

Intergovernmental Oceanographic Commission

Workshop Report No. 28

Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes

**organized by FAO as a contribution
to the IOC Programme of Ocean Sciences
and Living Resources**

Lima, 20 April - 5 May 1980



Unesco

**REPORT AND SUPPORTING DOCUMENTATION OF THE WORKSHOP
ON THE EFFECTS OF ENVIRONMENTAL VARIATION ON THE
SURVIVAL OF LARVAL PELAGIC FISHES**

**Held from April 20 to May 5, 1980
Instituto del Mar del Peru
Lima, Peru**

**(Workshop contracted by the Food and Agriculture
Organization of the United Nations)**

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FOREWORD

There have been several efforts in the past few years to draw the many facets of the Peruvian anchoveta experience into a coherent picture from which the complex interactions between the environmental fluctuations and the biological changes might be resolved. Recent examples include the IOC/WMO/CPPS joint working group meeting in October 1978. At this meeting regional fishery and oceanographic interests were joined by a SCOR working group to develop a research plan which would address the impact of El Niño events upon the regional resources. The following year the joint Peruvian-Canadian research project (ICANE) met to evaluate their research programme results. These studies included research cruises focussing on event-scale processes where biological sampling at scales ranging from Owen's micro-sampler (20 cm intervals) up through metre scale samples by Sameoto's multiple sample net system to standard net tows were collected such that continuous physical oceanographic data obtained from BATFISH and standard hydrographic stations could be directly related. Laboratory studies on larval fish feeding behaviour and survival were also undertaken to start controlled research on anchoveta physiology and feeding behaviour.

The IMARPE staff research contributions and results are outstanding examples of broad spectrum approaches to the problems inherent to marine resource studies. Recent conclusions drawn by Guillén about the anti-El Niño (La Niña) where the cold anomalies are also correlated with reduced recruitment have considerably broadened the scope of the monitoring necessary to explain or predict resource fluctuations. Indeed, looking at the time series of only temperature anomaly data shows quite clearly that the "average" conditions, which one can assume are beneficial to anchoveta survival, are rarely or infrequently observed. This is an obvious and compelling feature of this region's oceanographic variation, hence resource fluctuations.

Also the dynamic interaction between the major pelagic species and their development has recently resulted in a tremendous abundance increase and range extension through colonization by the sardine, and an increase in the apparent abundance of both jack mackerel and hake in the offshore area. This clearly requires one to step back and take a serious look at the relevance of single species models, particularly as they represent the potential to be derived from the Peruvian Current or any other marine system.

There must be a starting point or basis from which to begin, and this logically should include the early life history stages of individual species and any direct relations between ambient processes and subsequent survival of the eggs and larvae up through recruitment into the harvestable biomass. The following report and supporting documentation is presented in an attempt to combine our present knowledge of some of these processes into a useful basis for beginning more directed and relevant research into these important resource fluctuations.

G.D. SHARP

PREFACE

The Initial Basis

"I have the view that the most critical theoretical part of a theory designed to guide interaction with the real world is the initial basis."

Oscar Kempthorne^{1/}

Kempthorne's comment above came in response to Kiefer's (1977) exploration of the ways in which statisticians make decisions based on the general concept that "the taking of observations is supposed to give evidence (whatever that means)". The most commonly used method is based upon applying the two-decision accept-reject rule leading to the doublet (α, β) used to characterize statistical decision errors of the first and second kind. Given α , one proceeds to maximize β . But "The question of how one chooses α was never addressed." Kempthorne notes that the tackling of the problem which the mathematical statisticians posed for themselves has "been a great stimulus to one species of mathematics even though the solution of the problem has no relevance per se to the problems of applied statistics, whether of making a terminal decision or of stating a statistical conclusion." And finally, he points out that the amount of brainwashing required in order for teachers to convince students that a decision-making process has been derived when in fact it had not, was "utterly fantastic".

The general area of biological-environmental interactions seems to me analogous in many ways. Each of us separates out, or defines particular sub-problems which are, at least theoretically, solvable by themselves but we have never come to grips with the real issue of determining the "problem" or the initial basis. That initial basis is not, or should not be, a detailed and highly complex diagram of all of the effects and interactions which define some sort of deterministic or stochastic model. Put simply, it is, or should be, a precise definition of the problem for which a solution is being sought.

We gathered together in Lima from around the world because each of us believes in some vague way that "relationships" exist between certain biological parameters, e.g. year class size, and mortality, and environmental parameters such as temperature, winds, currents, etc., and we think we understand some of the mechanisms. Success in defining such relationships has been sporadic and fleeting. And relationships which seem to hold for one species fail for even closely related species in seemingly similar environments (see, e.g., Ahlstrom, 1965).

The possible reasons are many: the parameters may be measured too imprecisely; the wrong parameters may be measured; multi-species and/or life-stage interactions may be dominant. The lack of success so far has not been for want of trying. When one considers the amount of time and effort already expended in analyses, the number of attempts to relate environmental variation to changes in biological processes seems quite remarkable. With modern, fast, efficient computers we will be derelict in our duty if we do not examine and re-examine data already available for any hidden clues. But first, we must have an initial basis. Even if this workshop finds no solutions, the time will be well spent if we are able to reach some consensus on the problem.

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REFERENCES

1. AHLSTROM, E.H. 1965. A review of the effects of the environment on the Pacific sardine. Intl.Comm.for the Northwest Atlantic Fisheries, Spec.Publ., No.6;53-74
2. KIEFER, J., 1977. Conditional Confidence Statements and Confidence Estimators Journal of the American Statistical Assoc. 72, No. 360

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REPORT OF THE WORKSHOP ON EFFECTS OF ENVIRONMENTAL
VARIATION ON SURVIVAL OF LARVAL PELAGIC FISHES

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INTRODUCTION

This report is the result of a workshop held from 21 April to 5 May 1980 at the Instituto del Mar del Perú (IMARPE) under contract from the Food and Agriculture Organization of the United Nations. The topic of the workshop was the effects of environmental variation on the survival of eggs and larvae of pelagic fishes. The Agenda for the workshop is given in Appendix I, page 61.

The emphasis of this workshop was limited to exploration of the conditions, modes and mechanisms which allow larval fish to survive and grow to adulthood in order to be utilized by mankind. In the long run, the results of this and subsequent efforts will depend upon which of two things is basically true: 1) important events in the early life history of fish may be usefully described in terms of a few measurable parameters or 2) any attempt to describe (model) the mechanisms of complex biological-environmental-behavioural interactions of an organism in an uncontrolled ecological niche is futile.

While the latter may well be true, the former should not be dismissed without careful examination. We should, however, consider the possibility that simple but more intensive sampling could obviate both the concern about mechanisms and the selective (non-random) nature of the data elements. In addition we should consider the likelihood that purely empirical methods of data analysis may succeed where more conceptual methods fail in determining biological-environmental relationships. A most remarkable phenomenon in data analysis is the high frequency with which models "fit" the data in spite of the fact that no logical interpretation of the parameters can be made. We should hope that while considering the usefulness of models we also consider their decided limitations and whether they are necessary at all. The answer is by no means obvious. The question is being posed within the highest councils of the statistical community where it has been recognized that all too often and even for such simple cases as linear regression, the model becomes part of the information.

The major discussions during the workshop centred on the descriptions of existing larval survival models which were developed from energetic principles based on laboratory and field studies; the conceptual and practical studies of environmental properties of oceanic current systems which support major commercial resources; the available physical oceanographic models for describing and analytically evaluation stabilizing and mixing processes; and the development of requirements for a generalized model of the interaction of the physical and biological processes which might lead to qualitative forecasts of recruitment, given that this might be an important objective in some fisheries.

Several background documents were provided by the attendees, to which much of the discussion and most of this report will refer. These are listed in Appendix II, page 63.

These documents summarize our understanding of relevant biological and oceanographic properties at the various scales of occurrence of events which are presently considered to be important to the survival and general abundance of various commercially important pelagic species' eggs and larvae.

It was emphasized throughout the workshop that there was little point in extending the modelling efforts beyond the first feeding period at this time, since it is nearly impossible to appreciate the importance of predation effects at this and later stages, given present knowledge.

UTILIZATION OF RECRUITMENT FORECAST INFORMATION

The "Stock-Recruitment Problem" has received much attention in fishery research. For small, short-lived species of fish with corresponding high natural and fishing mortality rates, recruitment can contribute more than half of the total fishable stock. If recruitment is highly variable as is often the case for such species, the stock will also be variable. The associated fisheries tend to be unstable, in some cases critically so, with catches declining to nil for extended periods. The California sardine fishery still has shown no signs of recovery since its virtual disappearance twenty years ago. On the other hand, the Japanese sardine fishery suddenly recovered from nearly undetectable levels to a present level supporting a multimillion ton fishery. Perhaps the mostly widely followed fishery system has been that of Peru, which has experienced a remarkable degree of instability during the 1970's. The Peruvian system provides a useful focus for the study of recruitment determining processes, and their relationship to management of the fisheries.

The objectives of fishery management in Peru are primarily directed toward economic optimization and maintenance of social benefits such as employment. Fisheries make an important contribution to the nation's economy, and both government and industry face the problems of long-term planning in an uncertain environment. There is a demand for a forecasting ability providing at least a six-month lead time for decision-making regarding both resource conservation and fishery operations.

Anchoveta has been the historically pre-eminent species harvested in Peru. However, the substantial changes in the composition of the fish community since 1972 have now produced a condition where anchoveta is virtually a secondary species. Sardines (*Sardinops sagax*), horse mackerel (*Trachurus symmetricus murphii*), chub mackerel (*Scomber japonicus*), and larger predatory fish are now the major management concern, but the functional relationship of anchoveta as competitor and prey remains a difficult but important area needing investigation.

The present workshop has concentrated on anchovies (*Engraulis* species), due to the large amount of scientific and fishery information which has been gathered on the genus, especially the California and Peruvian resources. The biology of Peruvian anchoveta limits the predictive information and methods which could be employed. Under typical conditions, recruitment strength becomes apparent only at the beginning of the fishing season in March, when the two major recruitment modes are 6 and 12 months old respectively. A three-month lead time could possibly be gained by a scientific pre-recruitment survey (small juveniles). The feasibility, cost and precision of such a survey requires research and methodological development. This information could also be supplemented by monitoring and analysis of young fish appearing in the last months of the preceding fish season. Another useful quantity which may provide some forecasting information is oil content of anchoveta. A failure of the oil content to decline during the period of normal spawning activity, could be interpreted as increasing the likelihood of low egg production, hence low recruitment.

The possibility of a six-month forecasting ability based on environmental monitoring remains an attractive but perhaps elusive possibility. This workshop has helped assess the present feasibility of such forecasts, but a large amount of scientific activity would be necessary to produce these forecasts in any case. Recruitment forecasts based on environmental monitoring are unlikely to provide useful information to the commercial sector in the immediate future. Government and industry planners are seldom cognizant of the nature of uncertainty that is inherent to scientific studies of natural processes. Therefore it is unlikely that an imprecise forecast would be interpreted in the proper manner: most likely the forecast would initially be valued too highly, and when the imprecision became apparent, the forecast would be considered to be generally worthless. Recruitment forecasting would therefore best remain an internal activity in the scientific establishment until a time when precision is substantially increased by:

- 1) The development of a dependable monitoring scheme
- 2) The availability of a formal management policy
- 3) A reasonable period for validation has passed

This is not to imply that this research is primarily of academic interest, on the contrary, it is of direct relevance to both industry and management decision-making processes. There is very much the problem, given a forecast of "good" or "bad" recruitment, of what does one do or decide in response. These are questions which have little relevance to the workshops activities *per se*, they are more in the domain of managers and processors. What is apparent is that until a better understanding of the mechanisms directly affecting larval fish survival is obtained, the uncertainties facing the managers and processors decry their decision-making abilities. The credibility of the scientific community has suffered from over-emphasis of assessment tools utilizing "equilibrium" or "average" concepts which are not sufficiently representative of the observed dynamic processes in marine ecosystems.

Single species models are slowly being displaced by more complex formulations where the expected totals are less than the sum of the parts. Far more emphasis should also be given now to the analogies between man's fishing activities and the higher predator behaviour and responses to ecosystem fluctuation. With these thoughts in mind, the question becomes "What is the problem, and what is its basis?"

THE PROBLEM: POPULATION ABUNDANCE VARIATION

Variations in natural population abundances manifest themselves in many fashions, some of which are directly observed, others only inferred. There are only a few series of observations over sufficient time and area of coverage that permit the significance and magnitude of these fluctuations to be fully appreciated. Kondo (in press) has documented the catch records from 1905 to 1976 (recent years' data have been added) to show the full rise, peak and decline of the Japanese sardine (*Sardinops melanosticta*), along with the recent re-establishment of this stock to levels comparable to the 1936-1937 peak period. Sharp (this volume) has discussed these data along with the distribution maps showing the corresponding changes in habitat occupied from 1936 up until 1977. Sharp also tabled 25 species of commercial pelagic fishes whose relative catch varied by more than 5 times in the period 1970-1977. Of these, 15 were positive increases, 8 were decreases, and two both declined and subsequently rose to levels exceeding the low catch observed by more than 5 times within the eight years' period. The Japanese sardine catch increased by eighty-four fold during this time while the Peruvian anchoveta (*Engraulis ringens*) catches declined to less than a million tons (under regulation of catch), one sixteenth of the level of the 1970 catch.

In the past the major downward trends in apparent abundance of commercial fishes has been attributed to either overfishing, poor recruitment, or both. It is extremely difficult to explain positive increases over more than a few years given present fishery monitoring methodology and concepts. The search for relationships between stock size and recruitment, ignoring most other factors, has been a major occupation for many years. Sharp (this volume) and Bakun and Parrish (this volume) arrived at similar conclusions regarding this nearly fruitless quest. Both concluded that it is the proportional change in biomass resulting from recruitment that should be investigated rather than absolute numbers of recruits, and that the opportunity to observe any relations between recruitment and stock depends upon our ability to define the "system state" (e.g. carrying capacity and extent of utilization of the spawning grounds) as a variable to be used for deriving the stock size dependence of recruitment.

There is abundant literature on this topic, most of which fails to define the appropriate time scale or numbers of observations which might eventually permit one to extract the stock dependent recruitment processes from the environmentally induced effects. In a sense this workshop was a response to the void in effort to combine the more realistic view of environmental variation with modern concepts of feeding limitations as a major obstacle to be overcome if survival and subsequent recruitment is to be observed, or forecast with any degree of accuracy.

A. Classical stock and recruitment considerations

General biological knowledge of stock and recruitment relationships in most fish species is poor. However, we do know that the mean recruitment level is almost constant for some species over a large intermediate domain of variation of the parental stock (see Figures 1 to 3).

For example, in the case of North Sea herring, it follows from Figure 2, that this intermediate range comprises at least an interval corresponding to 10^{13} - 10^{14} eggs. The mean recruitment level is about $8 \cdot 10^9$ one-year-old fish. Thus the probability of an egg developing into a one-year-old fish is about 0.0001 or 10^{-4} . This value is not considerably lower than those characteristic of many fishes (e.g. *Engraulis* species). It is also important to note that this rate of survival has nothing to do with fishing since we are considering the total rate of mortality in the pre-exploited life-history stages. The effect of fishing is a reduction of the spawning potential not necessarily by changing the pre-recruit survival parameters. It is only when the rate of fishing is increased beyond a certain

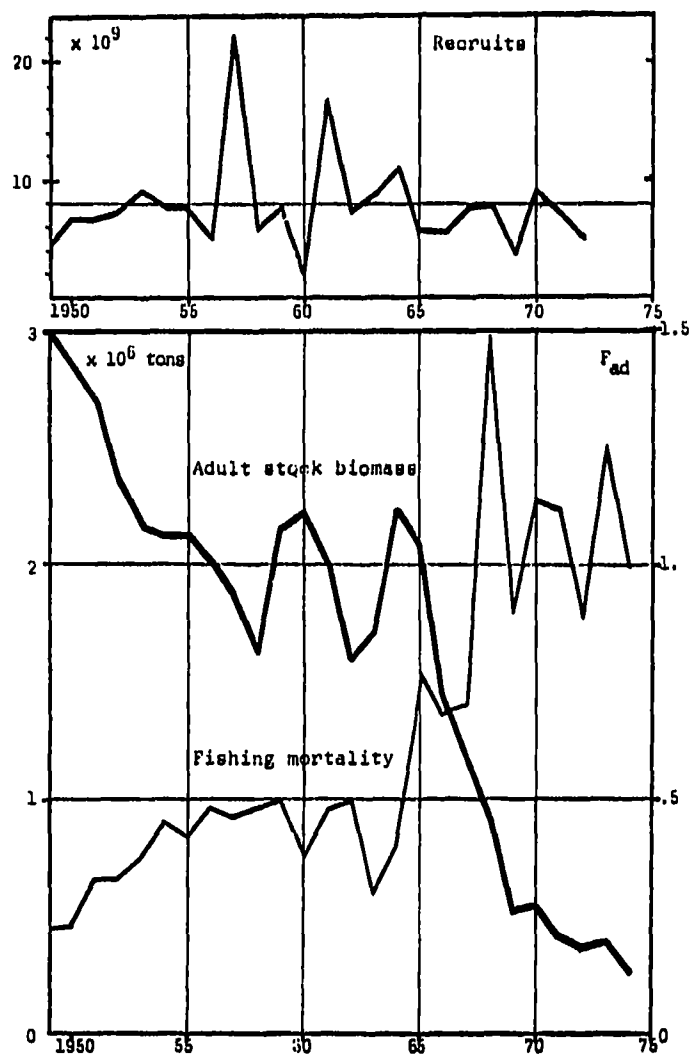


Fig. 1. North Sea herring

Top picture: recruitment numbers of one year old herring in the period 1949-72. Longterm mean (7.9×10^9) is shown. Bottom picture: adult stock biomass (3-9 years of age) at 1 January and adult fishing mortalities. Note at the strong 1956 and 1960 year-classes temporarily arrested the depletion of adult stock biomass and that the fishing mortality doubled from the early to the late 'sixties. (Based on calculated data given in ICES Documents C.M. 1972/H:13 and C.M. 1975/H:2).

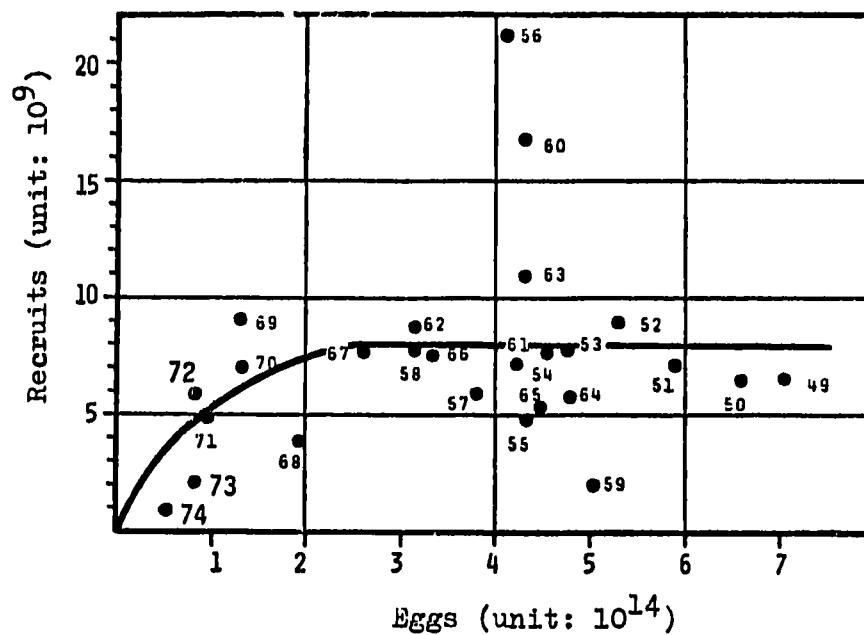


Fig. 2. Stock and recruitment plot of North sea herring. One year old herring against spawning potential (stated years). Based on data derived from single species VPA with $M = 0.1$ as given by ICES Working Group Reports.
After Beyer (1979). Redrawn

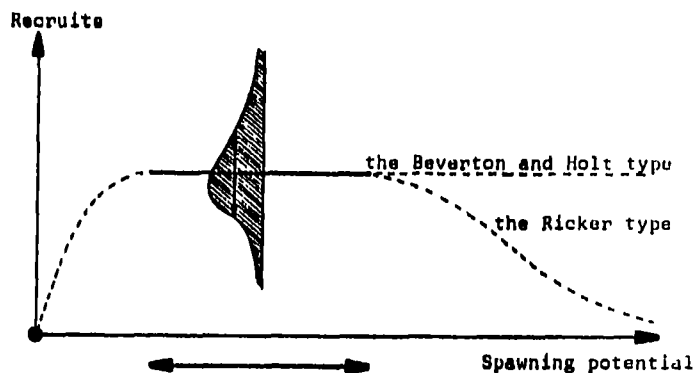


Fig. 3. Basic knowledge on the form of a recruitment curve. The mean recruitment level is almost constant when the parental stock (i.e. spawning potential) varies in a large intermediate domain. The log-normal distribution shown indicates variation in recruitment about this mean level. There is only one point on the recruitment curve that is known for certain and that is the point of extinction.

Table 1. Recruitment variation in North Sea fishes 1963-1975. Numbers adjusted to a value of 100 for the most outstanding year class of each species. "Ratio" is the ratio between the numbers in the strongest and weakest year classes. After Ursin (1979b).

Year Class	Gadoids					Plattfishes		Clupeids		Sandeel	Mackerel
	Cod	Haddock	Whiting	Saithe	Norway Pout	Plaice	Sole	Herring	Sprat		
1963	52	1	14	17	4	100	100	100			10
1964	49	1	26	23	6	29	21	53			26
1965	70	2	30	18	.5	28	11	47			43
1966	63	12	37	50	7	25	11	66	59		62
1967	20	100	100	51		21	18	65	62		10
1968	19	6	33	55	2	27	9	36	37		16
1969	82	2	30	29		32	26	78	41		100
1970	100	14	33	29	45	25	6	62	20	100	9
1971	18	21	68	30	7	20	14	41	19	21	17
1972	35	4	90	40	16	62	19	19	46	47	4
1973	31	21	63	100	100	40	18	47	91	28	15
1974	51	40	92	27	38	25	7		100	86	11
1975	27	9	37	50	18	37	22		79	41	4
Ratio	6	100	7	6	200	5	17	5	5	5	11

level that recruitment is affected (i.e. recruitment overfishing according to Cushing, 1971, 1974). In species with high natural mortality rates (i.e. *Engraulis mordax* $M = 1.1$) reproductive overfishing is very likely to occur before growth overfishing. In case of North Sea herring, however, a transition from growth overfishing to a type of recruitment overfishing seems to have taken place somewhere in the 'seventies'. But, in principle, we do not know very much about the proper location of this transition zone in the recruitment graph. There is only one thing that is known for certain, and that is the absolute point of extinction on the graph.

We know little about the other extreme of the recruitment curve. Beverton and Holt (1957) suggest the following type of recruitment,

$$R = \left(\frac{E}{E + \beta R_{\max}} \right) \cdot R_{\max} \quad (1)$$

where the number of recruits (R) increases towards an asymptotic level ($R_{\max}$) when the egg production (E) increases. This model is derived from a simple density dependent mortality model, i.e.

$$\frac{dN(t)}{dt} = -M(t) \cdot N(t) \quad \text{and} \quad M(t) = \mu_1 + \mu_2 N(t)$$

where $N(t)$ is the number of survivors or the size of the year class (population) at age t , M the instantaneous rate of mortality, and where μ_2 is a mortality rate due to competition and or intra-cohort cannibalism, and μ_1 is the density independent mortality rate.

Eq. (1) is the solution of this differential equation if

$$R_{\max} = \left(\frac{\mu_1}{\mu_2} / (\exp(\mu_1 t_r) - 1) \right)^{-1}$$

where t_r is the age at recruitment. In this formulation recruitment is dependent only upon current abundance.

$$R = \alpha E e^{-\beta E} \quad \text{maximum level of } \frac{\alpha e}{\beta} \quad \text{when } E = \frac{1}{\beta}$$

In the Ricker type of recruitment,

$$R = R_1 \cdot E \cdot \exp(-R_2 \cdot E) \quad (2)$$

where R_1 and R_2 are constant parameters, the number of recruits decreases from a maximum level (of $R_1 e^{-1}/R_2$ when $E = 1/R_2$) toward zero as the production of egg increases. This recruitment decline ($-R_2$) can be explained by the particular case of cannibalism of the young by adults in some species and other factors in other species (e.g. disruption or interference with eggs on salmon spawning grounds by other adults). These matters are described more fully by Ricker (e.g. 1954). We merely note here that the basic assumption underlying Eq. (2) is that pre-recruit mortality rate is linear function of spawner abundance or initial egg production.

This is about all that is known explicitly about recruitment. Almost all available data on stock and recruitment refer to the medium range of variations in the spawners. It is here that many species appear to maintain a relatively constant mean recruitment level and this constitutes the motivation for the assumption of constant recruitment in classical fish population dynamics. The most remarkable fact, perhaps, is that recruitment only shows relatively small variations about this mean level in many fishes considering the great reduction in numbers from the egg stage until maturity (Ursin, 1979b). There are, however, many species which do not exhibit this apparent stability in recruitment.

B. The stability of recruitment

Table 1 gives relative recruitment variations for 11 commercially important North Sea species in the period 1963-75. The table is based on recruitment figures from ICES Working Groups reports with the exception of Norway pout (Jones and Hislop, 1978) and the first data for mackerel (Hamre, 1978). We see, for example, that the cod year classes show a factor of six in variation from the weakest to the strongest year class. In order to consider this variation range in the light of the range of population reduction of cod during the first year of life we may apply the following consideration as an approximation of the situation in the 'seventies'. The mature cod stock comprises 200 000 tonnes, half of which are females. Once a year each female spawns 10% of its body-weight as eggs giving a total annual production of 10 000 tonnes eggs or 20 000 billion eggs ($2 \cdot 10^{13}$) since each egg weighs about 1/2 mg wet weight. The mean recruitment level, however, is only $2 \cdot 10^8$ one-year-old fish. Thus on the average only one egg out of 100 000 survives and grows into a one-year-old cod. The factor of six in recruitment variation implies that the probability of a fish dying (or surviving) the first year of life at most changes from 0.999 997 ($3 \cdot 10^{-6}$) for a bad year class to 0.999 983 ($17 \cdot 10^{-6}$) for a good year class. This is not a very great difference to explain. However, this also suggests that in a bad year a larva is 16% more likely to die at any given instant than in a good year. This is an interesting difference.

We could also consider stability in terms of recruitment to the mature stock. During its life time a mature female cod must produce an average of one mature female and one mature male. Only extremely small deviations from this number (2) are, on average, feasible if the cod stock shall retain approximately its present abundance as it apparently has done for the last 150 years or more. This approximative one-for-one replacement between successive generations holds at least as long as the mature stock is within the medium range of variation as referred to above. Thus, whether we are considering a situation of heavy fishing, where the mature cod female on the average produces, say, two million eggs in its short life time, or whether we are considering an average production of 40 million eggs per female at a low fishing intensity, the number 2 still holds. We do not yet know what causes this enormous reduction in number from the egg stage and leads to the apparent fine adjustment of recruitment to maturity.

Note that North Sea haddock and Norway pout show a remarkable variability in recruitment (Table 1). It could be that stabilizing mechanisms of the same effectiveness as those of cod do not exist in the North Sea for these two species. We shall not here, however, go into a specific discussion of what might cause the differences in relative recruitment variation among the North Sea species, but rather end by considering the stock and recruitment problem from general points of view.

C. The reason why $\ln R/S$ is a useful form for studying stock-recruitment relationships

The relationship of recruitment to parental stock is essentially one of survival from early stages (spawned eggs) to later stages. We can represent this process by coefficients of mortality rate for each stage or for the total process. If we begin with the number of eggs released (E), the number surviving to recruitment (R) is related to the coefficient of mortality rate (M_{overall}) for the total process.

$$\ln (R/E) = -M_{\text{overall}}$$

If we assume a common fecundity (f) for members of the spawning stock (S), we have

$$E = f S$$

We can combine these two equations to give

$$\ln (R/S) = \ln f - M_{\text{overall}}$$

This provides us with a convenient tool for studying effects of spawning stock size, environment, etc., on the two processes by which recruitment is determined: the number of eggs initially released per unit stock (which may also be a function of other variables); and their subsequent rate of survival to recruitment.

Mortality during stages or events in the life of a cohort of larvae may be shown by

$$\ln (R/S) = \ln f - (M_1 + M_2 + M_3 \dots)$$

$$\text{where } (M_1 + M_2 + M_3 + \dots) = M_{\text{overall}}$$

and where each M_i has a long term mean and variance (i.e. a probability distribution) which is conditional on such factors as adult stock (e.g. cannibalism), larval density (competition), food density, predation, temperature, etc.

A change in any M_i has an equivalent effect on recruitment no matter what the larval stage, while the actual numbers of larvae may be vastly different at different stages. The final convolution of the probability distributions of M_{overall} (i.e. the probability distribution of $\ln R/S$) may be extremely complicated. There may even be strong covariances between sequential values of M_i . For example, successful first feeding requires high concentration of esculent particles, which also indicates a higher likelihood of subsequent successful feeding. This may lead to juveniles which may not require as high a density of food at later stages as for those arising from larvae which had less food available initially.

Alternatively, the sum of many such probability distributions (particularly if larval density is not an important factor) may approach normality, according to the central limit theorem. This would tend to make R itself be distributed log normally. Through either empirical observations or detailed studies of cause-and-effect mechanisms, we may be able to derive conditional probability distributions which appreciably reduce our uncertainty of relative recruitment. Until recently, the only condition that has been investigated has been parental stock size, but this has not provided a very useful reduction in the unexplained components of the variance. Now we are beginning to examine the physical and biological environment, in the hope that a reduction in uncertainty can be obtained from these sources of information.

D. Toward modelling recruitment

It is difficult to attack recruitment problems in a sensible way by means of statistical tools because of the small amount of useful data that in general seems to be available. We presently only achieve one new recruitment data point per stock per year. Thus, in this situation, to explain recruitment variability such as the occurrence of extremely strong year classes, we may advance a great variety of conflicting hypothesis, all of which lead to different conclusions but none of which can be rejected on the basis of the data available (Beyer, 1976a). The situation is not better with respect to explanations of recruitment stability. Often it is not possible to distinguish between empirical recruitment models such as those given by Eq. (1) and Eq. (2) neither is it possible to sort out beforehand unimportant mechanisms of mortality regulation from available data. Apparently we need to obtain more biological knowledge on the causes of natural mortality in the first year of life and incorporate them into the recruitment models.

Andersen and Ursin (1977) conclude that the mechanisms which regulate mortality in early life should conform to the following requirements:

- 1) A high mortality shall be induced at the eggs to larval and postlarval stages.
- 2) Species with a large egg production (i.e. species with small eggs) should be hardest hit.
- 3) Survival should be an increasing function of food availability (this may not be a realistic requirement in general, however).

And, as an interim representation, they introduce an instantaneous larval mortality coefficient ($M_3(t)$) of the following type for each animal species:

$$M_3(t) = \frac{N(t)}{R_0} \cdot \frac{1}{w(t)} \left[\frac{dw(t)}{dt} \right]_{\max} \quad (3)$$

where $N(t)$ is the number of live fish with body weight (w) at age t and $(dw/dt)_{\max}$ is the highest possible growth rate at age t . R_0 is a recruitment parameter (a number of fish) maintaining the stock sizes. Thus, due to the first part of Eq. (3) mortality will be a function of the number of eggs hatched. The mortality will gradually decrease during the larval stages as the second part - the maximum relative growth rate at age t - decreases with increasing size of the fish (cf. $dw/dt = Hw^m - kw^n$) with $m = 0.56$ and $n = 0.83$ as the values used in Andersen and Ursin's work). However, if growth is impeded by food scarcity then mortality will remain high for a long period. This is intended to simulate mortality due to starvation.

The hypothesis that starvation can account for most mortality at the very early life-history stages was advanced by Johan Hjort in 1914 in relation to his investigations of year-to-year fluctuations in the stock of the Atlanto-Scandian herring. However, it was not until about 1970 that attempts were made to formulate this idea mathematically (Jones, 1973). More recently Lasker has directed his research efforts toward a more complete evaluation of the first feeding requirements (Lasker 1975, 1978a, 1978b, 1979).

Since Jones' initial attempt there have been several different approaches taken including those of Vlymen (1977), Beyer (1976a and b) and Beyer and Laurence (1980) to explain the effects of feeding behaviour, food availability and effectiveness of fish larvae in feeding to account for survival and growth. This is probably not an appropriate starting point for predicting recruitment, as it is obvious that from year to year the eggs must be differentially deposited in amicable locations, and that there is certainly predation upon them before hatching occurs.

Just how much of this predation is effected by other species and/or by the subject species needs to be determined.

Mac Call (this volume) has developed a model for anchovy egg cannibalism, which relates effective egg production to measurable variables. This model also provides an analytical basis for Csirke's (1978) stock-cpue-recruitment model for Peruvian anchoveta, which includes stock density as an important factor.

During active filter feeding, each individual anchovy filters v/V of the habitat volume (V) per unit time. The filtration rate per fish (v) may be approximately 3 l/min for a 20 g *E. mordax* (extrapolated from Leong and O'Connell 1969). The portion of time spent effectively filtering (p) is difficult to determine. It may be as little as 0.12, based on gut volumes and plankton densities given in Mendiola *et al.* (1969), with an assumed 4 hour time for gut clearance, or as much as 1.0 in conditions of low food density. The complete cannibalism model takes the form of a Ricker curve based on anchovy abundance (N):

$$E = fNe^{-mt_e - pvtN/V} \quad (4)$$

where E is effective egg production, f is fecundity (based on all fish including males and filter-feeding juveniles), m is natural rate of mortality and t is time to hatching. The above equation shows a maximum effective fecundity at $pvt N = V$, that is, when the population filters a volume of water equivalent to the habitat volume exactly once during the length of time it takes for the eggs to hatch. Note that the location of the maximum is independent of the natural mortality rate, although the value of the maximum is not. Assuming a habitat depth of 39m, and a p of 1.0, the optimum population density is 3 fish (at 20 g) per m^2 of sea surface, or 60 tons/ km^2 (150 tons/ mi^2). If p is as low as 0.12, the optimum increases to 480 tons/ km^2 (1200 tons/ mi^2). These are common anchovy densities according to acoustic surveys (Johannesson and Vilchez, this volume), and densities greatly exceeding these values have been observed. For example, in 1976, densities of 1 500 to 3 000 tons/ mi^2 were common, and this almost certainly indicates a harvestable excess of fish over optimal spawning densities.

Csirke's (1978) empirical model of the Peruvian anchoveta remains the only usable model of anchoveta stock-recruitment which recognizes density effects. For Mac Call's model (this volume) to be useful, several variables require better estimation, in particular, individual filtration rates, fraction of time spent filtering, and occupied habitat volume. Each of these may vary according to external conditions, such as distribution and abundance of food organisms for the adults.

Anchoveta larvae are also subject to cannibalism (Mendiola, 1978). Therefore the egg cannibalism model should be extended to the early larval period as well. There are several complications that make this phase more difficult to model. Larvae are fed upon by particulate feeding rather than filter feeding. The volume of habitat corresponding to filtered volume must be redefined, and because filter feeding and particulate feeding are mutually exclusive processes, eggs and larvae will generally not be fed upon at the same time. Because larvae decompose rapidly in the anchovy gut, quantitative estimates of larval mortality due to cannibalism are difficult to make. Csirke's empirical model also includes all the cannibalism on larvae as well.

The problems of modelling growth and mortality of fish larvae is a whole chapter by itself. We will not go into that here but merely note that the starvation hypothesis seems to constitute the most promising entrance to the recruitment problem. New models are under development and investigation (e.g. Beyer, 1976b, c; Vlymen, 1977; Beyer and Laurence, 1979, 1980) and in the near future we may hope to be able to exchange the mortality $M3(t)$ given in Eq. (3) with an expression that is based on a biologically acceptable way of modelling mortality due to starvation, and proceed on to define other mortalities.

CAUSES OF CHANGES OF POPULATION ABUNDANCE

A. Life history stages

From the previous discussion it should be clear that there are many points in the life history stages of fishes which can and do exhibit extreme sensitivity to very minor changes in relative mortality, whatever the source. Sharp (this volume) points out that the problem of "placing" the eggs into an appropriate environment is the life's work of a fish. The options for maximizing the chances for the eggs' development and subsequent larval survival really depend upon a long time series of events which cannot be "forecast" by the parental pelagic fishes. Many eggs must be lost due to short term changes in "appropriateness" of habitat, a function of local physical processes.

Given that there is an appropriate, amicable larval fish habitat for the eggs to develop toward, the survival from the hatch to more mobile stages depends on daily, local processes. If the survival criteria (food density and edibility) are not met then the larvae die, no matter whether due to starvation or predation. Achieving the more mobile stages alleviates the "local" physical limitations and increases the habitat variation available to individual larvae. (There is no predation in this present scheme, except for the larvae on their prey, due to the near absence of appropriate data to begin meaningful discussion on this topic). The important differences in the "solution" to egg and larval "placement" by the various species is summarized by Theilacker and Dorsey (this volume). The diverse strategies employed to deposit the eggs in appropriate places where hatching and subsequent larval survival are probable cannot be generalized, hence any attempts to develop a "general model" of larval fish survival must offer options for egg location, development time, first feeding capabilities, etc. as functions of species, ambient characteristics (e.g. temperature, oxygen availability), physical processes (e.g. current shear, mixing, stratification) and eco-biological prospectus (e.g. production at various trophic levels).

B. Variations in biological characteristics in the Peruvian anchoveta fishery

The Peruvian anchoveta fishery has provided many opportunities for fishery biologists from all experiences and backgrounds to speculate regarding the rise and fall of this important resource. The onset of the decline may well have preceded any indications from the behaviour of "traditional" stock status estimators. The present evidence indicates that there are at least two relatively isolated reproductive stocks, one in the north of Peru and one in the south, shared with Chile. In the developing fishery there were two major fishing areas centred off Chimbote and Callao. In the early sixties the fleet grew and spread southward to exploit the southernmost population centre. Valdivia (this volume) relates the observed decline in production in the central region (off Callao) as the exploitation increased in the south. In 1972 the recruitment to this area was the lowest recorded to date, which led to rapid abundance changes which have been hailed as the onset of the demise of the anchoveta stocks.

However, there were several events prior to the 1972 recruitment failure which suggest that the decline in anchoveta abundance was "facilitated" well before all the necessary conditions were in place. The growth and transition of the fleet operations from the central area of overlap of the northern and southern stocks, to the southern area was an event which led to the decline of anchoveta abundance. Not to say that fishing this stock was necessarily a bad thing, but with the "failure" of the northern stock recruitment, and the concentration of effort in the central and southern regions, the resilience of the biological system was stressed. The opportunity for the stocks to reestablish production was decreased by the intense localized exploitation in both the northern and southern "source" areas.

Also, the 1971 year spawners did not spawn at previously observed levels. The proportion of sexually mature individuals in the potential spawning size fish ($>9\text{cm}$) was only 40% as compared to 90% in previous years. The fat content of the 1971-72 catch was anomalously high and remained high over the fishing season. Although 1971 was judged to be a "normal" oceanographic year, the stimulus to transfer accumulated body fat to gonad products did not occur. Recruitment was apparently poor as a result of this physiological "anomaly", although recruitment rate (i.e. recruits per egg) may not have been particularly poor. It is important to recognize that there is no information on what stimulates spawning in these fishes, and that it will be difficult to interpret variations in apparent abundance without a better understanding of the interactions between the food, fish and exogeneous processes.

The distribution of phytoplankton abundance in the Peruvian system is concentrated on the borders of the upwelling areas (Santander, this volume). These are quite similar to the distributions of good areas of spawning. Mendiola and Gomez (this volume) show that high egg density (abundance) may yield low recruitment, even with high phytoplankton abundance. On the other hand, in 1975 there appeared to be both low food and low egg abundance, which yielded a relatively high recruitment. The interesting "anomaly" in this year was the high concentration of *Gymnodinium*, over 100 particles per ml were measured in one spawning area. *Gymnodinium* are considered to be excellent food for first feeding larvae. Their size and nutritional quality and general appropriateness (esculence) likely provided the first feeding larvae a boost, even though the spawners producing the 1975 eggs were considerably below the typical size-weight expectation. This size condition was likely due to a low abundance of phytoplankton in the pre-spawning period.

There are several characteristics of the anchoveta eggs and larvae which vary with latitude. For example, egg size increases as latitude increases, yielding larger larvae. As the larvae develop into juveniles, even more diversity in available food, and basic behavioural and physiological differences manifest themselves between the two areas. These are primarily reflected in size specific diets, which vary with area and season as the quantities and qualities of zooplankton and phytoplankton also vary between seasons and areas.

Among the several changes in reproductive properties of the anchoveta which appear to contribute to the uncertainties in the recruitment picture for the recent years is the observed shift in dominance of peak spawning period. In "typical" years the peak spawning occurs on the relaxation cycle of the upwelling season, from August to October. In 1972, 1973 and 1976 the peak spawning period shifted to the secondary period of typical years, peaking in February rather than the August to October period.

Tsukayama and Alvarez (this volume) have shown an effect of warm years on the proportions of reproductive females. Their data indicate a strong decline in proportions of females in pre-reproductive state with increased biomass in warm years. Other years yield a somewhat trendless proportion which varies from 8.0% up to 24.4%. The warm years range from only 4.1% to 10.5% at large adult biomass ($>12 \times 10^6 \text{ mt}$), and 6.7 to 30.0% at lower adult biomasses.

These observations indicate that several inter-related changes have occurred in response to climatic, oceanographic, and/or fishery related pressures. The problem is to try to develop, if possible, plausible explanations leading to testable hypotheses which might illuminate the cause and effect relations in this complex picture. Bakun and Parrish (this volume) also point out that although a hypothesis might be plausible, it might not necessarily be true. This leads to a basic procedure of constructing hypotheses based on more cause and effect (rational) input, which also leads to more testability and ultimately greater understanding of underlying principles and processes involving the biological effects of physical events.

C. Evaluation of variability, considering the problem of availability inherent to fisheries

One of the major problems in most fisheries research is the over-emphasis of fishery associated sampling, and lack of appropriate fishery independent biological and environmental information. Fisheries are notoriously biased samplers of resource populations and often yield misleading results if not carefully evaluated in comparison with other data sources.

In fisheries, the term availability is used conceptually to indicate that a variable portion of any population is susceptible to capture, and hence to measurement. This problem is present implicitly if not explicitly in all data collected from natural populations where "effective randomness" (with respect to the resource) in the allocation of sampling effort cannot be assured. For commercial catches of adult fish, i.e. the fishery, availability is an important parameter because the range of vessels or preferred fishing areas often restrict effort to a small proportion of the potential range of the resource. Scientific investigations such as egg and larval or acoustic surveys, are also by nature selective, and low levels of sampling effort make them highly susceptible to the effects caused by the universal tendency of organisms to aggregate, actively or passively, in time and space.

Thus uncertainty regarding the "population" actually being measured is added to the inherent variability in the distribution of a population. The availability factor, perhaps more than any other, appears responsible for the fact that simple intuitive concepts concerning relationships among apparent stock size, recruitment, egg and larval survival, etc. fail so regularly and dramatically. The most basic of these intuitive concepts is that associations should be stronger the smaller the interval between two events, say between recruitment and late larval stages as opposed to recruitment and eggs. This has never been demonstrated on a consistent basis. This failure seems to contradict what would seem most logical, and has resulted in attempts to by-pass the biological processes and information completely by relating apparent stock size or apparent recruitment to environmental factors alone. It has also led to the conclusion that a management strategy cannot realistically be based on any single indicator of stock size or stock condition (i.e. catch per unit of effort, egg and larval abundance).

Independent acoustic estimates (Johannesson and Vilchez, this volume) of distribution and abundance of pelagic fish biomass, particularly anchoveta in the Peruvian system have yielded remarkable insights into the changes in behaviour and occurrence within and among years which cannot be evaluated from fishery catch and effort data alone. There are many inherent assumptions in this source of information too, but the concurrence of some data collections and analysis from both acoustic and fishery sources certainly make a clearer picture available regarding population abundance variations.

The responses of populations to subtle oceanographic ambient changes is often not apparent from fishery related data. Use of several independent methods, like acoustic surveys and research cruises, often yields contrary pictures of resource condition in comparisons with fishery activities, particularly where there are preferred fishing areas and species, or conditions which promote high vulnerability through aggregation (e.g. shoaling of habitat, Sharp 1978).

Perhaps the best indications of resource status is the distribution area (or volume), and the abundance or aggregation sizes within this range. Fisheries operating only upon large aggregations tend to sample the distribution of the resource poorly adding to the uncertainties of stock status in the absence of independent methodologies.

D. Primary productivity and fishery production

Quillén (oral presentation) has related the overall primary production from the four major areas in the Peru Current to the total catch taken in the fishery. He has shown a relation between an upwelling area off Chimbote, with fishery production and the hydro-acoustic survey results. For the few available years data (1972-1975) he has also shown a

relation between total eggs and/or total larvae from the surveys from 4° to 18°S and primary production off Chimbote. He envisions that a change of units to carbon equivalents might give a better estimate of relative egg-larvae input as a function of primary production. His observations also include the fact that changes in peak primary production periods and areas correspond with the changes in spawning peak periods and areas.

The Chimbote area differs from the other Peruvian upwelling areas in that it has more moderate upwelling rates, over a longer period (i.e. February through October) than any other area. Adult fish appear to be able to cope with the transport rate induced by both the winds and upwelling and stay within the system, and thereby add back the ammonia required for high primary production rates. Also as it appears that a "cooling" trend in the spawning season leads to an increased survival of larvae (e.g. larval density increases), the longer descent period of the temperature in the Chimbote area may provide a survival advantage over the other upwelling areas where the temperature range is comparable, but the rate of change is greater.

E. Physical transport and faunal variation

Similarly, Parrish, Nelson & Bakun (MS) have correlated long term (e.g. evolutionary time scale) oceanographic phenomena with the zoogeographic properties of the California Current System. The fluctuations in horizontal advection, convergence or divergence, and stability of the water column on a seasonal and annual basis can be shown to correlate highly with success of reproductive strategies of the fishes in the various oceanographic regimes. For example, fishes living in the areas of high offshore transport processes are dominated by live-bearing species (e.g. *Sebastes*), whereas the onshore and eddy systems are the major reproductive habitat of species with pelagic eggs and larvae (e.g. anchovies and sardines).

F. Patchiness in the availability of larval fish habitat

One of the major questions arising from evaluation of survival experiments in laboratory studies of larval fish is, "Where would one find the necessary concentrations of esculent foods for larval fish?" Owen (this volume) has explored the scales of physical events which promote "patch" phenomena which can lead to appropriate densities of esculent larval food. It is obvious that the seasonal and areal distributions of large scale patches (e.g. eddy or upwelling systems) vary, and that "on the average" if their contents were well stirred as at times they can be assumed to be, few or no larval fishes could find appropriate survival conditions. Below this scale, Owen has measured microstratification of the appropriate order to promote larval fish survival.

To date 33 vertical and 4 horizontal microprofile sets have been obtained from mixed and stratified coastal waters in the Southern California Bight and on the Peru shelf under all but full storm conditions. Of these, all except a single horizontal set made in the mixed layer exhibited variations beyond sampling and measurement error of one or more of the parameters measured over the 2 m interval.

The incidence of microstructure was high; significant, fine-structure existed (as defined by statistically evident disparities in abundance of various constituents from different sampled strata at any given sampling) in 16 of 22 particle profiles and 11 of 21 nitrate profiles and in both of two ammonium profiles. These data suggest that small planktonic organisms overcome dispersive processes such as diffusive mixing to a degree sufficient to form laminae on the cm scale. Their vertical variation is pronounced in density-stratified water but detectable in the mixed layer as well. By water movement, reproductive rate and/or behaviour, plankton become differentially layered in what may prove to be microniches.

Incidence of plant pigment microstructure was quite high. All of the 23 sets analyzed showed variation of chlorophyll concentration indicating microstructure of the phytoplankton community as a whole. Fewer (19%) showed cm-scale variation of phaeopigments. However, of the 23 profiles, 14 exhibited unrelated profiles of chlorophyll and phaeopigments and 4 exhibited inverse relationships. This inconsistency demonstrates a degree of independence on the microscale which is not apparent in pigment concentration profiles from the usual sampling intervals of 5 to 10 m. This independence may be due to local effects of grazing or to differential rates of local production and sinking of the two particle types. These measurements thus may reflect the spatial scales on which these processes are first apparent.

Microstructure was not, of course, always detected. Sample series from the wind-mixed upper layer of the Southern California Bight showed less variation of organisms, particulates and nutrients than did sample series from density-stratified waters. However, significant microstructure of motile and non-motile organism populations, as well as of detrital particles, was detected in 2 of 4 casts made within the mixed layer in the absence of measurable density gradients, when mixing by wind was not in progress. The nutrient salts, phosphate and nitrite-nitrate exhibited low incidence of microscale variation over distances less than 2 m in both regions sampled. Widely varying values of silicate concentration suggest microstructure for that nutrient but occasional wide disagreement between replicate samples vitiate the case for silicate microstructure. Salinity (5 sets) varied monotonically in the presence of nutrient and organism microscale variation. Temperature microvariation was not measured.

Despite the dynamic conditions encountered, microstructure of organisms enumerated was at least as pronounced in the "mixed layer" near Peru's shelf-break as in the more stable layer at the same depth near the coast. None of the variations were in the form of stepped trends but were all of sub-meter extent. Small ciliates (20-50 μ m) were less numerous but varied proportionately with the small ciliates.

Yet to be determined is the extent to which physical mixing mediates the microstructuring process. Dye studies by Kullenberg (1974) and Woods (1968) conducted elsewhere in the density-stratified waters, show that cm-scale layers persist for at least a day in the absence of storm-force winds and that disruptive processes can operate on the same time and space scale.

Far more study is required before we can claim a full appreciation of the processes and events leading to a wide-spread availability of these "larval fish habitats".

Fasham (1978) stated clearly that studies of patchiness in the ocean have been too integrative to allow us to discuss phenomena on scales below hundreds of metres from literature observations. Owen, Mackas (1976) and others are beginning to apply more sensitive and discrete sampling techniques which might lead to a more informative class of data collection which could allow us to investigate more directly the distributions of larval fish habitat. This is presently not practical on any but the very short term and too integrative distance scales for reasonable investigations of changes of available larval habitat in time and space for broadly distributed resource populations.

Another series of questions which pose themselves are what, where, and how are appropriate patches of esculent larval fish food formed? Then, of course, what could change their relative availability? The first few questions can only be treated cursorily, and for only a few species where "appropriate" foods have been identified. The destruction of patches or stratified water will be dealt with in a later section regarding models available for evaluating larval habitat distribution.

G. Density dependent egg cannibalism

The number of eggs hatched successfully into the larval environment (here called effective fecundity) is likely one of the strongest density-dependent elements of the recruitment relationship for anchovies. Effective fecundity can be divided into pre-spawning and

post-spawning components: virtual fecundity is the actual number of eggs released into the water, but subsequent cannibalism as well as natural mortality will reduce the number of eggs which eventually hatch and become larvae.

Tsukayama and Alvarez (this volume) have addressed an important aspect of virtual fecundity. The fraction of the adult population (i.e. the stock) that is actively engaged in spawning, as determined by frequency of advanced gonadal states, decreases with increasing population size in warm-water years. During normal and cold years, the fraction spawning remains rather constant over a wide range of population sizes. In the latter case, the proportion of spawners is independent of stock size, but in warm years there is a declining relationship, with the maximum number of spawners occurring at an intermediate stock size. This relationship is hypothesized to be regulated by food availability, which may be reduced by the grazing pressure from the anchoveta itself during warm years, when plankton volumes are low.

Another dimension to virtual fecundity was suggested by Theilacker and Dorsey (this volume). Egg size varies due to biotic and abiotic factors, and particularly, there may be an inverse relationship between egg size and fecundity (e.g. see Bagenal 1971) even within a local population. While a relatively small increase in egg diameter may not seriously affect egg survival, the associated larger egg volume of large eggs may have a considerable effect on the size and survivability of the subsequently hatched larvae.

Survival of spawned eggs is dependent on the probability of mortality acting over the time to hatching. Time to hatching is a fairly deterministic function of temperature, decreasing with increased temperature. High temperatures do not necessarily result in high survivorship, however. High temperature is associated with increased occurrence of aborted development (Theilacker personal communication), and warm water places high metabolic demand on subsequently hatched larvae, probably requiring higher densities of prey for sufficient feeding to promote growth. Larval predators must also consume more at high temperatures due to their increased activity and metabolic demands.

Mortality due to predation on eggs is conveniently assumed to be independent of, for example, anchovy stock density. However, there may be a correlation of unknown sign: adults may tend to congregate and spawn in areas of high food supply, and egg predator abundance may also tend to be high; or anchoveta may reduce egg predator abundance by feeding on them. Evaluation depends on the relative species composition of the adult anchovies' available food.

Cannibalism of spawning products by filter feeders such as sardines and anchoveta has received attention in the past (e.g. Mendiola *et. al.* 1969), but the low number of eggs and larvae in anchovy stomachs have not appeared to be significant. However, if the number of eggs consumed between spawnings is calculated, a sizeable percentage of virtual fecundity may be lost. Hunter and Kimbrell (in press) have calculated that 32% of the total mortality rate of *E. mordax* eggs may be accounted for by cannibalism.

THE ROLE OF MODELLING IN PREDICTING SURVIVAL OF FISH LARVAE IN THE OCEAN ENVIRONMENT

A. Models and fishery management

Computer technology has made possible virtually unlimited complexity in the development and application of environmental, biological and economic models. That sophistication does not, however, lead necessarily or even usually to a greater understanding of the process(es) under investigation. More often than not, many of the parameters in the models either defy measurement entirely or can be measured with so little precision that they can only be utilized for examining the sensitivity of the overall model to changes in particular set or subset of parameters. Thus the dynamic range of the model system can be evaluated but in the absence of measurable or reliable parameter estimates, simulations of real-life experience may be impossible.

The important quality too often missing in fishery models is an underlying basis for investigating and resolving relevant questions. That is to say, a lack of true cause and effect relations and interactions based on observable principles.

A hierarchy of biological models can be defined as those which describe: (a) individuals, (b) single species populations, and (c) multi-species populations. In addition, the models can be classified as deterministic (or mechanistic) and stochastic (or statistical). So far in fisheries work, models have been mainly quasi-stochastic descriptions of individuals and single species populations. True stochastic models, i.e. models which consider the variability inherent in the parameter estimates as a fundamental part of the description of any natural process have rarely been used.

Cornfield (1974) described as well as any the difference between statistical and non-statistical quantitation:

"The distinction between statistical and non-statistical quantitation is elusive, but it seems to depend essentially on the complexity of the system being quantified; the more complex the system, the greater the need for statistical description.

Once, many people believed that the necessity for statistical description in a system was due solely to the primitive state of its development. Eventually it was felt that biology would have its Newton, then psychology, then economics. But since Newtonian-like description has turned out to be inadequate even for physics, few believe this any more. Some phenomena are inherently incapable of simple description."

The direct implication is that complex phenomena can sometimes be described only in terms of statistical averages and probabilities of occurrence. It is indeed ironic that statistical methodology has played such a small role in fisheries, perhaps one of the most complex areas of scientific investigation.

The primary value of most models is to identify estimable parameters to which some overall objective is likely to be sensitive. Care is required and simplicity desired. For example, most of the traditional growth equations or models contain at least three highly correlated parameters which usually describe the growth curve precisely but which are individually insensitive to changes in the pattern of growth. The parameters of a simple exponential model on the other hand while inadequate for describing the true growth trajectory will in general be a more sensitive index of change.

Many fishery scientists who have had to deal with the fishery management sector are well aware of the endless and circulatory arguments which arise when data collection and its design are not tied directly to well defined objectives. Brander (1975) noted that "The importance of collecting data and the amount of time and money worth spending on it can only be assessed if the objectives of fisheries management are fairly clearly defined".

B. Benefits and limitations of model building

The reward for model building is the identification of the important processes governing phenomena and a quantitative analysis of how these processes operate. With insights gained from the model, fisheries oceanographers may improve the design of their field and laboratory experiments.

To be used correctly, one must be aware of limitations of models. A model which successfully reproduces existing data may not necessarily be a good predictor. The model may assume a constant parameterization of processes which evolve or change in the real world. By "parameterization" we mean incorporating into the model the effect of a process not explicitly represented in the model. For example, a fisheries model may assume a constant recruitment to the fishable stock. Spawning success and fish larval survival up until the recruitment period could be parameterized in the model as a continual addition to the existing stock.

One way to improve the predictability of a model is to reduce the level of parameterization of important processes. One may do this in fishery models by including more explicit description of the reproductive process and the dependence of larval survival on the physical environment.

The biological modeller is less fortunate than the physicist in that he has fewer generally quantifiable, verified principles on which to base his formulations. However the biologist may be successful in significantly improving the predictability of models by reducing the level of parameterization only slightly. For example, spawning success and larval survival might be better expressed as probability distribution functions rather than deterministic functions which are "guessed" from some poorly related source.

C. Types of models

There are three levels of sophistication in modelling, which we will call (1) "back-of-the-envelope" calculations, (2) over-simplified models and (3) complex "ecosystem" models. However, the most complex ecosystem model is not necessarily the most illuminating. If one has little understanding of the processes involved, an order of magnitude estimate may be the best one can do. For example, to predict reproductive success one could simply multiply the spawning stock S by a constant reproduction parameter, r . However, this may not be a very accurate predictor, especially if the value of the parameter r is not well known. If parameter r is not constant in time, one will obtain totally inaccurate predictions of reproductive success. This is an example of what can be done, roughly, on the back of an envelope.

Over-simplified models involve more mathematical computations than type 1 models (i.e. they take more than one "envelope"), but are still too simple to relate directly with field data. An example in the context of predicting spawning success would be a fisheries model which incorporated environmental influence on values of recruitment rate. A fisheries biologist may use both his intuition and experience to formulate the reproductive rate of the fish stock as a function of environmental parameters such as sea water temperature, plankton, productivity, etc. The benefits of such models are that they are relatively easy to solve and the model results are easy to comprehend. The limitations of type 2 models are that they still may not be accurate due to the high level of parameterization. Also the model output may not be directly comparable to field observations.

The opposite extreme from "back-of-the-envelope" calculations is the ecosystem model. Here a fishery model would include a high level of complexity and a larger number of mathematical computations would be performed in the name of realism. Optimistically, the model output could be directly compared to field data as both should inherently include a similar degree of complexity. However, because of the large number of factors included in the model, it is often difficult to sort out the most important processes. It is often difficult

or impossible to derive an analytical sensitivity analysis of the model equations, and therefore one must generate a large amount of model output by iteration to completely understand how all the factors interact. Finally, the ecosystem type model may be no better a predictor of events (e.g. reproductive success) than a type 1 model, particularly if the basic parameterization is wrong.

There is one important step to take before entering into model building. That is to decide, on the basis of experience and intuition, which processes are likely to be fundamental to the problem. For example, biologists, physicists and meteorologists who individually understand single factors which may influence spawning success and fish larval survival need to decide collectively how best to formulate the problem. All factors cannot be included in detail. The ultimate fishery ecosystem model might include a prediction of larval survival encompassing all environmental possibilities. This model could take longer than a year to run on the computer to forecast the next year's recruitment. Even if we could derive an analytically time-efficient ecosystem model, there are fundamental limits to predictability.

In non-linear, open thermodynamic systems such as the ocean and the atmosphere, variances on small spatial scales can grow and manifest themselves as large scale variability through non-linear dynamics of the system. For example, in numerical weather prediction the limit to predictability of the local weather is at best a week. Predictability of ocean events relevant to fish larval survival are necessarily much less than one week. Thus some degree of parameterization is necessary.

It is likely that the most successful models to describe reproduction of fish stocks will lie somewhere between oversimplified models and ecosystem models in complexity.

Remembering that the role of modelling is to identify and quantify the important factors governing recruitment in fisheries rather than to merely provide a predictive capability, one will not be tempted to become over-involved with the model output which often leads to disenchantment with model building. Ultimately, modelling is used to develop understanding, and characteristically, with understanding comes predictability.

D. Scale analysis: a back-of-the envelope model

Scale analysis is a mathematical technique which has long been used by oceanographers and meteorologists to quickly identify the dominant processes governing various physical phenomena (O'Brien and Wroblewski, 1973). The technique may be applied here to demonstrate that the oceanic environment should not be neglected when considering larval survival. Scale analysis can be used to define the circumstances under which physical factors are critical and when biological processes such as behaviour, physiology and predation primarily determine larval survival.

Consider the general equation for the distribution of fish larvae F in the sea,

$$\frac{\partial F}{\partial t} + \nabla \cdot \underline{v}F - \nabla \cdot (K \nabla F) = \text{biological processes} \quad (5)$$

Where t is time, $\underline{v}$ represents the horizontal and vertical water velocities, and K is the coefficient of eddy diffusivity. The first term is the local change in F , the second represents advection of F and the third represents turbulent mixing.

Let us choose a Cartesian coordinate system in which x and y designate the horizontal position and z increases with depth. The advection terms in Equation (5) can be rewritten

$$\nabla \cdot \underline{v}F = u \frac{\partial F}{\partial x} + v \frac{\partial F}{\partial y} + w \frac{\partial F}{\partial z}$$

Where we have assumed non-divergent flow. If the horizontal and vertical coefficients of eddy diffusivity can be assumed constant, the diffusive terms can be rewritten.

$$\nabla \cdot (K \nabla F) = K_h \frac{\partial^2 F}{\partial x^2} + K_h \frac{\partial^2 F}{\partial y^2} + K_v \frac{\partial^2 F}{\partial z^2}$$

One can compare the relative influence of the physical and biological processes in determining the distribution of larvae by scaling all terms in Equation (5).

Let $x = Lx'$; $y = Ly'$; $z = Hz'$; $u = Uu'$; $v = Vv'$; $w = Ww'$

Where L and H are characteristic horizontal and vertical length scales respectively, U is a typical value of the organized horizontal flow and W is a typical value of the vertical velocity. Primed quantities are dimensionless.

If time is scaled by $1/\alpha$, the critical time scale for larvae survival, then scaled time $\tau = t/\alpha$. Finally, if F is a typical value for F so $F = \bar{F} F'$, Equation (5) becomes

$$(SBP) = \frac{\partial F'}{\partial \tau} + \left(\frac{U}{L\alpha}\right) \left(u' \frac{\partial F'}{\partial x'} + v' \frac{\partial F'}{\partial y'}\right) + \left(\frac{W}{H\alpha}\right) \left(w' \frac{\partial F'}{\partial z'}\right) - \left(\frac{K_h}{L^2\alpha}\right) \left(\frac{\partial^2 F'}{\partial x'^2} + \frac{\partial^2 F'}{\partial y'^2}\right) - \left(\frac{K_v}{H^2\alpha}\right) \left(\frac{\partial^2 F'}{\partial z'^2}\right) \quad (6)$$

SBP = Scaled Biological Processes

The magnitude of the nondimensional coefficients in Equation (6) defines the importance of the advective and diffusive terms relative to the biological terms which have been scaled to be of the magnitude unity. When $U/(L\alpha)$ or $W/(H\alpha)$ is much greater than one, advection plays a dominant role in determining the distribution of larvae (i.e. larval drift). If the coefficients $K_h/(L^2\alpha)$ or $K_v/(H^2\alpha)$ are large, turbulent transport of larvae is important.

Since L and H occur in the denominator of these non-dimensional coefficients, clearly for small length scales (metres) the physical processes of advection and turbulent diffusion are very important relative to the biological processes. For the Peru upwelling region, we estimate that U is 20 cm/sec and W is 0.01 cm/sec. The width of the upwelling zone L is about 20 km and the average shelf depth H is 50 m. For these length scales, appropriate values of K_h and K_v are 5×10^5 cm²/sec and 10 cm²/sec respectively. If the critical time scale for larvae survival, $1/\alpha$, is about one day,

$$\frac{U}{L\alpha} = 1.0 ; \quad \frac{K_h}{L^2\alpha} = 0.01 ; \quad \frac{W}{H\alpha} = 0.2 ; \quad \frac{K_v}{H^2\alpha} = 0.04$$

The biological terms in Equation (6) have been scaled to have a magnitude near unity. This equal importance of advection and biological processes implies large variability can be expected in larval survival in upwelling regions. Currents and turbulence become less important as the critical period $1/\alpha$ lengthens.

E. Available conceptual models for evaluating environmental effects on fish survival

Parrish, Nelson and Bakun (MS) have examined the plausible explanations over evolutionary (long term) scale events for the various reproductive strategies observed in the California Current System. There are direct cause and effect relationships proposed to exist regarding oceanic transport and species dominance by region in this system.

Csirke (1980) has shown a relation between adult distribution area (where area could be related fairly closely to volume in this case) and density dependent recruitment in the Peruvian anchoveta. MacCall (this volume) has given a supporting model of the density dependent process (cannibalism) underlying such a system.

All of the above models can be related to environmental-distribution properties of the subject species, the first indicating that populations which survive various transport regimes have the necessary pre-adaptations in the early life history stages to cope with the system, the second and third showing an effect of concentration of the adults into smaller areas, by whatever ambient force, such that predation of their own eggs and larvae results in lowered reproductive potential.

Another class of available conceptual models provides insights into what conditions must exist for larval fishes to survive. These are the laboratory-based models of Vlymen (1977) and Beyer (1979). Both models give as output the kind of food densities necessary for larval survival, given some basic information on the behavioural and physical characteristics of the subject species. Vlymen's model allows one to describe the required food patch geometrics as a function of appropriate particle size, and required ingestion rate of the larvae. Beyer's approach is to relate the successful feeding of a fish larvae to the probability distribution of an array of prey sizes and geometries. A combination of both approaches would be useful in defining appropriate "patch" characteristics which would lead to survival of individuals of species with known feeding characteristics and energetic expenditures.

On a different scale, what Andersen and Ursin (1977) have done on a population, multi-species level would appear to be an ideal, but perhaps unachievable objective. Their approach can only be effective given that one can monitor and quantify the numerous life history stages from initial egg deposition in one generation, to ultimate egg hatching and survival of the two required survivors in the life span of an original parental pair.

Bakun and Parrish (this volume) have described the requirements for realizing the most information regarding effects of environmental variation on fish populations. The developmental stages require that a realistic series of rational (cause and effect) processes be incorporated into the hypotheses relating biological processes and physical events, and that the "test" of the relationship can only be realistically achieved by comparison with another data series than that used to generate the models, or within limits, by comparison in another system (e.g. models developed in the California Current System might be generally applicable in eastern boundary current systems with similar species arrays).

The complexity of the physical and biological interactions may even preclude these comparisons, but only trying will provide any progress. Guillén's primary production-fishery production hypothesis may be quite reasonable in the Peruvian system where the transport processes retain most of the production nearshore, but the California Current System primary production is not retained to the same degree, and this alone may account for the differences in fish production between the two systems. Bakun and Parrish hypothesize that the offshore transport of the phytoplankton and zooplankton (as well as eggs and larvae in some areas) could preclude the availability of the egg and larval requirements. The adults would not be so drastically affected because of their mobility and because the adult requirements are far less in proportion to available food than is the accessible larval habitat to the larvae.

F. The problems of species interactions in a varying environment

There are several aspects of most fish survival models (or stock assessment models) which at present cannot be generalized beyond a few statements. The effects of interactions between two or more species in the form of either competition or predation is not well studied and only a few attempts have been made to integrate these processes into fishery evaluation schemes. Favorite, Laevastu and Straty (1977) have constructed a large simulation system which partitions species and predator-prey relations by area in the North Pacific Ocean. Andersen and Ursin (1977) have produced a complex multi-species, predator-prey model for the North Sea which incorporates growth, fecundity and other biological functions in an attempt to model the effects of varying species abundance on target species. Both of these approaches require immense amounts of data for realistic evaluations. They provide ample experience to show the relative merits of each approach, and clearly, either is potentially much more realistic than the single species approach which has dominated fishery science for several generations. The question becomes whether fishery assessment programmes are really ready for integrated efforts to resolve the problems of evaluating the condition and relationships of the various commercial species status. Doing less appears to be integrating out most of the important processes, resulting in very large uncertainties regarding fishery variations. However, to construct and implement a realistic multispecies, interactive model may be far too demanding for available resources. The problem lies in the enormous sampling programmes and analyses which would be needed to develop and verify the models, where today's research programmes tend to emphasize the simple, desk-top science approach. The resolution of this dichotomous situation will be left in the hands of resource evaluation

programme leaders, and will ultimately depend on the resources, in both expertise and finances, which are available to them. Of course the problems also cross the bounds of biology and will necessarily include oceanographic and climatologic research. The opportunities and need for taking this large step are clearly present, the only reluctance seems to stem from lack of the broader view of the problems and their means of resolution at the programming level, including funding and cost-benefit.

The apparent failure of most stock assessment programmes to evaluate resources, and management to implement their recommendations, thereby providing effective resource management (Saetersdal, in press) certainly argues for an improved approach. This should include a better environmental monitoring scheme in direct measurement of parameters of relative importance to fish biology, including such measurable qualities and quantities as habitat stratification, distribution, and variations in time and space. The need for developing multi-disciplinary fishery data collection programmes has been long recognized and responded to in many countries (e.g. Japan) with long standing fishing cultures. The generalization of this approach seems warranted. Of course these improvements are only worth the effort if there is an effective management implementation from which to begin.

G. Integrating physical and biological models

Formulating the critical period concept of larval fish survival in the ocean environment requires the integration of models of physical and biological processes. Vlymen (1977), Beyer (1979) and others have built models of the behaviour and physiology of fish larvae during the period when they are most susceptible to starvation. Kullenberg (1977), Woods (1979) and other physical oceanographers have modelled the physical processes which govern stratification and mixing in the upper layer of the ocean. Stratification of the water column permits phytoplankton to exist in sufficient concentration to enable the larvae to obtain sufficient food for the effort expended in searching and still permit sufficient excess nutrients for growth. Wind mixing of the water column can dissipate these food concentrations to levels which may limit food availability to such a degree that growth and survival are not possible.

To integrate separate physical and biological models is no simple task. However, it can be done successfully as demonstrated by Walsh (1975) and Wroblewski (1977) who have modelled plankton productivity in the Peru and Oregon Upwelling Systems respectively. Their approach was to combine existing physical models of the upwelling circulation with formulations of phytoplankton growth, nutrient uptake kinetics and zooplankton grazing and excretion. They were careful to merge the physical and biological models on compatible time and space scales.

Current knowledge concerning the effects of physical factors on patch structure is limited mainly to their effect on dispersion and/or destruction. In order to usefully integrate this knowledge in terms of individual larval survival, the initial conditions of patchiness need to be defined. This can be accomplished only when effective methods are developed for measuring and counting appropriate patches on a continuous basis.

Defining an appropriate food patch is the first requirement in this complex problem. Studies in the laboratory as well as in the field have been summarized by Theilacker and Dorsey (this volume). The Peruvian anchoveta food and feeding habits have been described by Mendiola (1969 and 1973) and Mendiola and Ochoa (1973). Far more knowledge regarding particle size for each food species, their relative mobilities, and reproductive rates are needed to complete a realistic model of the patches of esculent foods for larval fishes.

At present, we can only model larval fish survival as a predator-prey system, with growth and survival resulting from the difference between energy expended and energy gained in each feeding event, less the metabolic costs for maintaining the larvae.

For particulate feeders, the energy gained E_{IN} can be expressed in calories per unit time as

$$E_{IN,L} = \sum_{i=1}^{N_{\Delta t}} SS(D_i) \cdot cal(D_i) \cdot S_C^* \quad (5)$$

where $N_{\Delta t}$ is the number of attacks in the interval Δt by a larva of length L , $cal(D_i)$ is the caloric value of organisms of diameter D_i , $SS(D_i)$ is the size specific rate of successful capture^{1/} and $S_C^* = 0$ or 1 as the density of prey organisms is below or above the critical level required for feeding C^* .

Depending on the size specific energy requirements for capture, processing and maintenance, E_{IN} will or will not exceed the limit $E_{S,L}$ sufficient for survival and/or the limit $E_{G,L}$ required for growth. The critical element in terms of the population is then the relative frequencies with which

$$E'_{IN,L} > E_{S,L} \quad \text{and} \quad E_{IN,L} > E_{G,L}$$

From equation (5) it is clear that the input energy $E_{IN,L}$ depends only on the product $SS(D_i) \cdot cal(D_i)$ i.e. high risk-high gain is equally as viable an alternative as low risk-low gain. In the absence of detailed information concerning size specific rates of success and the caloric value of the prey, the most effective strategy cannot be assessed.

Since the larvae most probably react to any prey when the concentration C is greater than the level C^* and when given D_L is the lower threshold size and D_u the upper acceptable size

$$D_L < D_i < D_u$$

the number of attacks in the interval Δt depends upon the characteristics of the environment in which the larvae is found. In particular the number of attacks will be related to the average distance between prey organisms, i.e. to the patchiness of the environment.

In natural environments, patchiness is caused by both physical and biological factors. For passive organisms physical effects are primal while for actively swimming organisms, behavioural effects may be inextricably confounded with environmental factors. Using an artificially constructed model of prey contagion, Vlymen (1977) showed that growth rates of feeding anchovy (*E. mordax*) larvae from 4 - 20 mm in length could vary from 20 to 70% with changes in patch size and density. The applicability of his work to the prediction of larval survival at sea is, at present, unknown because methods for quantifying patchiness at levels relative to the larvae are not yet available. Spot sampling methods such as described by Owen (this volume) have been used to demonstrate micro structure at levels less than 1 m but the amount of effort required to adequately describe large areas of the sea by this technique is too great for its utilization as a monitoring tool.

A complete description of the larval environment requires knowledge of the relative frequencies with which patches of particular sizes and concentrations occur. In dynamic environments these frequency distributions are in constant flux and contain biological and physical elements of long term development, growth and stability as well as elements of long and short term dispersion and destruction. The problem of relating survival of individual

^{1/} $SS(D_i)$ includes the ability to capture food and the willingness to attack, i.e. $SS(D_i < D_L) = SS(D_i > D_u) = 0$, where D_L is lower acceptable limit and D_u is the upper size limit.

actively swimming larvae to quantitative measures of patchiness seems insurmountable, too large a number of rational and non-contradictory hypotheses can be established for the way in which biological behaviour may complement or counteract the physical processes.

For passive organisms such as first feeding larvae, the problem seems more tractable; without ability to actively seek out patches, they are likely most susceptible to aggregation mechanisms of the thermocline. If this is so, then survival may be directly related to the physical processes which determine the degree to which patches formed at the thermocline are able to persist in the mixed layer.

H. Time and length scales of physical motion

In general, the identification of the physical processes in a system is made by referencing the time and length scales of interest (which we normally call scaling). The range of possible scales is immense, time scales from seconds to decades, vertical length scales from centimetres to a few kilometres and horizontal length scales from centimetres to 1 000's of kilometres. However, not all of the possible scale combinations are relevant. We tend to associate the longer time scales with the larger length scales.

For the purposes of this discussion, we shall use vertical length scales as our reference and discuss the corresponding horizontal length and time scales and the physical processes and models we associate with these scales. The smallest physical scales we shall consider are 1 cm. At centimetre scales, molecular viscosity and diffusion are important. Horizontal length scales are the same magnitude as the vertical. Traditional isotropic turbulence models provide an adequate description of the fluid motions. The production of turbulence at these scales is nearly equal to the rate of dissipation of turbulent kinetic energy. Thus, in the absence of production, the turbulent motion will be damped on a time scale equal to the time it takes to travel a distance equal to the length scale, seconds to minutes, and then molecular diffusion time scales will apply. In the absence of turbulence, fossil structures will persist for a long time, but they are easily destroyed by turbulence.

At 10 cm, the world is no longer isotropic. From dye studies, the rate of horizontal to vertical scales is 100 to 1000. The generation of turbulence through processes like shear instability is still approximately balanced by dissipation suggesting time scales of minutes for actively turbulent regions. However, the fossil structures associated with mixing events can be much longer lived, which is the thermal fine structure of the ocean.

At 1 m, the strong horizontal anisotropy still exists with 100 to 1 000 times larger horizontal than vertical scales. The expected time scales of minutes to hours includes internal gravity wave motions as well as turbulent motions.

At 10 m, we begin to find that we can no longer isolate the relevant horizontal length scales and time scales from larger vertical scales in any simple fashion. For these vertical scales, we can describe near surface turbulence by mixed layer models where changes in the structures occur over hours and days and horizontal variations over 10's of kilometres.

At 100 m, we expect the mixed layer models to still apply with associated time scales of days-months-year and length scales of 10's to 100's of kilometres. At this order vertical scale, the geostrophic circulation becomes important and this circulation must be included in a model of the environment.

The largest vertical scales of interest are of the order of the ocean depth 1 km. The associated length scales are of order 100 km to ocean basin width with time scales of days-years. Eastern boundary current systems, weather patterns and El Niño are features to be described on these scales.

I. Distribution problems of biological variables in relation to physical oceanography conditions

1. Problem statement

Assuming that some important questions are related to how (where and when) critical concentrations of suitable food are generated, a problem is to formulate physical mixing models which can identify significant environmental parameters, and thereby obtain criteria for the probability of food concentration generation.

The food concentrations can be in the form of layers at or below the surface, more or less homogeneous patches characterized by fairly sharp horizontal and vertical boundaries.

A conceptual framework can be a stratified environment where biological activity occurs and the physical mixing events are below some level in frequency and force, so that food concentrations can build up. The relative timing of physical and biological events is critical, as is the ability of the physics to build up as well as destroy a stable stratification.

2. Mixing model for layered patches

We will first assume that the stratification is stable and that food concentrations in the form of layered patches exist. A simple mixing model may then be formulated by treating the "patch" as a line source on which horizontal and vertical mixing acts, assuming the "food" to be a passive tracer.

The horizontal mixing can be given by a diffusion velocity P and the vertical by a diffusion coefficient K_z , assumed to be constant over the layer in question but not over the entire water column (e.g. Kullenburg, 1974). The concentration C may then be given as a function of time t

$$C(t) = \frac{M_0}{\sqrt{2\pi} \cdot H_0 \cdot L_0 \cdot P \cdot t} \cdot e^{-\frac{\pi^2 \cdot K_z \cdot t}{H_0^2}}$$

where M_0 , H_0 , L_0 are the initial mass, thickness and length of the "patch", P and K_z are the mixing parameters and H is the layer thickness at time t . This is assumed to be virtually constant over limited periods of time.

The parameters P and K_z are known to vary with environmental conditions. Typical ranges may be

$$0.01 \leq P \leq 2.0 \text{ cm s}^{-1} \text{ and} \\ 0.01 \leq K_z \leq 200 \text{ cm}^2 \text{ s}^{-1}$$

It is quite clear that this variability will influence the biological system very much and that we should be able to locate potentially favourable areas if we can predict the mixing conditions on the basis of easily observable environmental parameters. To some extent this can be done.

3. Mixing in relation to environmental parameters

The vertical mixing in the top layer of the sea may be related to the wind, the stratification and the vertical current shear by a relation as (Kullenberg, 1971; 1974)

$$K_z = \text{constant} \cdot \frac{\overline{W_{10}^2}}{N^2} \left| \frac{dq}{dz} \right|$$

where W_{10} is the average wind speed at 10 m, the stratification parameter $N^2 = -\frac{g}{\rho} \frac{d\rho}{dz}$ with ρ the density of water and g the acceleration of gravity; q is the horizontal current vector. The numerical constant $= Rf \cdot c_d - \frac{\rho_a}{\rho}$ is about 10^{-7} (Rf is the flux Richardson number, c_d the surface drag coefficient, ρ_a density of air).

This expression can be used for conditions where the wind is blowing during 1/2 day or more and is valid for the surface layer down to the base of the wind-mixed layer.

The rate of deepening of the layer due to entrainment of water from the deeper layer can be estimated over time scales of hours and an expression for the momentum transfer coefficient and the entrainment velocity, i.e. the rate of deepening, can be obtained through energy arguments (e.g. Denman, 1973; Kullenberg, 1976, 1977; Richman and Garrett, 1977).

For very low wind speeds or calm conditions the heat input from the sun will be able to suppress the vertical mixing considerably, provided no other mixing energy sources exist. During such conditions the lowest vertical mixing rates are found. Generally, the vertical mixing can be related to the internal stress, current shear and stratification, where, however, it is very difficult to observe the stress.

Other mechanical energy sources are the tidal energy internal waves and shears related to frontal zones.

The horizontal mixing can be related to the current fluctuations or to the current shears. Over scales of meters to hundreds of meters or several kilometers the vertical shear diffusion has been shown to be an important process (e.g. Bowden, 1965; Kullenberg, 1972; Okubo, 1967).

Considering a line source internally, we are interested in diffusion, laterally out of the line. This may be related to the current oscillations and the current shear as

$$\sigma y^2 \times \left(\frac{dv}{dz} \right)^2 \cdot \frac{K_z \cdot t}{\omega^2}$$

with σy^2 being the lateral concentration variance where $\frac{dv}{dz}$ is the shear of the oscillating current component perpendicular to the line source and ω is the frequency of oscillation.

The model is based on the assumption that the vertical shear effect dominates the mixing. The variance may be related to the diffusion velocity P as

$$\sigma y = P \cdot t$$

Based on these brief considerations one can conclude that wind, current shear, stratification, alternative mixing energy sources and solar radiation are important environmental parameters.

Information on these can be obtained fairly easily, assuming that one can average vertically over some tens of centimeters up to meters.

The discussion also brings out the coupling between these environmental factors, which it is critical to understand.

In particular, this may concern what may be called the pre-conditioning phase. During this phase the required environmental conditions of nutrient supply, vertical stratification in relation to the euphotic zone and light conditions, are built up. These conditions are required for triggering the primary production followed by zooplankton development.

4. Areas and times of suitable conditions

Such areas are basically defined by the physical and chemical conditions acting during a pre-conditioning phase so as to build up the requirements for primary production. Such regions can to a large extent be defined based on the dynamical (physical) conditions and their stability in occurrence (in time) can be judged on climatological conditions. Clearly some of these regions are large, like the upwelling areas and frontal zones at continental slopes, but may also be more limited like the seasonal shelf sea fronts.

The point is that primary production is large over extended areas and within these patchiness on a variety of scale will be generated by local physical conditions as well as zooplankton development and grazing. These patches can have horizontal scales from metres to tens of kilometres and vertical scales from tens of centimetres to the mixed layer depth.

The regions of high primary production are governed by dynamic processes on climatological scales whereas the patchiness is to a large extent governed by local conditions.

5. Stratification and vertical mixing in the surface layer

It is important to realize that the heat input from the sun during a not too cloudy day and weak winds can suppress vertical mixing and generate stratification in the surface layer.

The wind generates two effects related to vertical mixing: i) mechanical energy transferred directly through the action of the wind stress and indirectly through breaking waves; ii) surface heat loss increases with increasing wind. This latter effect can be very important since a large surface heat loss will imply that convective motion can be set up in the surface layer.

Woods (1980) investigated this effect in detail and showed that the sun heat input over most areas of the ocean will suppress the convective motion during the day for weak winds not generating breaking waves, say less than $2-3 \text{ m}\cdot\text{s}^{-1}$

In such conditions stably stratified layers will develop near the surface. During night time the layers will be deepened. However, during the warm season the stratification is not necessarily destroyed, and cold, clear nights will likely break down the stratification to the depth of the (normal) thermocline. During the following day of heat input a new thin stable layer can be generated and so on. Several stable layers can thus be generated in an originally well-mixed surface layer, and these may persist until a strong wind-event or cooling event breaks them down. The thickness of the stable transitions between the layers will vary, but a likely range is 20-100 cm. High concentrations of various matters (chlorophyll, passive tracers) can be built up in these transitions or interface layers.

6. Radiation model

In order to obtain the vertical distribution of heat absorbed in the water column a radiation model can be used. Assuming that the important part of radiation in the present context is the direct sun light, the simplest radiation distribution for zenith sun in the surface layer (euphotic zone) of not too clear water is of the form

$$E = E_0 e^{-az}$$

where E_0 is the irradiance just below the surface, a is the light absorption coefficient and z the depth.

The sun elevation can be taken into account in the form

$$E = E_0 e^{-K(90^\circ)z/\cos\theta}$$

where $K(90^\circ)$ is the vertical attenuation coefficient and θ is the sun zenith angle under water.

In waters of primary interest in the present context the absorption will be due to the water itself, suspended materials and their distribution and dispersion properties, and dissolved organic substances.

The absorption is strongly wave-length dependent, with a minimum in productive waters around 520 nm wave-length (e.g. Jerlov, 1976).

J. Aggregation and disaggregation in relation to physical processes

When considering the dynamics of particles, both passive such as eggs and active such as flagellates, in the upper ocean, it is convenient to discuss time scales shorter and longer than 1 day separately. In the settling model we will find that passive particles can only collect at their neutral density level, which will probably be in the seasonal thermocline. Particles in the mixed layer at very low turbulence levels will settle out of the mixed layer, but at normal turbulence levels they will be dispersed throughout the mixed layer. We can generalize this result. If the amalgamation of particles (high density patches) must persist for longer than 1 day, then these patches cannot occur in the region we normally call the surface mixed layer and which we can adequately treat by one-dimensional mixed layer models as reviewed by Niller and Kraus (1979).

For these long time scales, the surface mixed layer is effectively well-mixed in terms of persistent patches. Below the mixed layer in the seasonal thermocline, the turbulence levels are much lower (open ocean work by Dillon and Caldwell, 1980) and layers can persist for long times, at least as great as 3 days, as observed in dye studies by Kullenberg.

Where a particle resides in the seasonal thermocline will depend upon its actual density and swimming ability, if any, and/or resistance to settling.

For time scales less than 1 day, the temporal development of the surface mixed layer must be considered. The levels of turbulence within the mixed layer will be determined by the strength of the wind stress, the rate of surface heating and the stability of current shears in the mixed layer. During the day time, we expect heating to occur at the surface and restratification of the water due to the addition of heat and formation of a shallow mixed layer on top of the previous mixed layer from the day before. The behaviour of this mixed layer should conform to the one dimensional mixed layer models mentioned earlier. At night, penetrative convection can occur and the depth of the new mixed layer will depend on the net amount of heating or cooling over the whole day and the strength of the wind. If solar insolation exceeds the back radiation and the wind strength does not increase, then the new mixed layer will be shallower than the old and a step in the seasonal thermocline will be formed. The process observed by Lasker (1975), e.g. the destruction of the chlorophyll maximum at the base of the mixed layer, represents a strong wind event deepening the surface mixed layer into the seasonal thermocline and their formation of a layer structure during the next day with the diurnal mixed layer.

K. A simple mixed layer model applicable to wind-driven surface, and tidally driven bottom mixed layers

Simpson and Hunter (1974) developed a simple model of mixing of solar heat energy by tidal streams in shelf seas:

Consider that an amount, q , of heat is introduced into the upper boundary of a water column of depth h , and an initial density ρ . This heat produces a density change $\Delta\rho$, in a thin layer Δh . To mix the column vertically to a uniform density ρ' in a depth h' the potential energy must be increased by an amount equal to:

$$\frac{\alpha q g h}{2c}$$

assuming density is a linear function of temperature, and neglecting salinity as a source of buoyancy input (giving $h=h'$) where:

α = linear expansion coefficient
 c = specific heat
 g = acceleration due to gravity

For a rate of heat input Q , the demand for potential energy to maintain mixing would be:

$$\frac{\alpha Q g h}{2c}$$

Energy is fed into the column, by stress on the upper or lower boundary, at a rate equal to:

$$\tau_B U_D$$

where τ_B is the boundary stress

and U_D is a "slip" velocity at the boundary (this is the wind drift velocity for the wind mixed layer, or the tidal velocity for the bottom mixed layer).

Now $\tau_B U_D = k \rho_B U_B^2 U_D$ where k is a drag coefficient in the quadratic friction law, and ρ_B and U_B are the density and velocity relevant to the medium generating the stress (water for the bottom mixed layer, air for the surface mixed layer).

A fraction ϵ of this kinetic energy is considered to be available for increasing the potential energy of the water column, so that at transition there is a balance defined by:

$$\frac{h}{U_B^2 U_D} = \frac{2C \rho_B k \epsilon}{\alpha g G}$$

In the original paper it was assumed that the right-hand side of the above equation was constant in time and space and tidal mixing only was considered, hence $U_B = U_D$. A critical value of $\frac{h}{U_B^3}$ was then shown to be associated with the transition between stratification and

full vertical mixing (and hence the occurrence of fronts) in the Irish Sea. This parameter has subsequently been shown to define the position of all the significant sea fronts over the northwest European shelf (Pingree and Griffiths, 1978).

The above result may be used to define the kinetic energy required to vertically mix a layer of depth h under a heating rate Q . Vertical mixing is ensured if:

$$\frac{U_B^2 U_X}{Qh} > \frac{\alpha g}{2C\rho_B k\epsilon}$$

A larger input of kinetic energy may hence support mixing over a greater depth and vice versa.

For tidal mixing in summer on the northwest European shelf, the above inequality becomes approximately:

$$\frac{U_B^2 U_D}{h} = \frac{U_B^3}{h} > 13 \quad (\text{cgs units})$$

(Pingree and Griffiths, 1978, where above U_B is the tidal velocity)

If we assume the same parameters apply to the surface mixed layer then:

$$\frac{U_W^3}{h} > 7 \times 10^5 \quad (\text{cgs units})$$

where U_W is the surface wind velocity.

Modelling of stratification and frontal structures in shelf seas is continuing with the inclusion of an interaction between the stratified shear flow and the efficiency factor (ϵ) (Simpson and Bowen, in press). Such a mechanism accounts in a simple way for the sharpness of tidally induced fronts, and for the fact that their positions do not fully adjust to the variation of flow over a Neap-Spring cycle.

The biological importance of shelf sea fronts as areas rich in healthy phytoplankton has also been demonstrated (Simpson, Edelston, Morris and Tett, 1979).

L. Settling model

We may model the settling of passive particles in a fluid of different density using Stoke's law (assuming low Reynolds number).

Let $\Delta\rho$ = density difference between particle and water
 r = particle radius
 η = molecular viscosity of water
 g = acceleration due to gravity
 w_s = settling velocity

Hence force on particle = $6\pi\eta rw_s$ (Stokes law)

= $\frac{4}{3}\pi r^3 \Delta\rho g$ (weight of particle)

Hence $w_s = \frac{2}{9} \frac{r^2 \Delta\rho g}{\eta}$

Now $r \sim 10^{-2}$ to $10^{-2.5}$ cm
and $\partial\rho \sim 10^{-4}$ (in mixed layer) cgs to $\sim 10^{-3}$ (below mixed layer) cgs
and $9 \sim 10^3$ (cgs), $\eta \sim .01$ (cgs)
then w_s is in range 2×10^{-4} to 2×10^{-5} cm/sec
(in mixed layer)
or 2×10^{-3} to 2×10^{-4} cm/sec
(below mixed layer)

(The values of $\partial\rho$ have been obtained by assuming a neutrally buoyant particle is displaced either within the seasonal thermocline or below the seasonal thermocline.)

The settling velocities are hence very slow and we may infer:

- For a length scale of 3000 cm (the thickness of the surface mixed layer) the corresponding settling time is greater than one week.
- Active particles (e.g. dinoflagellates) can overcome density effects if their swimming speed is in excess of 2×10^{-3} cm/sec.

M. Interaction of settling and mixing

Solution of the diffusion equation in the vertical for a particle with settling velocity w_s , in a fluid of diffusivity K , yields a layer of e-folding thickness equal to.

$$\frac{K}{w_s}$$

Values of K range from: 10^{-3} cgs (molecular)
to 100 cgs (in a turbulent mixed layer)

The above thickness is hence in the range

$$\begin{array}{ll} .5 \text{ to } 5 \text{ cm} & (K = 10^{-3}) \\ 5 \times 10^5 \text{ to } 5 \times 10^6 \text{ cm} & (K = 100) \end{array}$$

The thickness is equal to 3000 cm (the approximate thickness of the surface mixed layer) for K in the range:

$$\begin{array}{ll} .06 \text{ to } .6 \text{ cgs using } w_s \text{ } 2 \times 10^{-4} \text{ to } 2 \times 10^{-5} \\ .6 \text{ to } 6 \text{ cgs using } w_s \text{ } 2 \times 10^{-3} \text{ to } 2 \times 10^{-4} \end{array}$$

Hence, unless the level of turbulence is very low, particles "trapped" by density in the thermocline will be mixed upwards throughout the surface mixed layer; thus beginning the cycle of "salting" organisms throughout the mixed layer where they might find opportunity to encounter nutrients, light, food, etc. The importance of this process is paramount to the production cycle in the sea.

CONCEPTUALIZING GENERAL MODELS OF LARVAL FISH SURVIVAL

Perhaps before formalizing a larval survival model, one should consider the necessity for obtaining a reasonable recruitment forecast, and the sampling philosophies one would then choose. Quite clearly there are some species where studying larval survival models is not likely to provide useful management information, nor would one be able to find direct information regarding the input parameters. In this case a good example is the relatively nomadic skipjack tuna (*Katsuwonus pelamis*) which is only available to most of its fisheries for a short, late portion of its juvenile stage. Upon reaching maturity the adults become relatively unavailable, and their eggs and larvae are poorly known. Developing a realistic larval survival model would be relatively futile for this type of broad-ranging fish at present. However, a wind-drive turbulence index in the Central Pacific spawning habitat appears to be a useful forecasting tool for recruitment of the juveniles into the Eastern Pacific fishery.

For species of secondary economic importance, such as some long-lived demersals, the poor availability of their adult or reproductive age fish protects them from high exploitation and the recruitment, although contributing considerably to the fished population, may not yield great variations in overall biomass in contrast to some shorter-lived species. This type of fish might be readily evaluated from less refined models, perhaps only the more integrative $\ln S/R$ as a function of adult biomass (given that it can be measured) could be adequate.

More complex estimations, such as Csirke's anchoveta recruitment as a function of area and stock density might suffice for many situations, but the uncertainty inherent to the approach may not satisfy all interests, particularly where large capital investments are involved. In this case a persistent evaluation at the level of complexity inferred from the "Larval Survival" approach may be warranted.

Another consideration before leaping into the arena of larval fish survival models is whether or not all the necessary information can be collected over the range of the spawning population. Studying only a sub-region of the potential spawning area may not yield sufficient information for a realistic assessment of larval survival which might effect the exploited population and/or harvesting strategies. A bad estimate because of poor sampling, or inadequate understanding of the variables will in effect cost the investigators more than just time and effort. It will cost them credibility, a very significant loss in this already low period in fishery science performance.

A. Formulating the models

Given that one would wish to approach the larval survival question as a hybrid Vlymen-Beyer construct, then several important parameters need to be determined. For example, one would need to know:

- 1) Time to first feeding after hatching (Temperature, T, dependent)
- 2) Gut volume (L dependent)
- 3) Digestion/evacuation times (T dependent, food dependent)
- 4) Metabolic rate (T dependent)
- 5) Length/weight relation
- 6) Age/length (T dependent, food history dependent)

- 7) % successful capture (age dependent, particle dependent)
- 8) % body weight = ration per day
- 9) Gross growth efficiency (assumes constant energy expenditure)
- 10) Size specific prey selection
- 11) Seasonality of spawning - egg deposition
- 12) Behavioural information

Much of this requires intensive laboratory and field study at present.

The next series of questions would involve the physical system in which the specific target organism is to be modelled. Questions to be answered in this case are:

- 1) Seasonal and short-term wind speed and directions
- 2) Temperature distributions
- 3) Oxygen distributions
- 4) Primary productivity distributions and rates
- 5) Appropriate (esculent) food particle distributions
- 6) Stratification/mixing frequency related to (5)
- 7) Insolation rate
- 8) Tidal flux

B. Population aspects of the model

As an example, the dominant *Engraulis* stocks of the Peru and California current systems exhibit considerable similarity in their life history patterns. Both have their spawning peak periods near the winter-spring transition (except in anomolous circumstances such as reported by Santander, this volume), and a secondary peak near the summer-fall transition. The seasonal oceanographic cycles in these two eastern boundary current regions show similarities and differences. The seasonal temperature cycles are nearly identical with minimum temperatures occurring in late winter and maximum temperatures occurring in late summer. The upwelling maxima cycles show considerable differences in the two regions. The upwelling maxima in the Peru current (4° - 16°S) occur in the winter-spring transition. In the California current region the maxima occur in late spring (May, 30°N).

The dinoflagellates' and diatoms' annual cycles are closely tied to the upwelling cycles with maximum diatom concentrations occurring near the upwelling maxima and maximum dinoflagellate abundance occurring near the upwelling minima.

There are marked differences in the relationships between the spawning peaks of *Engraulis* in the two systems and the environmental, oceanographic cycles. In the Peru current, *Engraulis* spawns during the upwelling maxima, and during the diatom maxima. In the California current *Engraulis* spawns before the upwelling maxima, during the dinoflagellate maxima. Figure 4 gives the spawning periods of the four important pelagic species in the California and Peru currents, where known.

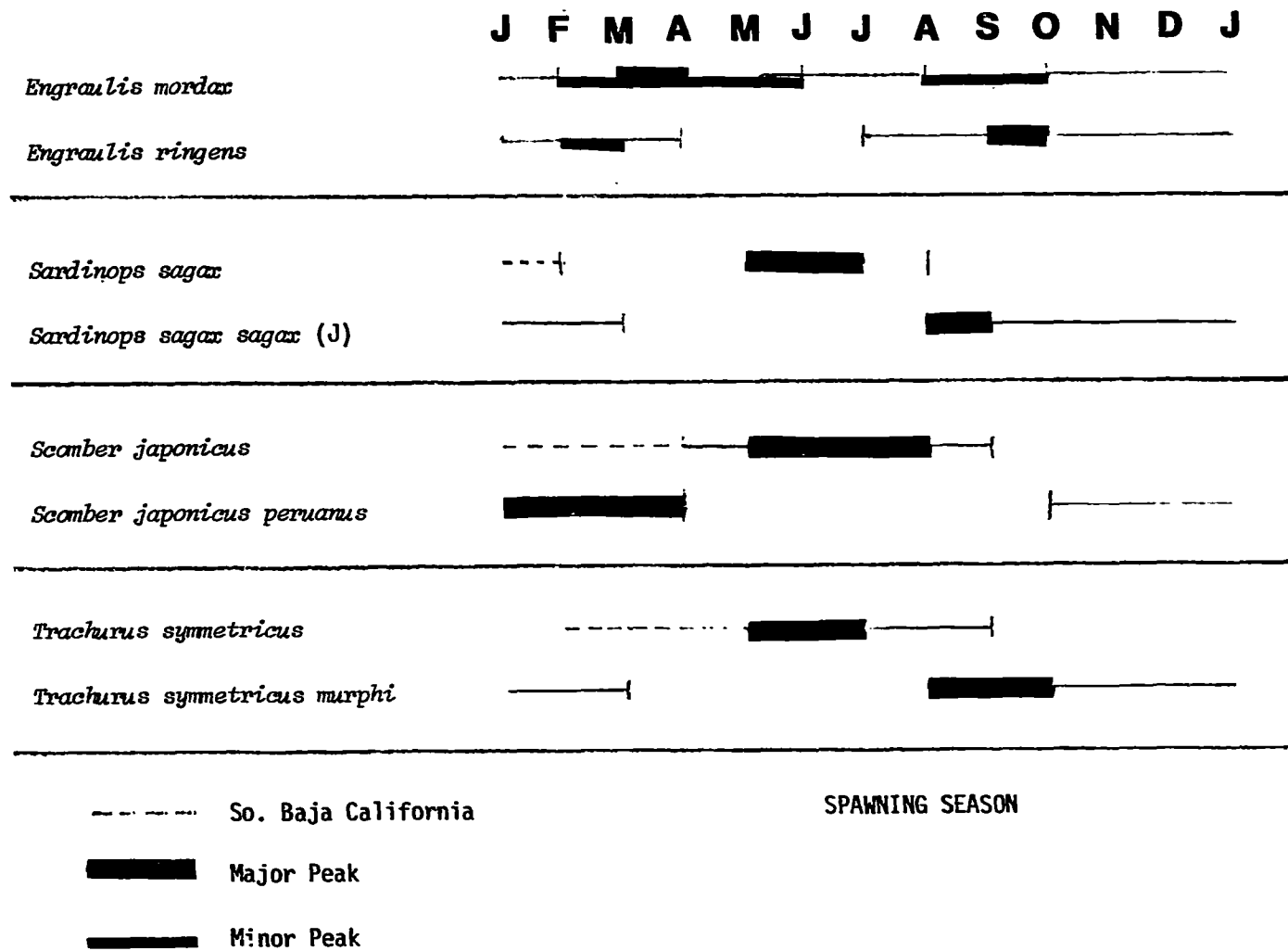


Figure 4

The early life history concepts developed at the workshop appear to lend themselves to testing by comparing the spawning cycles and environmental conditions occurring in the two regions.

If the early life history stages (first feeding, etc.) represent critical factors in determining recruitment or reproductive success, then a useful model should demonstrate why the two *Engraulis* populations in the two systems have such different spawning strategies in relation to the upwelling cycles of the two regions. It appears plausible to construct a useful model, but far more local monitoring of the environment over fairly small scale (1° latitude, longitude and sub-daily time) would need to be developed.

The important population information necessary to produce a meaningful larval survival model include:

- 1) Distribution of reproductive biomass
- 2) An estimate of regional density of (1)
- 3) The proportion of spawners in the total potential reproductive biomass (ã la Tsukayama and Alvarez, this volume)
- 4) Frequency of spawning (ã la Hunter and Goldberg, 1980)
- 5) Condition factor of reproductive individuals (e.g. fat content)
- 6) Size at spawning for relative fecundity estimation
- 7) Egg size and size of larvae at hatching
- 8) Predator abundance and distribution compared with egg and larvae distributions

From existing models there can readily be constructed system models which would be useful in testing the first feeding success leading to the larval survival hypothesis of Lasker (1975). Toward this goal the workshop has suggested several directions of information and research development which would provide a better test of the principles underlying this topic, which would also provide a realistic basis for research into the forecasting potential of larval fish survival as it relates to fishery recruitment.

SUGGESTIONS AND CONCLUSIONS

The trend in the past larval fish laboratory research has been a preoccupation with "care and feeding" which leads to maximum survival of eggs and larvae. The numbers of experiments which have not been written up because "too few" fish thrived is unknown, but the information content of such efforts could truly add another dimension to our knowledge of larval fish survival. It is clear that the next stages of larval rearing experiments should include defined stress conditions which might lead to a more realistic "typical" survival in contrast to the "excess" and "optimal" conditions offered and described to date.

Another need in larval fish studies is a series of standard methodologies and procedures so that results of various experiments, whether on similar species or not, can be compared. The chaotic collection of methods and treatments in available literature makes most studies nearly incomparable if not totally so. Even where similar species, methods, etc. are supposedly employed the results are often in total conflict. Among the many variables dealt with in eggs to larval studies such important variables as initial egg size and temperature variance over the study period are often not reported. These two variables alone can produce differences which if not accounted for would make experimental results diverge beyond reasonable, interpretable bounds.

Among the many questions needing attention regarding the physical processes which influence biological processes is the time dependence of local events. There are too few time series of data on appropriate scales to allow informed statements regarding such fundamental processes as layering or patch formation.

An interesting conclusion which was reached by the workshop was that if primary production and fish survival are correlated, then the physics may be the most important variable to monitor. Clearly the rate limiting steps need to be identified and monitoring schemes developed. Given that larval fish cannot survive without a first meal in their relatively immobile stages, then the physics of food concentration is an important rate limiting step. Once the larval fish obtain their first meals, they become more and more independent of "local" physics as growth and experience are obtained.

In fact, there may not be a truly "critical" period but as Sharp (this volume) suggests there are a series of hurdles to be met and cleared, all of which impart some probability of mortality.

One of the severe limitations to any predictions involving environmental states is the time dependence of the expected differences in state. The best short term prediction is: "about the same as present". The best long term prediction is: "it will be different". The scale of differences expected varies with our knowledge of trends and cycles (e.g. Spring tends to be warmer than Winter). Uncertainty in biological prediction can be attributed to poor understanding of cause and effects in the system and therefore lack of predictability really implies ignorance and/or large distances between available information sources and the events of interest. Prediction of any process is probability distributed and development of conditional probability predictors yield more specific event prediction, generally because this implies a knowledge of event or system "limits" (e.g. the specific events are better defined, hence more readily related to system variables).

This leads right back to Hjort's "critical period" hypothesis, and the need to evaluate the concept of food limitations, predation and physical variations as sources of mortality.

Models or conceptual constructs can only be validated given opportunity to devise and implement an appropriate sampling scheme. This provides the necessary feedback to permit progress toward a more realistic or better performing model. "Tuning" models without making "measurements" rarely results in a useful tool.

The need to scale up laboratory experiments to levels where very small differences in survival proportions as functions of ambient variations can be statistically evaluated seems to be the next shoreside stage in larval fish research. The at-sea evaluation of egg and larvae distributions at small scales (metres) and food distributions would improve our conceptual ability as regards eggs, appropriate food and larval survival. Clearly, definition of appropriate foods and development of culture techniques would provide tremendous opportunities for laboratory research, given a need to simulate natural processes in the laboratory to such fine detail.

The step away from single species studies needs to be taken, both in the laboratory and at sea. Predation processes, and competition aspects of larval survival need to be taken into account soon.

In order to speed the development of knowledge regarding physical processes relations to biological processes, a better evaluation of survival success as a specific function of time and location needs to be developed. The daily growth ring-otolith studies (Methot and Kramer 1979) appear to offer the best opportunities to determine time and event relations. Perhaps larval drift and transport processes can be monitored to yield probable location information.

The development of a high resolution particle counter, and subsampling system for definition of dense patches of potential food should be promoted. The distributions in time and space of esculent particles will certainly yield important insights into both the biology and physics of larval fish survival.

The major point in this workshop was not to "sell" modelling, but to try to evaluate the state of our abilities to formulate and describe the processes which appear to be important to the larval survival question. The shortcomings of available means are clear, and generally reparable. The motivation to better our understanding is high. The major task at hand is to convince the programming and administrative sectors of the world's fishery science centres, including climate and oceanographic science in this realm, that the uncertainties of population abundance prediction can probably be reduced by intense, integrated efforts to sample, study and interpret results of research at appropriate scales, namely tens of metres or less and hours to days, for individual larval fish problems, up through longer term, broader scale events to help reduce our uncertainties regarding population and ecosystems status.

POSTSCRIPT

This report represents not only the combined efforts of those attending the Workshop, but also many more individuals behind the scenes, back in the many research centre laboratories. Our goal was to evaluate present information and distill from this a realistic or representative picture of the interactions between ambient and early life history processes. This demanded a multidisciplinary approach. On day one of the meeting there were open misgivings expressed as to what could be accomplished, and how relevant each contributor's expertise was to such a complex problem. It became clear why it has taken fifty years to develop Johan Hjort's critical period concepts to a point where they can be dealt with in the laboratory or in the ocean. After two weeks of energetic discourse and intense effort, the patterns emerged, the task was faced and a basis for future investigations was produced.

Let us hope that it will not take another fifty years to reach conclusions regarding the sequential ecological processes leading toward a fuller understanding of the complex of resource species in the World Ocean.

REFERENCES

- ANDERSEN, K.D. and E. URSIN. 1977. A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. In print: Meddr.Danm.Fisk.-og Havunders.N.S., Vol.7.
- ARTHUR, DAVID K. 1956. The particulate food resources of the larval of three pelagic fishes, especially the Pacific sardine, *Sardinops caerulea* (Girard), Unpublished Doctoral Dissertation, on file in the Library of Scripps Institution of Oceanography, University of California, La Jolla, 231 p.
- BAGENAL, T.B. 1971. The interrelation of the size of fish eggs, the date of spawning and the production cycle. J.Fish.Biol., 3:207-219.
- BAKUN, A. and R. PARRISH. Environment inputs to fishery population models for eastern boundary current regions. This volume.
- BEVERTON, R.J.H. and S.J. HOLT. 1957. On the dynamics of exploited fish populations. Min. Agric.Fish.Food.Fish.Invest., Ser.2, 19:533 p.
- BEYER, J.E. 1976a. FISH I. Survival of fish larvae - a single server queue approach. IMSOR, 244 p.
- _____. 1976b. FISH II. Survival of fish larvae - a single server queue approach. IMSOR, 68 p.
- _____. 1976c. Ecosystems - an operational research approach. Part 1 of the Ph.D. dissertation. IMSOR, 315 p.
- BEYER, J.E. and G.C. LAWRENCE. 1980. A stochastic model of fish growth. Ecol.Modelling, 8:109-132.
- BOWDEN, K.F. 1965. Horizontal mixing in the sea due to a shearing current. Journal Fluid Mechanics, 21(1):83-95.
- BRANDER, K. 1975. Guidelines for collection and compilation of fishery statistics. FAO Fish.Tech.Pap., (148).
- CORNFIELD, J. 1974. From the Presidential Address. American Statistical Association, 27 August 1974.
- CSIRKE, J. 1978. Recruitment in the Peruvian anchovy and its dependence on the adult population. ICES Symposium on the Biological Basis of Pelagic Fish Stock Management. Aberdeen, Scotland, 3-7 July 1978.
- CUSHING, D.H. 1971. The dependence of recruitment on parent stock in different groups of fishes. J.Cons.Int.Explor.Mer., 33:340-362.
- _____. 1974. A link between science and management in fisheries. Fishery Bulletin, U.S., Vol.72, No. 4, 859-64.
- DENMAN, KIL. 1973. A time-dependent model of the upper ocean. Journal Physical Oceanography, 3(2):173-84.

- DILLON, T.M. and D.R. CALDWELL. 1980. The Batchelor spectrum and dissipation spectrum in the upper ocean. *J. Geophysical Res.*, 85(4):1910-1916.
- FASHAM, M.J.R. 1978. The statistical and mathematical analysis of plankton patchiness. *Oceanogr.Mar.Biol.Ann.Rev.*, 16:43-79.
- FAVORITE, F., T. LAEVAUSTU and R.R. STRATY. 1977. Oceanography of the northeastern Pacific Ocean and eastern Bering Sea, and relations to various living marine resources. Northwest and Alaska Fisheries Center Processed Report. June 1977. U.S. Dept. of Commerce, NOAA, NMFS, Seattle, Washington.
- HAMRE, J. In press. Biology, exploitation and management of the northeast Atlantic mackerel. ICES Symposium on the Biological Basis of Pelagic Fish Stock Management. Aberdeen, Scotland, 3-7 July 1978.
- HJORT, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapp.P.-v.Réun.Cons.Perm.Int.Explor.Mer.*, 20:1-228.
- HUNTER, J.R. In press. The feeding ecology of marine fish larvae. In J.E. Bardach (ed.), *The Physiological and Behavioural Manipulation of Food Fish as Production and Management Tools*. International Centre for Living Aquatic Resources Mgmt., Manila.
- HUNTER, J.R. and C.A. KIMBRELL. In press (prob. 1981). Egg cannibalism in the northern anchovy, *Engraulis mordax*. *Fish.Bull.* (U.S.): 78(3)
- HUNTER, J.R. and G.L. THOMAS. 1974. Effect of prey distribution and density on searching and feeding behaviour of larval anchovy, *Engraulis mordax* (Girard), pp. 559-73. In J.H.S. Blaxter (ed.), *The early life history of fish*, Proc.Int.Symp.Dunstaffnage Mar.Res.Lab., Scottish Mar.Biol.Assoc., Oban, Scotland 17-23 May 1973. Springer-Verlag, Berlin, Heidelberg, New York
- JERLOV, N.G. 1976. Marine optics. Elsevier Oceanography Series 14, 231 p. Amsterdam.
- JOHANNESSON, K. and R. VILCHEZ. A preliminary note on hydroacoustic observations of changes in distribution and abundance of some common pelagic species in the coastal waters of Peru, with special emphasis on anchoveta. This volume.
- JONES, R. and J.R.G. HISLOP. 1978. Changes in North Sea haddock and whiting, pp.58-71. In *North Sea fish stocks - recent changes and their causes*. ICES Symposium held in Aarhus, 9-12 July 1975, edited by G. Hempel.
- KONDO, K. In press. How has the stock of the Japanese sardine recovered? Biological basis of stock size fluctuations. ICES Symposium on the Biological Basis of Fish Stock Management. Aberdeen, Scotland, 3-7 July 1978.
- KULLENBERG, G. 1971 Vertical diffusion in shallow waters. *Tellus*, 23(2):129-135.
- _____. 1972. Apparent horizontal diffusion in stratified vertical shear flow. *Tellus*, 24(1):17-28.
- _____. 1974. An experimental and theoretical investigation of the turbulent diffusion in the upper layer of the sea. Institut Fysisk Oceanografi, University of Copenhagen, Report 25, 272 p.
- _____. 1976. On vertical mixing and the energy transfer from the wind to the water. *Tellus*, 28(2):159-165.

- KULLENBERG, G. 1977. Entrainment velocity in natural stratified vertical shear flow. *Estuarine and coastal marine science* 5, 329-338.
- LASKER, R. 1975. Field criteria for survival of anchovy larvae: the relation between in-shore chlorophyll maximum layers and successful first feeding. *Fish.Bull.U.S.*, 73:453-462.
- _____. 1978a. The relation between oceanographic conditions and larval anchovy food in the California Current: Identification of factors contributing to recruitment failure. *Rapp.P.-v.Réun.Cons.Int.Explor. Mer*, 173:212-230.
- _____. 1978b. Ocean variability and its biological effects - regional review - northeast Pacific. *Rapp.P.-v.Réun.Cons.Int.Explor. Mer*, 173:168-181.
- _____. 1979. Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California Current: contrasting years, 1975 through 1978. ICES/ELH Symp./PE:11. Submitted to the ICES Symposium on the Early Life History of Fish, 2-5 April 1979, Woods Hole, Massachusetts.
- LAURENCE, G.C. and J.E. BEYER. 1980. A stochastic dynamic model of growth and mortality in winter flounder larvae (*Pseudopleuronectes americanus*) reared in the laboratory under experimental conditions. ICES Symposium on Early Life History of Fishes 2-5 April 1979, Woods Hole, Massachusetts.
- LEONG, R.J.H. and C.P. O'CONNELL. 1969. A laboratory study of particulate and filter feeding of the northern anchovy (*Engraulis mordax*) *J.Fish.Res. Board, Canada*, 25:393-407.
- MACKAS, D. 1976. Horizontal spatial heterogeneity of zooplankton on the Fladen Ground. (C.M 1976/L:20, Plankton Committee), printed at 64th Statutory Meeting of ICES, Copenhagen, Denmark.
- MENDIOLA, B. 1978. The food of the anchoveta *Engraulis ringens* J. in an area of upwelling (San Juan). IMARPE Informe No.49:16 p. (In Spanish).
- MENDIOLA, B. and D. GOMEZ. Food, survival and time of inactivity of larval anchoveta (*Engraulis ringens*). This volume.
- MENDIOLA, B. and N. OCHOA. 1973. Observations on the food and feeding habits of the anchovy, *Engraulis ringens* J. made during cruise 6908-09. *Oceanography of the South Pacific* 1972. Comp. R. Frazer, New Zealand National Commission for UNESCO, Wellington pp. 457-461.
- _____. Phytoplankton and spawning of the anchoveta (*Engraulis ringens*). This volume.
- METHOT, R.D. and D. KRAMER. 1979. Growth of northern anchovy (*Engraulis mordax*) larvae in the sea. *Fish.Bull. U.S.*, 77(2):413-423.
- NIILER, P.P. and E.B. KRAUS. 1977. One-dimensional models of the upper ocean. In *Modelling and prediction of the upper layers of the ocean*, edited by E.B. Kraus, Pergamon, New York, 323 p.
- O'BRIEN, J.J. and J.S. WROBLEWSKI. 1973. On advection in plankton models. *J.Theor.Biol.* 38: 197-202.
- OKUBA, A. 1967. The effect of shear in an oscillatory current on horizontal diffusion from an instantaneous source. *International Journal Oceanology and Limnology* 1, 194-204.

- OWEN, R. Patterning of flow and organisms in the larval anchovy environment. This volume.
- PARRISH, R., C. NELSON and A. BAKUN. MS. Transport mechanisms and reproductive success of fisheries in the California Current.
- PINGREE, R.D. and D.K. GRIFFITHS. 1978. Tidal fronts on the shelf seas around the British Isles. J. of Geophysical Res. 83(C9):4615-4622.
- RICHMAN, J. and C. GARRETT. 1977. The transfer of energy and momentum by the wind to the surface mixed layers. J. Physical Oceanography 7:876-881.
- RICKER, W.E. 1954. Stock and recruitment. J. Fish. Res. Board Can., 11:559-623.
- SAETERSDAL, G. In press. Review of past management of some pelagic stocks and its effectiveness. ICES Symposium on the Biological Basis of Pelagic Fish Stock Management. Aberdeen, Scotland, 3-7 July 1978.
- SANTANDER, H. Fluctuations of spawning of anchoveta and some related factors. (In Spanish with English abstract.) This volume.
- SHARP, G.D. 1978. Behavioural and physiological properties of tuna and their effects on vulnerability to fishing gear. In G.D. Sharp and A.E. Dizon (eds.), The physiological ecology of tunas. Academic Press, New York, San Francisco, London, pp.397-450.
- _____. Colonization: modes of opportunism in the ocean. This volume.
- SIMPSON, J.H. and D. BOWERS. In press. Models of stratification and frontal movement in shelf seas, progress in oceanography.
- SIMPSON, J.H., D.J. EDELSTON, A. EDWARDS, N.C.G. MORRIS and P.B. TETT. 1979. The Islay Front: physical structure and phytoplankton distribution, estuarine and coastal marine science, 9:713-726.
- SIMPSON, J.M. and J.R. HUNTER. 1974. Fronts in the Irish Sea. Nature. 250 (5465):404-406.
- THEILACKER, G. and K.T. DORSEY. A review of larval fish behaviour, physiology and their diversity. This volume.
- TSUKAYAMA, I. and M. ALVAREZ. In press. Fluctuations in the anchoveta stocks during 1964-1978.
- VALDIVIA, J. A review of the Peruvian anchoveta population decline and the biological changes observed. This volume.
- VLYMEN, W.J. 1977. A mathematical model of the relationships between larval anchovy (*E. mordax*) growth, prey microdistribution and larval behaviour. Environ. Biol. Fishes, 2:211-233.
- WALSH, J.J. 1975. A spatial simulation model of the Peru upwelling ecosystem. Deep-Sea Res., 22:201-236.
- WOODS, J.D. 1968. CAT underwater. Weather, 23:224-225.
- _____. 1980. Diurnal and seasonal variation of the convection in the wind-mixed layer of the ocean. Quarterly Journal of the Royal Meteorological Society

- WROBLEWSKI, J.S. 1977. A model of phytoplankton plume formation during variable Oregon upwelling. *Sears Foundation: J. of Mar.Res.*, 35(2):257-394
- WROBLEWSKI, J.S. and J.J. O'BRIEN. 1976. A spatial model of phytoplankton patchiness. *Mar. Biol.*, (35):161-175
- JONES, R. 1973. Density dependent regulation of the numbers of cod and haddock. *Rapp. P.-V. Réun.Cons.Int.Explor.Mer*, 164:156-173
- JONES, R. and J.R.G. HISLOP. 1978. Changes in North Sea haddock and whiting. *Rapp. P.-V. Réun.Cons.Int.Explor.Mer*, 172:58-71
- MAC CALL, A. (This volume). The consequences of cannibalism in the stock recruitment relationship. p.201-220
- ROJAS DE MENDIOLA, B., N. OCHOA, R. CALIENES and O. GOMEZ. 1969. Contenido estomacal de anchoveta en cuatro areas de la costa Peruana. *IMARPE, Informe No. 27*, 33 p.

References were not available at time of publication for Ursin 1979, and Beyer 1979.

Appendix I

A G E N D A

21 April 1980	IMARPE	Opening of workshop
	G.D. Sharp	Introduction to fishery problems
	J. Wroblewski	Portraying bio-physical events
	B. Mendiola/N. Ochoa	Phytoplankton and anchoveta spawning
	H. Santander	Fluctuations of anchoveta spawning and some related factors
	R. Villanueva	Industry and scientific advice
22 April 1980	S. Zuta/O. Guillén	The Peruvian Current System
	A. Bakun/R. Parrish	The California Current System
	R. Owen	Small scale patterning in the ocean
	G. Kullenberg	Insolation model and stratification effects
23 April 1980	J. Zweifel	The California anchovy model
	J. Richman	Eddy scale models
	J. Hunter	Eddy scale models
	G. Theilacker	Larval fish diversity in Pacific coastal pelagics
	K. Dorsey	Larval fish diversity in demersal and Atlantic pelagics
24 April 1980	K. Johannesson	Distribution and abundance of pelagics in the Peru Current
	R. Parrish	Zoogeography and physics of California Current System
	I. Tsukayama/M. Alvarez	Fluctuations in the anchoveta spawning stock during 1964-1978
25 April 1980	A. Mac Call	Management information
	J. Beyer	Larval population modelling
	O. Guillén	Primary production and anchoveta recruitment

MODELLING INTERACTION WORKSHOP

28 April 1980	J. Wroblewski/G.D. Sharp	Summary and round table discussion
29 April to 2 May 1980	Larval models and small scale physical models of stratification and destratification	
	Eddy scale and smaller scale interactions	
	1. Current scale - Ekman and wind driven	
	2. Ocean scale - climate	
	Specific monitoring points and methodology relating to fish larval survival	
5 May 1980	Summary and Report	

Appendix II

BACKGROUND DOCUMENTS PROVIDED AT THE WORKSHOP

1. Environment inputs to fishery population models for eastern boundary current regions - Andrew Bakun and Richard Parrish
2. Larval fish diversity - Kathleen Dorsey
3. A preliminary note on observations of changes in distribution and abundance of some common pelagic species in the coastal waters of Peru, with special emphasis on anchoveta - Karí Johannesson and Ricardo Vilchez
4. Food, survival and time of inactivity of larval anchoveta (*Engraulis ringens*) - Blanca Rojas de Mendiola and Olga Gomez
5. Phytoplankton and spawning of anchoveta (*Engraulis ringens*) - Blanca Rojas de Mendiola and Noemi Ochoa Lopez
6. Patterning of flow and organisms in the larval anchovy environment - Robert Owen
7. Transport mechanisms and reproductive success of fishes in the California Current - Richard Parrish, Craig Nelson and Andrew Bakun (to be published elsewhere)
8. Fluctuations of anchoveta spawning and some related factors - Haydee Santander
9. Colonization: modes of opportunism in the ocean - Gary D. Sharp
10. A review of larval fish behaviour and physiology - Gail Theilacker
11. Fluctuations in the anchoveta spawning stocks from 1964-1978 - Isabel Tsukayama and Maria Alvarez
12. The variability and dynamics of coastal upwelling on "eddy" and smaller scales - James Richman (to be published elsewhere)
13. On the possible enhancement of oxygen depletion in the coastal waters of Peru between 6°S and 11°S - James Richman and Sharon Smith (to be published elsewhere)

SUPPORTING DOCUMENTS FOR THE REPORT OF THE WORKSHOP

The following manuscripts provide reviews of information, research, concepts and observations upon which the Report was based. Some of these manuscripts were contracted by FAO for presentation and discussion at the Workshop (e.g. Bakun and Parrish; Owen). Others were provided as information papers and subsequently revised or married with other materials (e.g. Theilacker and Dorsey; Johannesson and Vilchez) to provide useful reviews of important research findings.

The IMARPE staff provided informative experience papers and background information for the contributors not particularly familiar with the Peruvian system. Due to the exigencies of preparation and dissemination of this series of reports, no translation of the documents into other than original languages was possible. I would hope that this would not entirely inhibit readers from perusing the supporting tables and figures as substantive information for the texts is generally contained in these.

I take full responsibility for the rather dubious quality of the English abstracts. It is hoped that they adequately paraphrase the important messages in the texts to a sufficient degree to perhaps pique interested readers into making contacts with the respective authors for clarification and further development of some of the topics. There is much to be learned and much more known than can be expressed here in this limited text. I am sure that many will obtain a more eclectic view of the problems of Living Resource Science from careful reading of all of this documentation. This was the objective of this effort.

Gary D. Sharp

ENVIRONMENTAL INPUTS TO FISHERY POPULATION MODELS
FOR EASTERN BOUNDARY CURRENT REGIONS

by

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INTRODUCTION

Recent precipitous declines in important fishery stocks around the world have pointed out an urgent need for advances in fishery management science. A particular need is for realistic models which can predict and simulate effects of various management options. In most existing management models, the surplus production of a stock is assumed to be a relatively constant function of stock size. Recent events have shown this assumption to be inadequate under conditions of environmental perturbation.

Properly incorporating environmental effects in fishery models can be a difficult problem. There are two basic approaches: (1) the rational (cause-effect) approach which is based on an understanding of the physical and biological processes involved, and (2) the empirical approach in which the functional relationships are defined by analysis (by means of statistical regression, etc.) of available data.

A strictly rational approach is usually not feasible. The complex linkages between environmental processes and biological consequences are incredibly difficult to observe or to investigate experimentally; the quantitative information needed to construct rational models of those linkages is most often unavailable. On the other hand, the empirical approach is hampered by a chronic lack of sufficient data points. Fishery data characteristically yield one estimate of stock size or recruitment per year; the available time series generally does not exceed several decades and most often is of the order of 10 to 20 years. To sort out a multitude of possible environmental effects by statistical means from a series of 10 to 20 data points is not possible. Moreover, the time series often contain significant autocorrelation, indicating a lack of independence of data points, which further depletes the severely limited degrees of freedom.

Generally, a combination of the two approaches allows the greatest amount of available information to be incorporated. The rational approach is used to generate hypotheses and to test and quantify those processes which can be measured or addressed experimentally. Then the empirical approach is used for testing, verification, and calibration. The demarkation between the two approaches is important. Often in fishery science an hypothesis is generated on the basis of experience, and since rational explanations can be constructed (because of the multitude of possible interacting processes occurring in marine biological communities it is nearly always possible to find a rationalization for any empirical result) the hypothesis comes to be regarded as rational when in fact it is basically empirical. Then when the hypothesis is "tested" against the time series of available data, which nearly always contains the period of experience which generated the hypothesis, a "verification," not surprisingly, is indicated. When basically the same data is used to test a hypothesis as was used to formulate it, obviously no real test can occur. For this reason many published fishery-environmental "relationships" are in reality untested hypotheses; it should not be surprising that they often fail almost immediately after publication.

Even when there is considerable rational input available, it is necessary to limit the choices of explanatory environmental variables to minimize the chances of spurious "fits" to the very limited time series. Thus as much rational input as possible must be utilized in formulating pertinent environmental indicators. In the past, measured environmental properties have often been used to produce correlations with fishery data in the belief that the same environmental processes which alter the measured properties would also alter the fish stock parameters. However, the linkages between the environmental processes and the observed properties may be just as (or more) tenuous and subject to independent alteration, as those between the processes and the biological consequences of interest. Certainly, a property is easier to measure than is a process, and a property has the reassuring attribute of having a single scalar value at a given point in space and time. In addressing a process one must come to grips with a space - time continuum in which a choice of scale is critical. However, due to the lack of any excess degrees of freedom to deal with additional linkages it is advisable to focus as directly as possible upon the actual involved processes in formulating environmental variables for fishery modeling efforts.

Recently several promising rational hypotheses concerning environmentally-caused recruitment variation in fish stocks of eastern boundary current regions have appeared. (1) A sensitivity of reproductive success of pelagic fish stocks to the dissipation of fine-scale food strata by wind mixing during early larval feeding (Lasker, 1975, 1978) has been indicated through a remarkable series of

laboratory and field experiments. (2) A detrimental effect on coastal fish stock of offshore transport during the larval drift period has been suggested by comparative studies (Parrish, Nelson and Bakun, MS) of the seasonal and spatial characteristics of reproductive strategies and drift conditions in the California Current region. (3) Since it is generally thought that the massive fish stocks inhabiting eastern boundary current regions depend on the primary production supported by the vigorous coastal upwelling characteristic of these regions, it is expected that long time scale fluctuations in upwelling intensity would be linked to fish stock variations.

The four "classical" eastern boundary currents (Wooster and Reid, 1963) are the Canary Current off the Iberian Peninsula and northwestern Africa, the Benguela Current off southwestern Africa, the Peru Current off western South America, and the California Current off western North America. These also comprise the four main upwelling regions of the world, as cited by Cushing (1969). They are characterized by rather broad, slow equatorward flow, high primary productivity, and massive pelagic fish stocks which have experienced extreme fluctuations. Very similar assemblages of fishes appear to constitute the major portion of the exploitable biomass in all four regions. In each, there is an anchovy, pilchard (sardine), horse mackerel (jack mackerel), hake, mackerel and bonito. The species are very closely related and several of the species are found in more than one region (Table 1). The similarity of the pelagic fish community in the eastern boundary currents suggests that the processes occurring in these systems may be direct analogs. It is possible that the environmental processes which regulate the recruitment and population fluctuations of a species group, for example the anchovy (*Engraulis*), are similar in all of the eastern boundary currents.

TABLE 1. Dominant anchovy, pilchard, horse mackerel, hake, mackerel and bonito in the four eastern boundary currents.

CALIFORNIA CURRENT	PERU CURRENT	CANARY CURRENT	BENGUELA CURRENT
<i>Engraulis mordax</i>	<i>Engraulis ringens</i>	<i>Engraulis encrasiolus</i>	<i>Engraulis capensis</i>
<i>Sardinops sagax</i>	<i>Sardinops sagax</i>	<i>Sardina pilchardus</i>	<i>Sardinops ocellatus</i>
<i>Trachurus symmetricus</i>	<i>Trachurus symmetricus</i>	<i>Trachurus trachurus</i>	<i>Trachurus trachurus</i>
<i>Merluccius productus</i>	<i>Merluccius gayi</i>	<i>Merluccius merluccius</i>	<i>Merluccius capensis</i>
<i>Scorpaenopsis japonicus</i>	<i>Scorpaenopsis japonicus</i>	<i>Scorpaenopsis japonicus</i>	<i>Scorpaenopsis japonicus</i>
<i>Sarda chilensis</i>	<i>Sarda chilensis</i>	<i>Sarda sarda</i>	<i>Sarda sarda</i>

DEFINITION OF ENVIRONMENTAL VARIATION

If fishery environmental studies are to lead toward management systems which are capable of adapting to environmental variations, the data required to indicate these variations must be of a type that can be obtained on a continuing basis. Thus, it is advantageous to base these studies on the sort of data that are routinely gathered, or that can be obtained by a minimal survey effort.

Generally, the physical characteristics of the environment which are thought to have important effects on recruitment variations can be grouped into four major categories:

1. The field of horizontal advection,
2. The field of vertical stability,
3. The field of temperature,
4. The field of convergence and divergence of flow at the sea surface, which is linked to the field of vertical advection.

In addition there are available certain physical indicators which are sometimes considered as "integrators" of several (or many) environmental effects.

Horizontal advection

Biological processes in the sea tend to integrate very short-scale variations in the physical environment. For instance, in the case of transport of planktonic fish eggs and larvae, since spawning generally is distributed in time and space, and eggs and larvae may passively drift for an extended period, short-scale flow variations tend to be averaged out by the space-time continuum of drifting organisms (Parrish, et. al., MS).

On large time and space scales, flow in the ocean is well approximated as a simple combination of the geostrophic current field and the field of Ekman drift induced by the horizontal force exerted by the wind on the sea surface (Greenspan, 1968). The conceptual picture, therefore, is of a thin surface layer of Ekman wind drift which varies in phase with large-scale atmospheric weather patterns, superimposed on the deeper, more slowly varying geostrophic flow field. The Ekman layer is thought to extend no deeper than 50 to 100 meters below the sea surface, and most of the transport probably occurs in the upper 5 to 30 meters.

The geostrophic current at the sea surface is directly proportional to and at right angles to the slope of the sea surface. The constant of proportionality is a function of latitude, being a minimum value at the poles and increasing to an infinite value at the equator; thus the geostrophic approximation is useless directly on the equator but Montgomery and Stroup (1962) have indicated it to be a useful estimate of current velocity as near as several degrees of latitude to the equator.

The standard method for estimating the sea surface slope is by measuring the temperature and salinity of the ocean at various depths, thereby determining the field of density of the sea water. For water to be motionless at some deep level there must be no horizontal variation in the weight of the water column pressing down from above. Thus, the horizontal differences in thickness of the column, and thereby the sea surface slope, can be computed from the internal density field (Sverdrup, et. al., 1941). Although there is probably no level at which the ocean is completely motionless, the geostrophic velocities at great depths tend to be much smaller than those at the surface, and so this method provides an acceptable approximation.

Surveys using this method have been made in all the major eastern boundary current regions. In the California Current, the CalCOFI surveys have made regular observations since 1949. The flow patterns described are quite detailed. However, methods for applying this wealth of detail to biological problems are not well worked out; as yet, little use has been made of these data in explaining biological variations. Such surveys are expensive, and obtaining the required space-time continuity of coverage is a problem.

For some purposes a schematic picture of the normal seasonal variation of geostrophic flow is required. This is not necessarily easy to get. Simple averages of the few available samples of sea surface topography as done by Wyllie (1966) and Hickey (1979) can be dominated by atypical features. This procedure can also introduce spurious features that never occurred in any of the measured samples. For example, during a particularly warm year the sea surface would tend to stand higher than normal throughout a given region; this would not generate any current features since currents are related to the gradient of surface height. Since spatial coverage is seldom complete in any one year, if observations from the warm year are averaged with those from several more normal years, the locations containing data from the warm year would tend to be higher than other locations. The surface slopes thus generated would determine current patterns that never actually existed.

Parrish, et. al. (MS) used the long-term mean temperature and salinity summaries produced by Robinson and Bauer (1973) to produce a smoothed long-term mean geostrophic pattern for the California Current region in which atypical features are suppressed; however, lack of indication of the typical seasonally varying features is a major deficiency. Because temperature observations are much more numerous than salinity observations, Husby² has produced some interesting seasonal patterns by combining

2. Personal communication, David M. Husby, Pacific Environmental Group, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Monterey, California, 93940.

seasonal temperature fields with long-term mean salinity fields. Other approaches include the association of non-observed salinity values with observed temperature values through the use of a characteristic temperature-salinity (T-S) relationship (Emery, 1975) and the filling of data gaps by curve fitting to existing data points by harmonic analysis³.

An ideal situation is where the sea surface slope variations can be directly measured; the long-period variation in the difference in measured sea height between two sea level gauges on either side of an ocean current is directly proportional to the variation in the space-averaged geostrophic surface flow across a line drawn between the two gauge locations. Saur (1972) produced a very large space scale index of monthly variations in geostrophic surface flow between sea level gauges located in San Francisco and in Honolulu. Christensen et. al. (1979) used sea level differences between Guadalupe Island and the coast of Baja California to indicate flow variations on a scale which is probably more pertinent to coastal fish stocks. Wyrtki (1974) showed that an array of sea level gauges on tropical islands could successfully monitor changes in the equatorial current system of the Pacific.

In most cases there exists no convenient island located the proper distance offshore to indicate flow variations on a scale upon which they would be affecting fish stocks. In these cases it may be reasonable to assume that the largest sea level variations will be at the solid coastal boundary and thus that a single coastal sea level station can be an index of major alongshore geostrophic flow variations. The most likely offshore length scale to be involved in such an index is the baroclinic Rossby radius of deformation (Moore and Allen, 1973) which is of the order of 10 to 20 km in the subtropical eastern boundary current regions. For example, Smith (1974) and Reid and Mantyla (1976) found correspondence of coastal sea levels at certain California Current locations with measured variations in alongshore flow. Marthaler (1976) indicated that the monthly mean near-surface currents over the Oregon continental shelf could be estimated from a regression with coastal sea level to a precision of ± 6 cm/sec where the annual range is 60 cm/sec. Off the New England coast of the eastern North America, where the continental shelf is relatively wide, Beardsley and Butman (1974) found that, if they assumed a constant sea level at the shelf break, a coastal sea level measurement could indicate the alongshore geostrophic flow (averaged over the shelf width) to $\pm 15\%$.

Sea level measurements are available in long time series in all the major eastern boundary current regions. The Permanent Service for Mean Sea Level⁴ lists monthly mean values for the California Current since the turn of the century (e.g., San Francisco since 1897, San Diego since 1906), nearly as long for the Canary Current (Lagos since 1908, Santa Cruz de Tenerife since 1927), for the Peru Current since the early 1940's (eg. Matarani since 1941, Talara since 1942) and for useably long time series for the Benaguela Current region (eg. Walvis Bay, 1958-72). Sea level time series are subject to distortion by geological uplifting and downwarping of coastal regions but these are usually of much longer time scale than the fishery variations of interest, and so can be easily corrected by linear or first-order curvilinear detrending, or by low-pass filtering. Sudden discontinuities due to earthquakes, etc., are usually well documented.

The other major component of flow, the surface wind-induced Ekman drift, which combines with the geostrophic flow to determine the actual water movement in the ocean surface layer, presents a different sort of problem. It cannot be inferred from any signal that is measured within the ocean and varies rapidly, adjusting to wind variations on a time scale of less than a day (except very close to the equator). It can be estimated from the field of wind stress on the sea surface. This stress field must be constructed from scattered reports from ships at sea and from observations at coastal stations which may be distorted by effects of local land topography. Because of the rapid variation, frequent sampling is required, preferably at intervals of twelve hours or less. Standard reporting periods have been established by international convention to provide synoptic samplings which are disseminated globally. These are arranged into consistent analyzed fields by various national meteorological agencies, commonly at 6-hourly, or even 3-hourly intervals.

3. Method developed by Ronald J. Lynn, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, California, 92037.
4. Institute of Oceanographic Sciences, Bidston Observatory, Birkenhead, Merseyside L43 7RA, England.

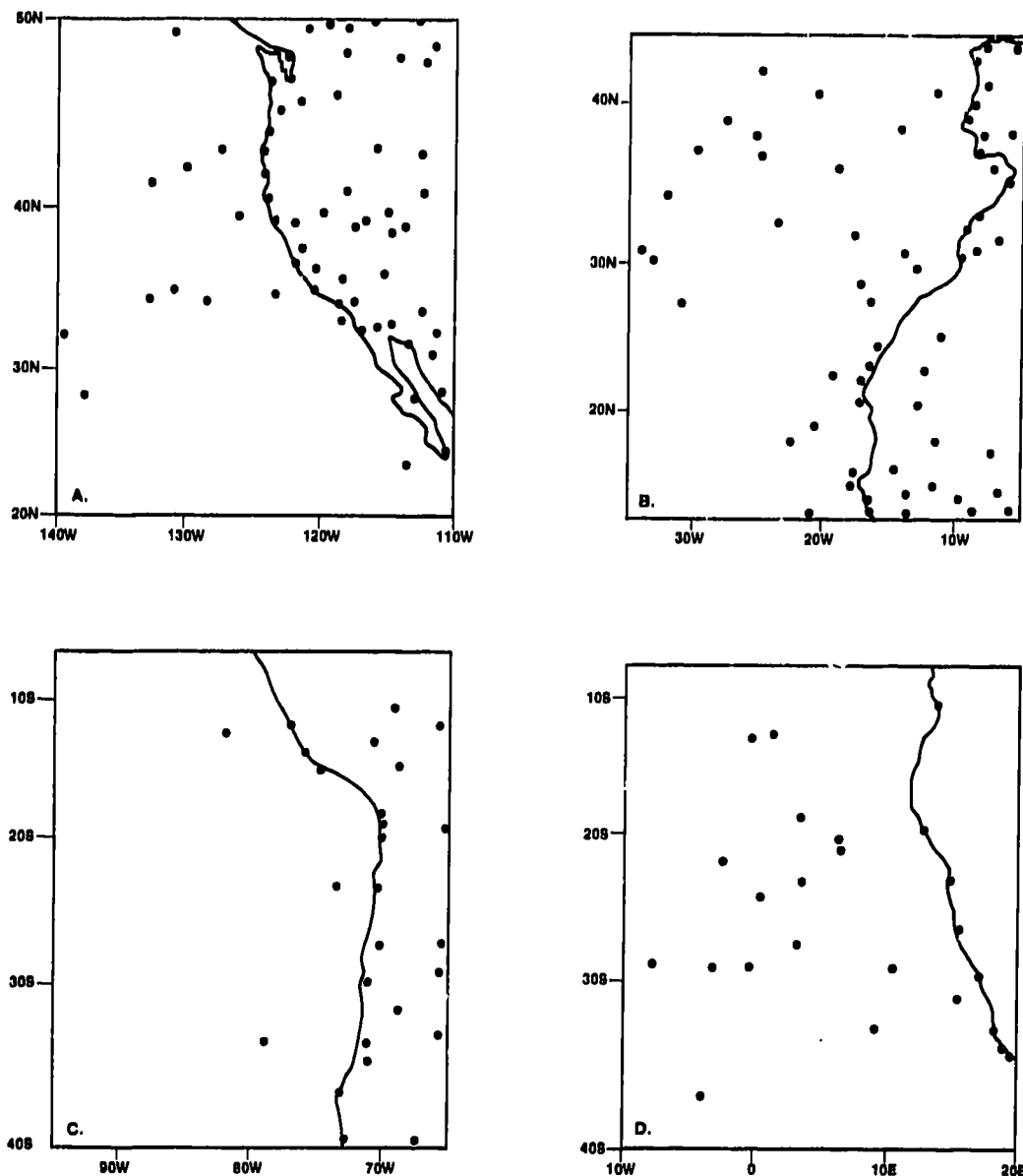


Figure 1. Typical synoptic report distributions in the four major eastern boundary current upwelling regions: A. the CALIFORNIA CURRENT (distribution shown is for 0600 GMT, Jan. 11, 1980), B. the CANARY CURRENT (0000 GMT, Feb. 12, 1980), C. the PERU CURRENT (1800 GMT, Feb. 7, 1980), and D. the BENGUELA CURRENT (1900 Gmt, Feb. 7, 1980).

The report density available in any synoptic sampling for any of the major subtropical eastern boundary current regions does not normally exceed several per 5-degree latitude - longitude "square" (Figure 1). In order to form consistent time series from such sporadic report distributions, it is necessary to spread the large-scale information represented in the observations to consistent geographical locations and to suppress measurement and transmission errors and small-scale information which is nonrepresentative of the large-scale. The analysis procedures used by meteorological agencies to prepare synoptic data fields for forecast purposes are designed to accomplish these same results, and thus provide a resource for the production of sea surface wind stress time series. Many of the standard analysis

procedures (e.g. Holl and Mendenhall, 1972) are designed for use in temperate latitudes and make use of the strong geostrophic coupling between wind and atmospheric pressure distributions to employ both types of observations and thereby increase the data base. In the tropics, where the geostrophic coupling becomes weak these methods do not work well. However, there are certain analysis procedures designed specifically for the tropics (e.g. Lewis, 1972) which are in routine use at the present time.

Once an estimate of the wind field over the sea surface is available it can be readily converted to an estimate of the surface Ekman transport field in the ocean. However it is important to note that the linkage of wind velocity to wind stress is non-linear. Thus, where time averages are to be made, the averaging should be performed after the stress computation. Bakun (1973) has shown that time series of monthly alongshore stress estimates computed from monthly mean winds at locations near the west coast of North America correlate highly with corresponding series of monthly means of synoptic stress computations. The high correlation is probably due, at least in part, to the effect of coastal topography in constraining the directional variation of the wind. Thus, although it seems likely that similar high correlation would occur in other eastern boundary current regions with coastal mountain ranges, it remains an untested assumption. In regions where the directional variance of the wind is high, in the mid-latitude central ocean, for example, such an assumption is probably unwarranted. Bakun (1973, 1975) has discussed certain other problems in using analyzed atmospheric fields near coastal boundaries.

A major unsolved problem is the assignment of "error bars" to the stress estimates computed from atmospheric analyses. The estimates appear to be quite adequate for defining variations on the energetic "synoptic atmospheric event" and "seasonal" scales, and to identify major interyear differences. However, their adequacy in defining subtle differences among groupings of years remains undemonstrated.

Ekman transport is calculated as the ratio of the wind stress magnitude to the local value of the Coriolis parameter and is directed 90° degrees to the right (left) of the stress in the northern (southern) hemisphere. The fine-scale vertical structure of the Ekman drift velocity field depends on vertical eddy viscosity characteristics which are not well known; however the total transport of water in the layer between the sea surface and the depth at which the drift velocity becomes negligible does not depend on these characteristics, and can be inferred from the wind stress alone. The depth of negligible Ekman drift velocities is likewise not well known. However, as mentioned above, most of the transport probably occurs in the upper 20 to 30 meters. It is unlikely that appreciable Ekman drift would penetrate below the surface mixed layer into the stratified portion of the water column. Aggregates of organisms which are continually being mixed over a depth range as deep as or deeper than the Ekman layer can be assumed to move with the Ekman transport; in this case a drift speed can be assigned by dividing the Ekman transport by the depth of mixing.

The upper portion of the Ekman layer would tend to move at a lesser angle to the direction of the wind stress. Classical Ekman theory, assuming a constant vertical eddy viscosity, predicts the free ocean surface to move at an angle of 45° to the wind. An analysis by Madsen (1977), in which he assumes an eddy viscosity varying linearly with depth, yields a surface deflection of about 10° . Empirical studies reported by Stommel (1954) found speeds of drift at the sea surface to be of the order of $1/20$ to $1/30$ of the wind speed, with deflection angles usually between 30° and 60° .

Detailed specification of the vertical distribution of Ekman velocity is not available. The classical Ekman spiral is not generally observed. The interaction of Langmuir-type circulations (Scott, et. al., 1969), etc., is not well understood. However, we can be quite certain that the Ekman transport concept is realistic, at least in a time- and space- average sense, both from dynamical necessities (Greenspan, 1968) and from climatological correspondences of wind and oceanic distributions (e.g. Wooster and Reid, 1963; Wooster, Bakun, and McLain, 1976). For fisheries applications, it appears necessary to make do with the concept of Ekman transport, modified by a somewhat vague notion that the very surface moves at an angle more directly downwind than does the depth-integrated transport. At the equator the Coriolis parameter goes to zero and so the Ekman transport relationship "blows up"; the evidence of equatorial divergence of ocean surface waters indicates some degree of Ekman effect acting even very near the equator.

Direct measurements of ocean flow cannot generally provide the required time and space coverage required for operational fishery management purposes. One type of direct measurement which has been useful in climatological studies of eastern boundary currents (Wooster, et. al., 1976; Bakun, et. al., 1974; Bakun and Nelson, 1977; Bakun, 1978) is the so-called "ship drift" observation. These are differences, attributed to ocean currents, between dead-reckoning and verified positions as recorded in ships log books. These have been gathered since the last century and have provided the basis for much of our knowledge of large scale ocean currents. The data contain a very large error variance, being based on differences between rather uncertain navigational fixes, estimates of ship speed, etc., and require a very large sample to achieve a meaningful estimate of mean current speed. Although observations are rejected when wind speeds are very high, the data are undoubtedly contaminated by the effects of wind on the ships superstructures. The data appear adequate to define long-term mean seasonal variations, but are not numerous enough to be useful in indicating interyear variability.

Vertical Stability

Recent work (Lasker, 1978) has indicated extreme sensitivity of anchovy reproductive success to the breaking up of fine-scale food strata by wind mixing during early larval feeding. We can estimate variations of wind mixing energy added to the water column from available analyzed wind fields; the energy added varies in rough proportion to the cube of the wind speed (Elsberry and Garwood, 1978). The stability of the upper water column, which would oppose such mixing might be estimated from vertical temperature and salinity structure. Little is known concerning the time scales of aggregation of food strata or the ability of the food organisms to themselves resist dispersion by turbulence. It is difficult to formulate a proper index of the wind effect in this case. A first impulse is to look at interyear variations in the cube of the wind speed averaged over a spawning season as the relevant factor. However, it probably is not the average intensity that is critical, but the existence of sufficient time-space "windows" within which wind-induced turbulence does not exceed a certain critical value. We do not know what the critical value is and we do not know the length of time required for formation of the food concentrations needed for successful first feeding of larvae. This appears to be a very fruitful ground for research. Application of recent advances in oceanic mixed layer modelling should be helpful in determining at what point turbulence would be initiated. Repetitive samplings of biological microstructure under varying wind conditions would begin to define time scales of aggregation and ability to resist dispersion. Perhaps comparative studies of conditions in areas where fish normally spawn (i.e. favorable to larval survival by natural selection), as opposed to conditions in areas where spawning does not occur, would yield some information on normal requirements for reproductive success. Such information might then be used to define a formulation to correctly indicate the effect on year-class success of interyear variations in wind-induced turbulence.

Temperature

Sea temperature is probably the most commonly used environmental variable in studies of biological variations. There are several reasons for this. Probably most important is that temperature has a direct physiological effect. The rates of biological processes increase and decrease with temperature, and extremely unfavorable temperatures can be lethal. Thus, temperature can define limits of occurrence; anomalous temperature conditions, by changing growth and maturation rates, can cause disruptions and mismatches in the timing of critical life cycle events. Of perhaps nearly equal importance is the availability of temperature data, due in some extent to the simplicity and ease of the measurement. Finally, temperature provides a signal of important ocean processes; for example in eastern boundary current regions, cool sea surface temperatures are often related to coastal upwelling or to horizontal advection from higher latitudes.

Sea surface temperature is routinely measured and reported by ships at sea. The observations are distributed internationally through the World Meteorological Organization (WMO). Subsurface temperature observations are much less plentiful, but these are also gathered and distributed by WMO and the Intergovernmental Oceanographic Commission (IOC) through the IGOSS program. Sea temperature is also routinely measured at many coastal stations. These observations have the advantage of being a generally continuous time series at a consistent location. They are sometimes subject to very local

influences, often being located in or near harbors and estuaries. Temperature signals from coastal stations located within a region occupied by a single fish stock can exhibit a disconcerting degree of noncorrelation.

This brings up the problem of how to choose from a variety of available temperature signals in attempting to define a useful relationship to biological events. The procedure of searching a number of possible signals to find the "most pertinent" one, i.e., the one that yields the best correlation, and then applying a standard significance test to the regression results in a misleading overestimate of significance. After all, a 95% significance level signifies only that the chance of an equivalent degree of correlation from unrelated random series is one in twenty. Thus if one tests four unrelated series the probability of finding a correlation significant at the 95% level is increased to one chance in five, corresponding to an 80% significance level which may be inadequate to confidently reject a null hypothesis of no relationship.

Various methods are employed to summarize scattered temperature observations to produce time series indicative of conditions in the environment. None should be used blindly. The space scales of temperature variation in the ocean may be quite small and not well sampled by the available distribution of observations. Thus the variation in distribution of reports may introduce spurious variability capable of obscuring the true variation. Averaging by areal segments of the ocean surface (e.g. McLain, 1978) can be a particular problem in coastal upwelling regions where horizontal temperature gradients are large.

Use of meteorological-type "objective analysis" procedures (e.g. Laevastu and Hela, 1970), where available data is spread to areas where data is lacking, may involve similar time series distortions. Often climatology is used in these procedures to fill large space-time data gaps. The resulting time series can be difficult to interpret; methods for establishing error limits are not available.

Recently there has been widespread use of empirical orthogonal function (or principal component) analysis in studies of climatic fluctuations (Preisendorfer, 1977). In this way temperature series from several locations can be combined into a single series, based on the linear combination which explains the largest fraction of the total variance of the individual series (Weare, Novato, and Newell, 1976). These techniques have not yet been widely used in fishery studies. They can probably be useful if properly employed. However, there should always be a firm physical basis for believing that the linear combination which contains the most variance is a more pertinent indicator of the effect upon the biological process of interest than is some other possible combination. Otherwise, one is simply adding another time series to a situation in which the major need is to limit the choices of explanatory series so that the concept of statistical significance can be meaningful.

Convergence, divergence, upwelling

An important aspect of the surface Ekman drift is that it is subject to strong convergences and divergences, convergence being a net gain of surface water at a point due to spatial gradients in horizontal transport, and divergence being a net loss. Thus sinking waters are generally found immediately below surface convergences, and rising waters below divergences.

Floating organisms would tend to be concentrated in areas of convergence and dispersed in areas of divergence. The rising waters in areas of divergence can aid non-motile phytoplankton in remaining in favorable light intensities for photosynthesis. Rising deeper waters replenish exhausted nutrient concentrations at the surface and cool the surface layers. Spatial gradients in surface convergence or divergence can tilt the subsurface density structure and establish sea surface slopes which alter the underlying geostrophic current field. Thus convergence and divergences in the surface wind drift affect the biological environment in a variety of ways and on a variety of scales; variations in the wind stress at the sea surface are probably the major external driving forces leading to biological perturbations.

The strongest convergence and divergence can occur next to a coastal boundary where transport gradients essentially reflect a step increase from zero on the continent to a finite value in the ocean. Where the surface transport adjacent to the coast is directed offshore, the result is locally wind induced

coastal upwelling. Bakun (1973) produced time series estimates of monthly variations in the onshore-offshore component of Ekman transport. These were called "upwelling indices" (after Wooster and Ried, 1963) to call attention to the fact that, lacking direct measurements of coastal upwelling intensity, the variations in the local driving force, the alongshore wind stress, may be the best available indicator of upwelling variations.

Recent research has indicated the likelihood of poleward propagation of upwelling characteristics. This appears to be less important, at least on the seasonal scale, in the higher latitude eastern boundary current upwelling regions (Smith, 1974; Bakun, et. al. 1974; Wooster, et. al. 1976) than in the lower latitude regions, for example, the Peru (Smith, 1978) and Guinea (Bakun, 1978) coasts. However, even in Peru, Smith (1980) finds that the onshore-offshore component of flow is well represented by the locally wind-induced Ekman transport.

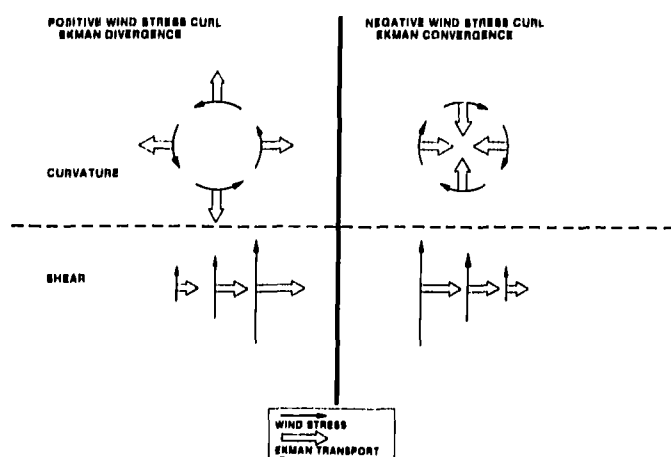


Figure 2. Wind stress curl and resulting Ekman transport. Positive curl expresses the anti-clockwise (cyclonic) rotation due to either curvature or shear in the wind field; since the Ekman transport is directed perpendicularly to the right of the stress the result is Ekman divergence in either case. Negative curl expresses the clockwise (anticyclonic) rotation in the field; the result is Ekman convergence.

The onshore-offshore scale of the coastal divergence is related to the baroclinic Rossby radius of deformation (Mooers and Allen, 1973) which is of the order of 10 to 20 km in subtropical regions, although features of the continental shelf topography may, under certain circumstances, cause seaward expansion of this scale (Huyer, 1976). Offshore of this coastal boundary region, the convergence and divergence of surface Ekman drift is controlled by the wind stress curl (Fofonoff, 1963), which is a measure of the "rotation" in the wind field represented by curvature or shear (Fig. 2). Monthly surface layer divergence indices based on wind stress curl estimates were proposed by Bakun and Nelson (1977). The problem of establishing expected error bars on these estimates is even more bothersome in this case than in the case of Ekman transport indices since the process of taking derivatives amplifies errors. This problem is presently unsolved and the significance of computed wind stress curl anomalies is uncertain at this point. However, Chelton (1980) has reported a significant relationship between wind stress curl

variations computed in this manner and low frequency variations in the onshore-offshore contrast in flow of the California Current, i.e., the tendency for the flow to be less southward (more northward) near the coast than in the offshore region.

The coupling of the surface convergence or divergence associated with the coastal boundary with that occurring offshore of the boundary zone presents possibilities for various combinations (Fig. 3) of probable biological significance. For example, a situation of coastal upwelling with negative wind stress curl causing offshore convergence (Fig. 3(d)) would favor concentration of drifting organisms upon being transported out of the coastal upwelling zone. This particular situation appears to be typical of the central Baja California upwelling center (Bakun and Nelson, 1977).

The effect of such couplings on the geostrophic current pattern can apparently have biological consequences. For example, the negative curl area off central Baja California corresponds to an apparent "blocking" of northward counterflow along the coast during the fall relaxation of upwelling-induced southward circulation (Bakun and Nelson, 1977). Semi-independent gyral circulations occur in the positive curl regions to the north and south (Fig. 4). These correspond to the areas of occurrence of separate subpopulations of California Current pelagic fishes including sardine (Clark, 1947), Pacific mackerel

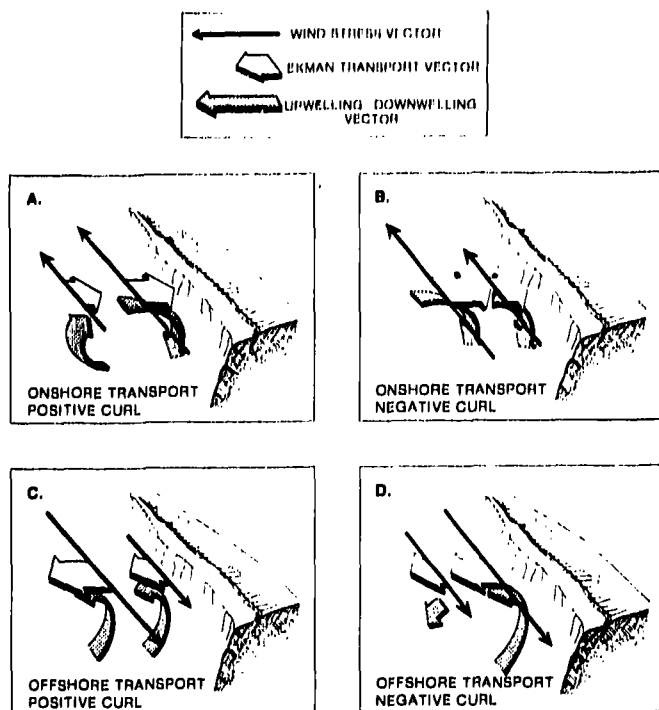


Figure 3. Types of couplings between surface convergence or divergence at the coast (due to the onshore-offshore component of Ekman transport) and that (due to wind stress curl) occurring offshore of the coastal boundary zone. A. Onshore Ekman transport and positive wind stress curl; convergence and downwelling at the coast, divergence and upwelling offshore. B. Onshore Ekman transport and negative wind stress curl; convergence and downwelling at the coast, continued convergence offshore. C. Offshore Ekman transport and positive wind stress curl; divergence and upwelling at the coast, continued divergence offshore. D. Offshore Ekman transport and negative wind stress curl; divergence and upwelling at the coast, convergence offshore.

The infra-red or microwave radiation sensors are not as yet accurate enough to define the subtle long-term variations which would be reflected in fish stock fluctuations. Satellite mounted altimeters may be capable of recognizing the existence of sea surface slopes characteristic of swift ocean currents such as the Gulf Stream; their precision does not yet approach that required to indicate fluctuations in broad-scale mean flow velocity in eastern boundary currents, although it may be adequate to recognize major eddy structures.

The wind sensing capabilities of satellites offer some very enticing prospects for uses in fishery management studies. The 50-km resolution which is designed for the microwave scatterometer which was placed on SEASAT-A would allow synoptic viewing of features the size of the negative wind stress curl lobe off central Baja California (Fig. 4(a)), i.e., on the scale that wind stress features may actually affect fish stocks.

(Roedel, 1952) and northern anchovy (Vrooman and Smith, 1971). This suggests the possibility that fluctuations of the wind stress curl pattern could influence exchanges between subpopulations. Indeed, Parrish and MacCall (1978) find variations in the wind stress curl in the region of separation to be significantly related to recruitment variations in the Pacific mackerel stock to the north.

The smaller scale features of the stress and stress curl (Fig. 4(a)) distribution produced by Nelson (1977) by compositing many years of data, cannot be resolved by the observations generally available in a synoptic sampling (Fig. 1). Thus time series indicators can only be produced on a considerably larger scale (Bakun and Nelson, 1977). Estimates of fluctuations of wind stress features of the size of the negative curl lobe must presently rely on an untested assumption that such features would fluctuate in phase with and in the same sense as the larger scale pattern in which they are embedded.

Satellite Measurements

Measurements from earth-orbiting satellites have been heralded as the answer to many of society's environmental monitoring data needs. Recently, the U.S. Government placed into orbit a satellite (SEASAT-A) specifically designed for ocean science purposes. Satellite measurements have been valuable in indicating sea temperature structures as a tactical aid to fishing operations; satellites have also improved the weather advisory services which are vital to the operation of a fishery. However, we are not aware of their use to date on the fishery management problem.

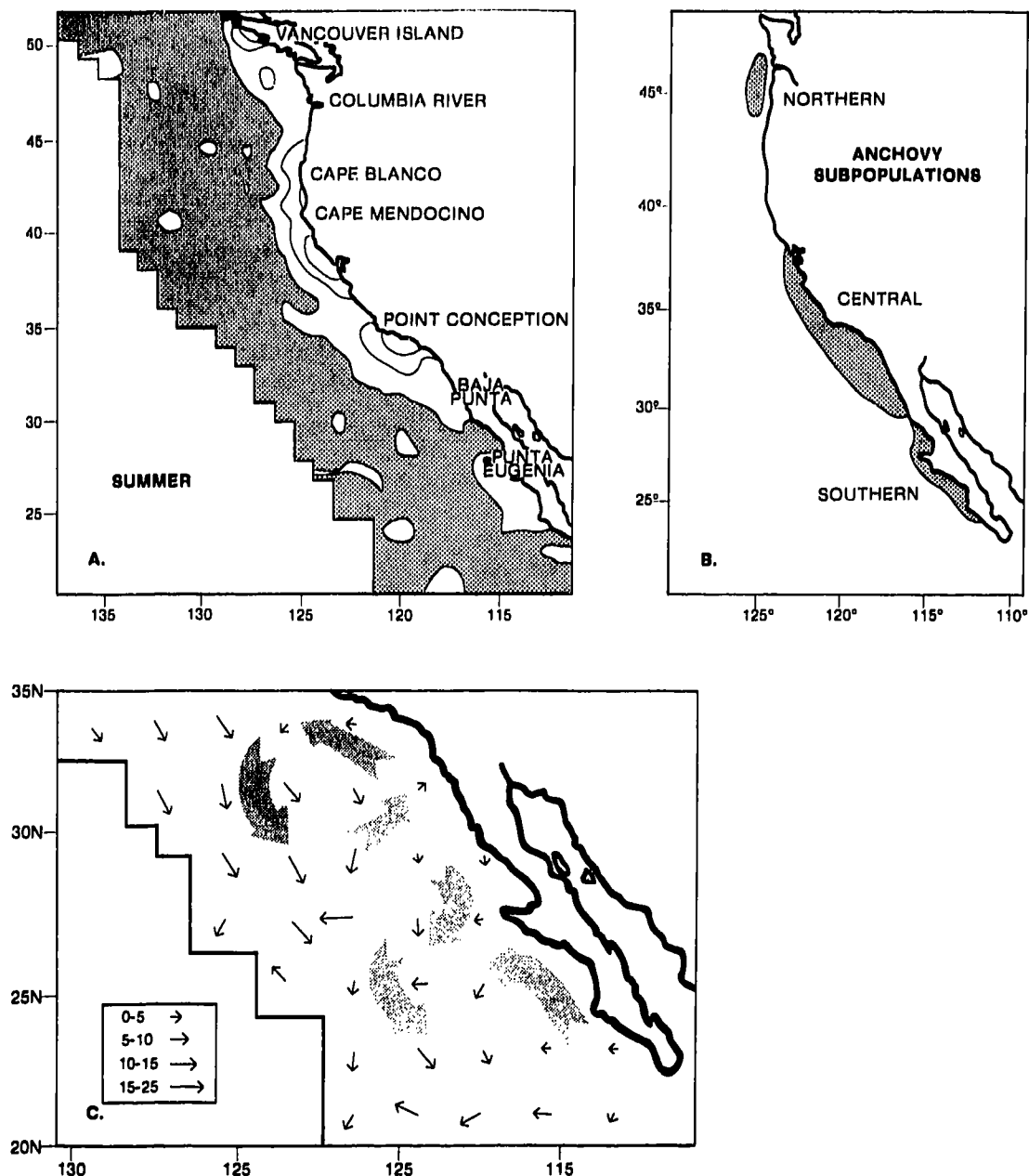


Figure 4. (a) Wind stress curl distribution during summer (June through August long term means). Contour interval is $0.25 \text{ dynes cm}^{-2}$ per 100 km. Negative curl values are shaded; positive curl values are unshaded (after Nelson, 1977). (b) Spawning distributions of the central and southern subpopulations of northern anchovy (Paul E. Smith, personal communication). (c) Ship drift during October, November, and December. The small arrows, indicating mean drifts, are scaled according to the key at the lower left. Large arrows suggest the inferred circulation pattern (after Nelson, 1977).

Another general requirement for wide application to fishery management is that a data source be available in long time series so that models based on it can be verified against observed fish stock variations. This necessitates some years lag between the introduction of new technology systems such as satellites and telemetering buoys, and their usefulness in this sense. This delay can be eliminated if the new available information can be used to "calibrate" existing time series. For example, if the ability to

view small scale wind stress curl patterns would allow us to define their relationship to the large scale synoptic weather patterns which can be defined by the density of synoptic ship reports available historically, models using the small-scale physical mechanisms could be based on the large scale time series.

Integrators of multiple processes

Where possible, it is preferable to use indicators of the particular processes which are actually affecting the organisms. Sometimes such indicators are either not available or else a precise notion of the relative importance of various processes may be lacking. In these cases, using time series which reflect more than one process or which are considered indicative of general environmental transitions may be the only resort.

An important example of this sort of time series is the Southern Oscillation Index (Bjerknes, 1969) which is indicative of major transitions in the coupled ocean-atmosphere system; Quinn (1978) has used this index to predict El Nino invasions off Peru. Indeed, El Nino itself has come to be regarded as an important index of Pacific-wide variations. Chelton (1980) has reported a correspondence between changes in the broad-scale background flow of the California Current and El Nino occurrence. Baumgartner, et. al. (1979) report that conditions in the Gulf of California are dominated by variations corresponding to El Nino occurrences.

Long time scale variations in atmospheric pressure are sometimes used as an explanatory variable in empirical studies of fish stock variation. (See section on Pacific mackerel, below.) It is unlikely that the actual pressure experienced by the organisms has any significant effect on survival; a change in depth of a couple of feet would involve pressure changes comparable to any atmospheric pressure fluctuations. However, just as barometric pressure is useful in indicating weather changes, it is related to variations in atmospheric effects on the ocean environment. Where low atmospheric pressure is related to occurrence of cyclonic storms, anomalous mean barometric pressure may be indicative of (1) anomalous Ekman transport conditions which disrupt upwelling normally produced at the eastern edge of a subtropical high pressure system, (2) negative wind stress curl, (3) increased wind-induced mixing of the upper ocean, (4) decreased solar radiation due to cloud cover, etc. However, each of these effects can be estimated separately; in our opinion it is preferable to indicate separately each process involved in as precise a manner as possible. If it is considered necessary, because of limited degrees of freedom, etc., to combine multiple processes into a single series this should be done in a rational manner, based on the available understanding of the interacting effects of the processes involved.

Other "integrators" which have been used in fishery studies include tree ring width (Cushing, 1979), sunspot activity (Favorite and Ingraham, 1978), and very long term average air temperature (Cushing, 1979).

Even carefully designed indices of individual processes can unavoidably become integrators of several interacting environmental effects. As described above, surface layer divergence indices indicate both the effects of the divergence or convergence of planktonic material and the linked effects of the wind stress curl on the geostrophic flow field. Upwelling indices are related to variations in upwelling or downwelling, offshore transport, and the near-coastal alongshore current. Sea temperature variations can be linked to biological variations through direct physiological effects, and through the dependence of temperature on upwelling, horizontal advection, and turbulent mixing. Obviously, the fishery-environmental problem is not simple, and in the situation of severely limited degrees of freedom, it is well to take great care to avoid generating statistical nonsense.

Independence of data points

Environmental time series are often found to contain a certain amount of serial correlation, i.e., a level of persistence affecting multiple data points. This can be caused both by real variations of period longer than the sampling interval and by inhomogeneties in the time series introduced by changes in sampling method, instrument location, etc. These causes are often difficult to separate.

For example, methods of producing atmospheric analyses such as are used as input data in Bakun's (1973) upwelling index computations have evolved from subjective hand analysis of reports in the 1940's and 1950's to fully automated objective procedures in recent years. In addition, the distribution of reports also changes over time; it is possible that the establishment of a reporting station in an area which was previously undersampled could cause a major disruption of the consistency of the indicator series. Even a direct measurement such as sea level is subject to vertical movements of the earth's crust upon which the gauge is mounted. Temperature series can be disrupted by such things as harbor construction near a measurement site, or by changes in the measurement technique such as the progressive conversion from bucket thermometers to sea water intake thermometers on reporting vessels.

Even when longer term features in a time series represent real environmental changes, they may be undesirable in an analysis. If a correlation is controlled by longer period features, the number of degrees of freedom assumed in order to estimate statistical confidence must be reduced to some fraction of the available number of data points. This represents a further limitation of the severely limited degrees of freedom typically available in fishery data series.

High-pass filtering of data series before testing for a relationship is one way to minimize the likelihood of arriving at unwarranted conclusions. If an apparent correlation disappears after high-pass filtering, then inhomogeneities must be considered as a source of error. The assumed degrees of freedom should be reduced to the number of observations which can be assumed to be independent of one another. (See section on Pacific mackerel, for example.)

POPULATION BIOLOGY CONSIDERATIONS

Population fluctuations of fishes are caused by an interplay between the biology of the organisms, (i.e. the genetic and age structure of the population) and the environmental conditions encountered by the population. In exploited stocks there is the further complication of alterations in the genetic and age structure of the population caused by selective fishing mortality. Before the understanding of a fisheries resource can go beyond rudimentary levels the stock structure of the resource must be adequately described. Knowledge of the number of reproductively isolated stocks, a description of their spawning grounds, distribution, and relative population size is a prerequisite to understanding their population dynamics. The lack of speciation in the pelagic fishes within the various eastern boundary current regions suggests that there is some degree of interchange within each region. In the pelagic fishes of the California Current region the number of reproductively-isolated stocks appears to be relatively small and these stocks appear to be separated into subregions which can be described by surface transport patterns (Parrish et al, Ms). Existence of smaller, reproductively-isolated units (stocklets) within the subregions has not been documented; however little research has been done to test this possibility. Once the stock structure is defined the principal research and management concern centers around the determination of fishing strategy that will maximize and stabilize long-term yield from the stocks or stocks. In small pelagic fishes the principal factor that prevents maximization and stabilization of yield is the high degree of variability in stock size.

Spawner-Recruit relationships

One of the most pervasive questions of fisheries biology is the relationship between parent stock size and reproductive success (usually referred to as recruitment). Near extremes of views on this question were presented in Clark and Marr's (1955) classic paper on the California sardine fishery. Clark suggested that at low and moderate stock sizes recruitment was directly proportional to parental stock size and that at high stock sizes recruitment declined with increasing stock size. Marr suggested that over the expected range of stock size recruitment was unrelated to stock size. These two views are shown graphically in Figure 5a. The relationship between parental stock size and reproductive success can be expressed in different ways. For example, is recruitment dependent upon parental stock size or is the rate of recruitment dependent upon stock size? In the first case the dependent variable is recruitment (i.e. numbers of recruits or recruit biomass) in the second case the dependent variable is the recruitment rate; (i.e. recruits per spawner or recruit biomass per spawning biomass). When viewed from the rate

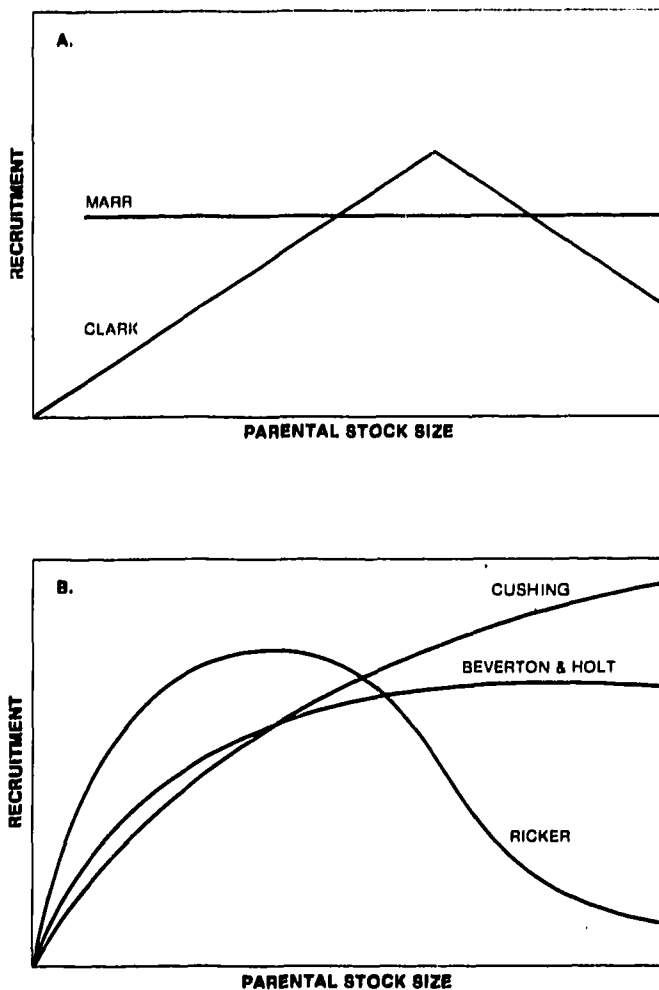


Figure 5. Stock-recruitment functions.

TABLE 2. Stock-recruit models

Ricker: $R = a P e^{-bP}$

Beverton & Holt: $R = P/(a + bP)$

Cushing: $R = aP^{-b}$

R = Recruitment

P = Parent stock size

a = density-independent coefficient

b = density-dependent coefficient

viewpoint Clark's model implies that recruits per spawner are independent of stock size at low and moderate parental stock sizes and are inversely dependent on parental stock size at high parental stock sizes. Marr's model implies that the number of recruits per spawner continuously declines as parental stock size increases; it is therefore density-dependent.

The recruitment rate can be viewed as the summation of a stock's reproductive, growth, and mortality rates up to the age at recruitment. If decreased stock size results in increased growth or reproductive rate or in decreased mortality, the recruitment is termed compensatory density-dependent. That is, the relative recruitment success increases at lower stock sizes. The mechanisms for this type of change include features such as intraspecific competition for food, lower growth rates, lower fecundity, and cannibalism at higher stock sizes. If the rate of recruitment decreases at low stock sizes the stock is said to have depensatory density-dependence. The principal mechanism suggested for depensatory density-dependence is increased natural mortality associated with smaller school sizes that might occur at small stock sizes (Clark, 1974).

The mathematics that have been used to describe the relationships between parental stock size and recruitment principally consist of alternative extinction curves. These extinction curves are used to describe the relationship between recruits per spawner and spawning stock size. The most commonly used models are those proposed by Ricker (1975: 282), Cushing (1971), and Beverton and Holt (1957: 49). These models are listed in Table 2 and shown graphically in Figure 5b. All three models have a density-independent term which can be envisioned as describing the intrinsic rate of increase, and a density-dependent term which is a compensatory term that has the effect of reducing the rate of increase as the stock size increases.

The Ricker (logistic) model has the largest compensatory term and implies that at high stock sizes recruitment is low; the potential shape of the Ricker curve is quite variable. The Beverton and Holt (asymptotic) model implies that at high stock sizes recruitment reaches an asymptotic maximum. The Cushing (allometric) model implies that recruitment increases with stock size but at a continuously decreasing rate.

The choice of which model to use for a particular stock should be related to the hypothesis that is envisioned to limit the stock. If there is good reason to believe that there are very strong density-dependent effects in recruitment, i.e. if the spawning grounds are much more limited in size than the feeding grounds or if cannibalism by adults is significant, the Ricker model may be appropriate. The anadromous stocks of salmonids for which the model was originally developed are a good example for the use of the Ricker model. If the "gate mechanism" is expected, i.e. if nursing grounds have a relatively constant carrying capacity, the Beverton and Holt model is appropriate. The plaice (Platichthys platessa), for which the model was originally developed are a good example for its use. If the critical stage (or match-mismatch) hypotheses is considered to be the principal factor controlling recruitment the Cushing model may be most appropriate. The California stock of sardine is a good example for the use of this model (MacCall, 1979).

The Ricker model, due to its flexibility of shape, can approximate the shape of all three of the above examples as long as it is only applied to the stock sizes for which there is sufficient data to justify its usage. Of course none of the regression fits should be extended beyond the range of the data to which it was fitted. The methods used for fitting the various models include linear regression, linear regression with transformed variables, and iterative nonlinear regression. Models fitted with logarithmically transformed variables are fitted to the geometric mean rather than the arithmetic mean and are biased towards low expected values. Corrections for this type of bias are described by Beauchamp and Ohlson (1973).

Life History Stages

Stock-recruitment models work best if the observed variation from the model is small and random. The models give biased predictions if the variation from the model is large, if it contains time series trends, or if there is autocorrelation in the residuals (Sissenwine, 1977). The predictive capability of stock-recruitment models has not proven to be of great value in stocks of small pelagic fishes which have high natural mortality rates. This type of stock, in which recruits comprise a large proportion of the exploitable biomass, appear to be susceptible to recruitment overfishing during unfavorable environmental periods (Paulik, 1971; Cushing, 1975; Murphy, 1972).

Research into stock-recruitment relationships requires extensive age composition sampling of the catch and many years of data at different stock sizes. Recruitment, while not easy to measure, can be reasonably estimated in stocks which have large fisheries and extensive sampling of the catch. The fact that only one data point is accrued per year puts a severe limitation upon the determination of factors influencing recruitment processes. Stocks which have extended spawning seasons with potential multiple peaks, such as the Engraulis stocks of the Peru and California Current regions, have special problems in estimation of recruitment. In the California Current only two pelagic stocks have enough data at different stock sizes to produce statistically meaningful stock-recruitment relationships (The California stock of Sardinops (Murphy, 1966; MacCall, 1979) and the California stock of Scomber (Parrish and MacCall, 1978)). In both of these stocks the stock-recruitment relationships are characterized by very flat curves with a large amount of scatter in the data points. In both, compensatory density-dependent processes appear to be minor and the Cushing model, which implies that highest recruitment occurs at large stock size, provided the best statistical fit. However, over the range of stock size that is likely to occur with heavy exploitation the Cushing, Ricker, and Beverton and Holt stock-recruitment functions would all produce similar curves.

If a significant portion of the variation in recruitment is associated with environmental fluctuations, spawner-recruit models can potentially be improved by inclusion of the associated environmental terms. Recruitment is therefore probably best described with models developed with multiple regression. The Cushing and particularly the Ricker models have several features that make them the best candidates for the development of density and environmental-dependent multiple regression models. As Ricker (1975) has pointed out the effect of environmental variation is expected to be multiplicative. The dependent variable in these two models are logarithmically transformed variables which allows the environmental terms to be exponential terms which have geometric effects. The Ricker model is particularly well suited

for the development of regression models as the dependent variable is the natural logarithm of recruits per spawner, or recruit biomass per spawning biomass ($\ln R/P$). Therefore the terms which best describe the survival rate are those included in the model. If the model that best describes " $\ln R/P$ " is developed with stepwise multiple regression with parental stock size and environmental variables as independent variables the model will be less biased than the case where the environmental variables are regressed against the residuals of the Ricker model (i.e., if the residuals are the dependent variable).

The final multiple regression model, incorporating both density and environmental terms, can then be transformed (by exponentiation) to an expression of absolute recruitment. If desirable the bias in expected value resulting from the fact that the model is fitted to the geometric mean of the observed data can then be avoided by nonlinear regression. The coefficients developed with the stepwise multiple regression can be used as starting values in an iterative nonlinear regression. Environmentally-related variation is likely to be the result of many biotic and abiotic processes. Due to the limited number of observations and attendant problems with degrees of freedom only a small number of terms can be statistically justified. Therefore unless the environmentally-related variations in the rate of recruitment are dominated by one or a small number of environmental processes or features the inclusion of environmental effects is unlikely to be of much benefit.

The processes regulating the populations of exploitable marine fishes break naturally into three stages, based both upon life history phases and data sources. These stages are the early life history, juvenile and post-recruit stages. The early life history stage is limited to the period when the organisms are largely planktonic. This stage is characterized by very high mortality. The bulk of information concerning this stage comes from egg and larval surveys, field studies and laboratory experiments. The early life history, as used here, ends at about the time that the larvae become mobile enough to avoid egg and larvae survey nets. The juvenile stage is essentially the stage that is unsuceptible to capture by either egg and larvae survey nets or commercial fishing gear. From a modelling viewpoint the feature that characterizes this stage is the lack of information. The post-recruit stage is the stage that is susceptible to capture by commercial gear. A large proportion of the knowledge of this stage consists of information gathered from the fishery.

Modelling of any one of these three life history stages is a difficult task and there presently are no stocks for which fully developed models of all three life history stages are developed. Modelling of the individual life history stages is dominated by models of the post-recruit stage with a lesser total effort on the early life history stage and practically no effort on the juvenile stage. Modelling of any one of the life history stages must necessarily ignore many of the relationships and processes that occur in the other life history stages. The following sections describe some of the weaknesses of models which concentrate on only one of the life history stages.

Post-recruit modelling

The bulk of the current population models of fish stocks is composed of models which are focused on the post-recruit stage. Adequacy of the models is primarily limited by first order approximations of the parameters which describe the growth, mortality, and recruitment rates. Population fluctuations occur through the alteration of one or more of these rates and the mechanisms that cause these alterations are largely related to differences in stock size, environmental conditions and age composition of the stock. Determination of relationships of the environmental state, stock age composition and stock size to growth, mortality and recruitment rates requires data from extensive long-term sampling programs. Such data are very sparse and most of our current information is from a few well-studied stocks.

Growth is the easiest of the three required rates to measure. In addition, large numbers of samples can be taken each year. Growth, therefore, is the best described rate. For purposes of describing age-dependent growth, samples are largely independent if taken through catch sampling programs or exploratory fishing. This independence does not extend to the testing of the relationship between stock size and growth rate or that between environmental state and growth rate. For the testing of these relationships only one observation accrues per year and these observations may be autocorrelated.

Documentation of changes in growth associated with changes in stock size of post-recruit fishes is not common in the literature (Murphy, 1977). This may be partially due to the fact that data is not often collected in a manner to show such changes. For example, weight at age is a more meaningful measure of growth than the more commonly used length at age. Of course a stock must also fluctuate over a wide range of stock size before a relationship between stock size and growth rate can be determined. Another reason that density-dependent changes in the growth rate are uncommon or relatively small is that when surplus energy is available it may be utilized for gonadal growth rather than somatic growth. Compensatory gonadal growth can occur through earlier age at maturity, increased batch fecundity or increased numbers of spawnings per year. Earlier age at maturity at lower stock size is a common feature in the stocks of small pelagic fishes of eastern boundary currents and has been described in the California stocks of sardine (Murphy, 1966) and mackerel (Parrish and MacCall, 1978) and the Peru stock of anchoveta (Valdivia, 1978). Verification of variation in batch fecundity or number of spawnings per year is presently unavailable and will be difficult to obtain. Fecundity is usually considered to be proportional to body weight and is often expressed as the number of eggs per unit body weight. If this is the case, even if there are no compensatory changes in the number of eggs per unit weight, fecundity will increase with compensatory changes in the condition factor such as described for the California stock of sardine (MacGregor, 1959). Availability of surplus energy can be the result of compensatory density-dependence or favorable environmental state; with a limited set of observations it is difficult to sort out the two factors. Mortality rates are very difficult to measure accurately and natural mortality in exploited stocks is confounded with fishing mortality. Essentially nothing is known of the dependence of mortality, in the post-recruit stage, upon stock size or environmental state. Heavily exploited stocks of small pelagic fishes often exhibit increased total mortality with increased age within the post-recruit stage (Paulik 1970). It is not known if this is due to increasing natural or fishing mortality.

Modelling juvenile fishes

The present information on the juvenile stages of the pelagic fishes of eastern boundary current regions is too incomplete to be of much use in population modelling. Information on mortality rates and on the processes affecting mortality is lacking. The available field data base is largely limited to general descriptions of geographical distribution plus some information on sizes of fish. Data is needed on the vertical distribution of juvenile fish. Laboratory data is largely limited to growth data which is not verified against field data; although with the new daily aging techniques (Methot and Kramer, 1979) this is an area of active research.

The stock-recruitment relationships discussed previously group the processes affecting the early life history and juvenile stages into a single process (i.e., recruitment). The relative effect of the early life history and juvenile stages in determining recruitment fluctuations is not known. And it obviously must be determined separately for each stock. Although the early life history stage is critical on the short time scale, in that it has very high mortality, there is little evidence that year class size can be predicted by the numbers or concentrations of large larvae. For example, Smith (1978) has shown that the ratio of large larvae was nearly constant over the period of 1952 - 1956 and has suggested that the largest source of variation in sardine year-class size occurred during the juvenile stage. One of the most perplexing problems concerning recruitment processes in upwelling areas is the contribution of the large concentration of larvae which are found well offshore of the slope.

Modelling the early life history stage

Modelling of the early life history stage involves problems comparable to those of the post-recruit stage in addition to those particular to the early life history stage. The value of post-recruit models is largely determined by how well they predict the potential yields to the fishery and their adequacy is very sensitive to the accuracy of their stock-recruitment functions. Early life history models will eventually be evaluated on how accurately they predict the number of larvae entering the juvenile stage. The adequacy of early life history models will in a similar way be sensitive to the accuracy of stock-egg functions.

Both juveniles and post-recruits have the potential to reduce the survival of eggs and/or larvae through cannibalism or competition for forage. They also have the potential to increase the survival of eggs and larvae through predation on potential egg and larval predators. However, the most obvious effects that the post-recruit stage has on the early life history stage are those associated with the production and spawning of eggs. The numbers of eggs, their quality, and their distribution in time and space are determined by processes affecting the post-recruit segment of the stock. Fecundity and egg quality can be altered by density-dependent or environmentally related variations in the growth rate, condition factor, age at maturity, number of spawnings per year, and age structure of the post-recruit segment of the stock.

The distribution of eggs in time and space is influenced by oceanographic conditions (i.e. temperature, currents, food availability, wind events) which affect the geographical distribution of the adults. Features which trigger spawning, although not well understood, could also include oceanographic conditions. Stock size also alters the geographical distribution of spawning as a stock may increase the size range, of its spawning grounds as stock size increases. The stock may also saturate the available spawning grounds in both time and space when the stock is large. If this occurs the variance in the stock recruitment relationship should increase as stock size decreases. The age structure of the stock influences the time of spawning as older fish often start spawning earlier in the season than first time spawners. With species that have multiple spawning, older fish may have a longer spawning season than first-time spawners.

The rates at which all of the above relationships between adults and their eggs and larvae occur are potentially density-dependent. Density-dependent rate increases are more likely when lowered population size is caused by exploitation rather than when it is caused by environmental changes which may independently affect the rates at which the processes occur.

Several extremely sophisticated larval fish models have recently been published. (Vlymen, 1977; Beyer, In press) These models are well designed to model individual spawning spots. Thus they are in many ways analogous to yield-per-recruit models in that they describe the survival and growth of a given amount of eggs or larvae. For the purposes of predicting reproductive success or recruitment of individual stocks for management purposes these types of models have severe limitations. The models were, of course, not intended for management purposes. The results of these models are dependent upon given environmental states. The limitations of the models are not primarily due to the structure of the models but rather to the lack of knowledge of the environmental variables in the models. Determination of the average environmental conditions encountered by eggs and larvae in a given year is beyond our present capabilities and resources. Even if we were able to establish the mean environmental conditions encountered by eggs and larvae it is likely that the use of mean data would not result in good predictive capability due to patchiness problems. The survival of individual eggs and larvae is dependent upon interactions that occur on very small space and time scales. These interactions are associated with processes which operate on a wide range of scales. Thus the survival from individual spawning spots is affected by a range of space scales from that of less than the size of a spawning spot to that of at least the size of the spawning grounds and a range of time scale from less than hours to at least the length of the spawning season plus the length of the early life history stage.

A possible solution to the integrating problem is the use of spatial compartment models to account for environmental state patchiness in the larger space scales. Smaller-scale patchiness could be accounted for by stochastic terms. Unfortunately while the environmental state may be considered to be an additive process the response of individual spawning spots to environmental conditions is not additive. For example the survival of larvae after two days of starvation is dependent both on the age of the larvae and the feeding conditions, (i.e., environmental state) on the days preceding the two days of starvation. The spatial compartment model must therefore include age groups. The fact that processes affecting egg and larval survival operate on short time scales implies that the models must be run with short time steps. Thus, the combination of requirements for adequate spatial detail, age composition, and short time steps will result in the requirement of a huge computer and considerable running time.

An alternative to the use of a large compartment model, which also requires less conceptual alteration of existing larval models, is to model individual spawning spots. The models could be moved around in fields of the environmental state as Lagrangian drifters.

Eastern boundary current pelagic fishes have such extensive spawning grounds and extended spawning seasons that integration of scales becomes a major, perhaps dominant feature of any predictive model of the early life history stage.

RECENT ADVANCES - CALIFORNIA CURRENT REGION

Anchovy

The data base on the northern anchovy Engraulis mordax is different from those for the other better known species in the California Current Region in that the majority of information comes from field and laboratory studies rather than being taken from the fishery. There is more information available on eggs and larvae than on post-recruits. Most recent larvae work is well discussed in companion papers in this volume; we will therefore limit our discussion of recent anchovy research generally to processes having a larger scale than that affecting individual larvae.

The anchovy is widely distributed throughout the California Current System. Blood serum studies (Vrooman and Smith, 1971) show that there are three reproductively-isolated stocks (Fig. 4(c)) which exhibit considerable differences in their seasonality of spawning. The spawning grounds of the stocks appear to be separated by oceanographic features. The northern and central stocks are separated at the Northern California upwelling maximum (Parrish et.al., MS) and the central and southern stocks are separated in the region where negative wind stress curl approaches the central Baja California coast (Fig. 4(b)). The bulk of the information available on the anchovy concerns the central stock which extends from about 29° N to 38° N.

The central stock of the northern anchovy, like the anchoveta of the Peru Current, spawns to some degree all year round, with peaks in February-March and August-September. In both the peak in the winter-spring transition is greater than the peak in the summer-fall transition.

Lasker and coworkers (Lasker 1975, 1978; Lasker and Smith, 1977; Lasker and Zweifel 1978; Smith and Lasker, 1978) have shown that first feeding is a critical period for anchovy. Success of first feeding is associated with the occurrence of small scale concentrations of dinoflagellates which can be dispersed by wind events. However, the fact that the anchovy has such a long spawning season makes it very difficult to predict recruitment on the basis of indices of wind stress or other environmental data. Good environmental conditions during any part of the year could conceivably dominate annual recruitment. A recent breakthrough on daily aging (Methot and Kramer, 1979) greatly enlarges the possibilities for analysis of the relationships between environmental conditions and larval survival. Adequate sampling of pre-recruits coupled with daily aging will allow assessment of the time of year and associated environmental conditions which result in significant recruitment.

MacCall (1979) has noted a correspondence between low second quarter (April-June) values of the upwelling index (Bakun, 1973) at 33° N in the period 1947 to 1952, and extremely low anchovy biomasses in the early 1950's. This corresponded to apparent recruitment failures in sardine in 1949-50 and Pacific mackerel in 1949-50-51 and to disappearance of bonito (Sarda chiliensis) in the late 1940's and their reappearance in 1954.

We might add that upwelling index values at 39N, which characterize the Cape Mendocino - Point Arena area where the most vigorous upwelling in the California Current system occurs, were chronically low through the second half of the 1940's. This may have adversely affected the general level of productivity throughout the entire system (See sardine model, below.) Thus the low spring upwelling of 1947-52 local to the Southern California Bight may have been superimposed upon poor conditions which were advected from the upstream upwelling maximum.

Two recent studies indicate direct interactions between adult and larval processes. Hunter and Goldberg's (1980) work on batch fecundity shows that the northern anchovy spawns approximately once a week over an extended spawning season, indicating that energy reserves and the availability of food to the anchovy may influence the number of spawnings per year. Hence total fecundity may be a function both of adult anchovy biomass and food availability. Hunter and Kimbrel (in press) found that approximately 17 percent of eggs spawned were cannibalised by filter-feeding anchovies, and they estimate that this may represent about 32% of the natural mortality of anchovy eggs.

Pacific mackerel

Substantial catches of Pacific mackerel commenced off California in the late 1920's. Economic conditions at the beginning of the 1930's caused a large drop in fishing effort, but a recovery of prices and demand resulted in rapid expansion of the fishery from 1932 to 1935. Landings reached a peak of 66,500 MT in the 1935-36 season. Thereafter, the fishery went through a long, fluctuating decline. In the 1953-54 season the fishery was nearly exhausted, but good recruitment in the 1950's (Fig. 6) rejuvenated the fishery for a while until a series of poor recruitments in the 1960's brought it to a temporary close. Recently the population has rebounded strongly.

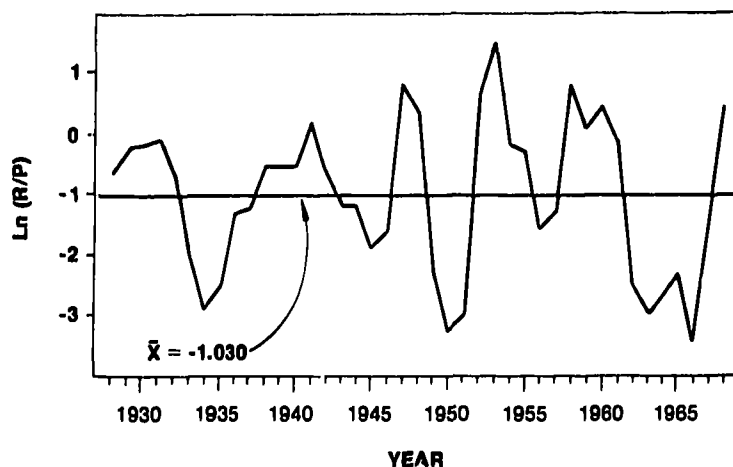


Figure 6, Time series of the natural log of the observed recruit biomass per spawning biomass in the California Current stock of Pacific mackerel, Scomber Japonicus.

A detailed analysis of the fishery, including population biology, cohort analysis, spawner-recruit models, and yield simulations, was presented by Parrish and MacCall (1978). Here we briefly abstract certain of their main findings concerning environmental dependence. These are in the area of empirical environmentally-dependent spawner-recruit models. Their post-recruit models do not address any environmental dependence, incorporating the usual assumptions of constant natural mortality rate, etc.

The authors consider a number of environmental variables, which are assumed to act mainly during the May-July spawning period. Thus, they are hypothesizing that environmental effects on Pacific mackerel recruitment occur at the spawner-egg and the early life history phases. Several linear combinations of months were considered, including (1) a simple average over the 3-month May-July period of peak spawning, (2) a simple 3-month April-June average to test for lagged effects (e.g. upwelling would provide suitable food particles only after some lag, assumed to be of the order of one month), and (3) "prorated" averages of both 3-month periods, where each monthly contribution is weighted by an estimate of the percentage of spawning which occurred during that month in each particular year of the time series.

The environmental variables for which these linear combinations produced the best correlations with recruitment are given in Table 3 (Parrish and MacCall's Table 18). Other variables tested which did not

yield significant correlations included Saur's (1972) index of very large-scale subtropical gyral circulation based on Hawaii to San Francisco sea level difference. Separate tests against all the individual monthly values produced lower correlations than those against the linear combinations (Table 3) considered characteristic of the entire spawning season.

TABLE 3. Correlation Coefficients of Linear Combinations of Monthly Values of Environmental Variables with logarithm of Pacific mackerel recruitment.

Variable	N	May-July mean	Prorated May-July	April-June mean	Prorated April-June
SPIER	41	.270	.416**	.276	.255
BARP	41	.030	-.165	-.007	-.059
SSTC	38	.434**	.432**	.432*	.392*
WINDC	38	-.354*	-.380*	-.289	-.306
SLLJ	41	-.542**	-.391**	-.514**	-.392**
SLEV	41	-.509**	-.348*	-.509**	-.366*
UP	23	.458**	.319	.575**	.713**
CURL	23	.528**	.610**	.486*	.584**

SPIER	-Sea surface temperature at La Jolla
BARP	-Barometric pressure at San Diego
SSTC	-Sea surface temperature, Marsden Square quadrant 120(2)
WINDC	- Wind speed, Marsden Square quadrant 120(2)
SLLJ	-Uncorrected sea level height at La Jolla
SLEV	-Sea level height at La Jolla corrected for atmospheric pressure
UP	-Upwelling index at 30°N
CURL	-Wind stress curl (surface layer divergence) index at 30°N
*	-Significant at 5% level
**	-Significant at the 1% level

The highest correlation of all was found with the April-June composite upwelling index, which is conceptually satisfying since upwelling would be expected to have a lagged effect. Highest correlations with sea temperature and with surface layer divergence (wind stress curl) were with the May-July prorated variables, again conceptually satisfying since these effects would seem to act directly on the larvae without lag. The correlation coefficients with temperature are positive, suggesting that warm temperature contributes to reproductive success; in this case the temperature appears to indicate a physiological effect, since a temperature-upwelling-productivity linkage would result in negative correlation coefficients with temperature. The correlations with surface divergence were positive; this is somewhat puzzling since one would expect convergence (negative divergence), by concentrating food organisms, to favor survival. Perhaps convergence could be detrimental by concentrating mackerel larvae in frontal structures where they would be highly vulnerable to predation. An alternative explanation could be that the relaxation of the blocking of northward coastal counterflow by the negative wind stress curl lobe off central Baja California could have allowed augmentation of the exploited northern subpopulation by the southern subpopulation (See subsection on convergence-divergence in the section on environmental variability, above). Negative correlations are found with coastal sea level; this could be related to the upwelling effect since strong upwelling would tend to depress coastal sea level.

Farrish and MacCall present a number of empirical models containing various formulations of density-dependence (including those presented in Table 1 and in Figure 5(b)) and the environmental variables (Table 3). Since the upwelling index and surface divergence index series are available only since 1946, models containing these variables treat only the latter part of the historical record of the fishery. In order to retain reasonable degrees of freedom for each explanatory factor these models were restricted to a density factor and two environmental factors. Models treating the total time series were allowed to contain three environmental factors in addition to a density dependent factor. None of the density dependent formulations were as significantly correlated with recruitment as were various environmental

terms; density dependence alone could account for no more than 24% of the observed variation. However, the authors felt that some form of density dependence was a conceptual necessity and so a density dependent formulation was forced to appear in each multiple regression model. However, the fitting of the density dependence was accomplished in concert with the environmental terms. This is a fundamentally different procedure than that used by Nelson, Ingham and Schaff (1977) who first fitted an assumed density dependence and then fitted environmental variables to the residuals. In our opinion the procedure of Parrish and MacCall is more valid, since fitting a density dependence before accounting for environmental variation assumes that environmental variability does not affect the fit; if this were the case there would be little need to include environmental terms.

A model containing a Ricker density dependence, and an upwelling index and a wind stress curl (surface layer divergence) index as environmental terms, was significant at much greater than the 99% level and explained 76% of the observed recruitment variation since 1946. A model containing sea temperature, coastal sea level and barometric pressure, as well as a Ricker function was again significant at the 99% level and explained 59% of the variation in the longer series covering the total fishery.

The two intense declines in the Pacific mackerel stock correspond to periods of poor recruitment in the late 1940's and early 1950's and in the mid, 1960's (Fig. 6). During the first period, there was an extended series of poor upwelling years in the upwelling maximum region off Northern California (Bakun, 1973). During the decline in the 1960's, anomalously low upwelling in the local Baja California spawning area was indicated. It is interesting to note that in the recent period, not treated by Parrish and MacCall, extremely vigorous upwelling is indicated for the mid 1970's, while excellent relative reproductive success in 1974 and 1976 has enabled the Pacific mackerel stock to rebound from its previous collapsed state.

The environmentally-dependent functions produced by Parrish and MacCall have allowed them to run simulations of management options containing a realistic spectrum of environmental variance, i.e. an aperiodic cyclic pattern as opposed to the random environmental noise usually assumed (e.g. Allen 1973, Walters, 1975). These simulations have been used by the State of California in establishing a management strategy for Pacific mackerel, which is now in operation.

Before concluding our survey of this work, a comment on independence of data points is relevant to the purpose of our present paper. The ratio of recruitment to parental biomass (Fig. 6) obviously contains substantial autocorrelation; the series in no way resembles random "white" noise. Rather, runs of multiple years of good and poor recruitment dominate. In this case the assumption of an independent data point each year probably results in a substantial overestimate of available degrees of freedom (Table 2). However, one can visually convince himself that there are at absolute minimum some ten or eleven independent data points determining the function in Fig. 6 and at least eight in the series since 1949 (by counting extrema or crossings of the zero line, etc.). A recomputation indicates that the significance of Parrish and MacCall's major relationships is still at an acceptable level even when the assumed degrees of freedom are so reduced. However, in cases where the relationships may be less pronounced, this issue of independence of data points may be critical. A formula for choosing the reduction in degrees of freedom in an autocorrelated time series is presented by Sutcliffe, Loucks, and Drinkwater, (1976).

Sardine

The Pacific sardine (*Sardinops caerulea*) fishery expanded rapidly in the years prior to World War II to become the largest fishery in the United States with 774,000 MT landed in the 1936-37 season. The exploited stock spawned in the region of stability and favorable transport south of Point Conception (Parrish, et. al., MS) but during the period of abundance migrated as adults to feed in the region of vigorous upwelling to the north, an important fishery arising as far north as Vancouver Island. A period of relative stability in the catch ended in 1945, whereupon the catches begin to decline disastrously to the point where the fishery essentially vanished in the early 1960's.

There are two sets of recruitment estimates published for this stock. Murphy's (1966) cohort analysis presented numerical values through 1960. In this analysis, Murphy assumed a change in natural mortality rate from 0.4 in the years previous to 1949, to 0.8 in subsequent years in order to match independent stock estimates based on egg and larvae surveys. MacCall (1979) showed that this change was unnecessary and presented recruitment estimates through 1965.

Since no studies of sardine which incorporate time series indices of environmental processes have yet been published, we here present results of a preliminary hypothetical model formulated to include density dependence and environmental effects represented by upwelling index and wind stress curl index time series. Four such time series were hypothesized as indicative of environmental effects on larval survival.

These included an upwelling index and a wind stress curl index computed at 30° N latitude (symbols: UP30 and CURL30), found by Parrish and MacCall (1978) to be the most significant variables in their Pacific mackerel model, and a wind stress curl index at 33° N latitude (CURL33), considered characteristic of surface layer divergence within the Southern California Bight and possibly related to the strength of the gyral circulation in that area. Each of these three index series was averaged over the 5-month period, February through June, of maximum sardine spawning (Murphy 1966).

A fourth environmental variable (UP39) is the average over the calendar year preceding spawning of the upwelling index computed at 39° N latitude. The inclusion of this variable, which does not characterize the specific season or the location of spawning, was motivated by correlations noted between longer-term upwelling index variations (Fig. 7) in the area of the Northern California upwelling maximum and indices of spring zooplankton abundance in the downstream areas extending from Central California to southern Baja California. A multivariate response such that strong upwelling off northern California during the previous summer and fall quarters was associated with highest zooplankton concentrations in the downstream offshore regions relative to the concentrations directly inshore of those regions was the most robust relationship found. The spring zooplankton concentrations in the various offshore regions along the coast have a tendency to vary directly with the northern California upwelling index but the various univariate relationships are less pronounced than are those which are associated with the multivariate nearshore/offshore contrast (significance: .90 v.s. .98).

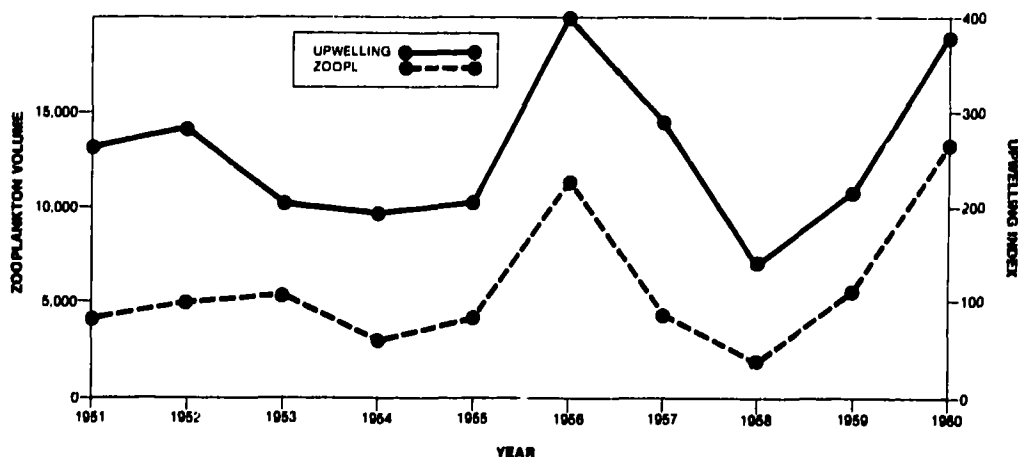


Figure 7. Central California offshore zooplankton abundance during spring (Paul E. Smith, personal communication v.s. upwelling index at 39N latitude (Bakun, 1973) averaged over previous 12 months.

Density dependent effects were incorporated by including parent stock size as a variable (STOCK). A final variable which was a simple linear trend (TREND) was added to reflect long-term changes, such as possible competition due to the rise of the northern anchovy population during the time period modeled. The modeled period covered only the decline of the stock since the upwelling and wind stress curl indices are not presently available for the period prior to 1946.

We expect the effects considered to alter the proportion surviving of whatever number of eggs were spawned rather than "killing" or "not killing" any fixed number. Since we wish as much weight given, for

5. Personal communication, Paul E. Smith, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, California, 92037.

example, to a halving of expected recruitment as to a doubling, a regression against the logarithm of the ratio of recruits to spawners is appropriate. The formulation of our model is therefore:

$$\ln(\text{RECRUITS}/\text{STOCK}) = a_0 + a_1 \text{UP30} + a_2 \text{UP39} + a_3 \text{CURL30} + a_4 \text{CURL33} + a_5 \text{STOCK} + a_6 \text{TREND}$$

Note that upon transformation to a prediction equation by taking the exponential of this model equation, the term containing the variable STOCK corresponds to a Ricker function (see Table 2).

The model was run on both the Murphy and MacCall population estimates; we look for results which are consistent in the analysis of both of the two separate sets as being perhaps less subject to distortion by deficiencies in our knowledge of the real population variations.

Against MacCall's estimates the full model was significant at 0.95. When the two least significant variables, UP30 and CURL30, were dropped from the model the significance improved to better than 0.99 ($r^2 = .7$). Regression coefficients were positive for variables UP39 and UP30, and negative for CURL30, CURL33, STOCK and TREND. Thus strong upwelling appears to favor survival, strong curl (surface layer divergence which would oppose formation of concentrated patches or organisms) corresponds to decreased survival. There appears to be compensatory mortality (negative coefficient for STOCK) and an apparent declining trend in survival over the period (possible competition from the increasing northern anchovy population). Of course the regression coefficients for UP30 and CURL33 should not be taken very seriously since significance increased dramatically when these variables were dropped.

The most significant variable by itself is UP39; the regression against this variable alone is significant at above .90. However, with STOCK and TREND in the model with UP39, UP39 is the least important of the three in reducing unexplained variance. The model with STOCK and TREND only is significant at .995; however, against either STOCK or TREND alone the regression is completely non-significant. The model with the three variables STOCK, TREND and UP39 is significant at better than .995 ($r^2 = .87$).

Murphy's (1966) estimates yield a series five years shorter than MacCall's (Fig. 8). This further depletes the seriously limited degrees of freedom. In this case the full model has an R-square of 0.92 and is significant at the 95 percent level. UP39 and UP30 have positive regression coefficients, STOCK and TREND have negative coefficients, as before. CURL33 has a negative coefficient as before but now CURL30 has a positive coefficient. This positive effect of a lessening of the ordinarily negative values of CURL30 is the same pattern noted by Parrish and MacCall in (1978) for the Pacific mackerel. The most significant single variable is STOCK, yielding significance at better than 90 percent and an R-square of .30. If TREND is then added, significance increases to the 99 percent level. If UP39 is introduced at this point its added contribution is significant at the 95 percent level. Subsequent addition of CURL30 to the model already containing STOCK, TREND, and UP39 is significant at somewhat better than 90 percent. The model containing the four variables, STOCK, TREND, UP39, and CURL30 is significant at better than the 99.5 percent level. R-squared is .92.

The variable UP39, which is designed to measure the effect of annual-scale variations in the northern California upwelling maximum, has appeared as an important factor against both population data sets. A period of generally weak upwelling commencing after the Second World War lasted through 1963, (Bakun, 1973) broken only during 1951 and 1955-56, which as a matter of fact were followed the next year by relative sardine year-class success (Fig. 8) and 1959, when the population was already at quite low levels. Murphy (1966) has reported a tendency for the spawning of sardines, before the population collapse, to be situated offshore relative to the spawning of anchovies. We have here noted the tendency for UP39 to reflect increases in offshore zooplankton concentrations relative to those near the coast during the spring spawning season. It seems a possibility that the long term variations in upwelling in the upwelling core of the California Current region could have been a factor in the rise of the anchovy at the expense of the sardine.

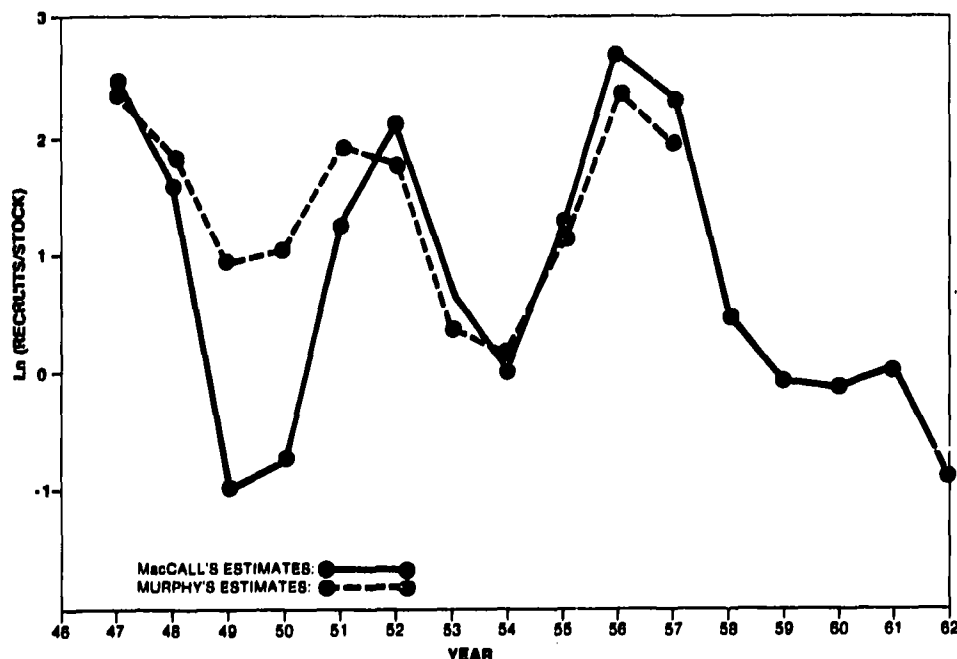


Figure 8. Natural log of the ratio of recruits (10^6 fish) to parental biomass (10^3 metric tons) based on the estimates of Murphy (1966) and MacCall (1979) over the modeled period of decline of the Pacific sardine fishery.

Regression analyses of both data sets indicate a compensatory effect of stock size and a negative trend in the rate of recruitment of sardine after 1946. The compensatory effect was obviously not strong enough to keep the population from collapsing under the combined effect of heavy exploitation and a declining trend in the rate of recruitment. The declining trend in the rate of recruitment could have been related to increasing competition with the rising anchovy population or it could be the result of overestimation of the potential spawning biomass due to an increasing proportion of sardines of southern origin as the stock declined as was suggested by MacCall (1979).

Again this is a situation where the data offer some tantalizing indications, but the available degrees of freedom in the historical time series are far too limited to yield final conclusions.

Hake

Substantial catches of Pacific hake (*Merluccius productus*) commenced abruptly in the mid-1960's. Smith (1975) has reported a geographical shift in larval hake abundance, coincident with the heavy fishing pressure, such that larvae became more abundant off Central California and less abundant off Baja California. He hypothesized a linkage whereby the fishery resulted in a relative depletion of larger sized fish, which may either have traveled farther south to spawn or have participated in multiple spawning, the latter of which would have occurred farther south along the annual migration route.

Bailey (In press) presented a model supporting this hypothesis and further showed that the offshore extent of larvae off Central California was correlated ($r = 0.70$, significance 0.99) with offshore transport as indicated by interyear variation of the January monthly upwelling index (Hakun, 1973) at 36° N latitude. Off Baja California no such correlation was found. Bailey suggests that, since hake larvae tend to be distributed near the top of the thermocline, a deeper surface mixed layer off Baja California could perhaps protect the larvae from offshore transport.

Bailey (MS) constructed an index of yearclass strength from annual trawl surveys by summing the percentages of the total age composition contributed by each cohort over the ages 4-6 years. Over 14 years of available data, January offshore Ekman transport is negatively correlated ($r = 0.73$, significance 0.997) to this year class index; offshore transport during the winter spawning season appears to be detrimental to reproductive success, in agreement with the hypotheses presented by Parrish et al (MS). If larvae spawned off Baja California are indeed relatively protected from offshore transport, and the shift of spawning intensity to the less protected Central California region was indeed caused by the operation of the fishery, this situation presents an additional mechanism by which fishing pressure may adversely affect resilience to environmental perturbation.

Temperature does affect the situation. Bailey (In press) indicates more northward spawning in warm years relative to cold years. In addition egg and larval survival seems to be better in warm years judging from numbers of large larvae found in the spring. Bailey found that when a temperature index was added as a second explanatory variable to the regression of year class strength against Ekman transport, 69% of the variance in year class strength ($r = 0.83$, significance 0.998) is accounted for.

Bonito

The Pacific Bonito, Sarda chiliensis, has been fished commercially in the California Current region since the beginning of this century. Collins and MacCall (1977) have summarized the available information on the population dynamics and biology of the California Current stock.

Historically, the landings have fluctuated widely. The population appears to be centered near Sebastian Vizcaino Bay in central Baja California while much of the exploitation occurs off Southern California. The Southern California fishery apparently operates on two stock segments, one of which migrates annually northward from the population center and the other of which is a transient resident population which becomes established during periods of particularly favorable local conditions. Thus it is difficult to separate fluctuations in stock size from variations in availability to fishing operations.

Collins and MacCall constructed an index of relative recruitment success from estimates of spawning biomass derived from aerial surveys and estimates of recruitment based on catch per unit effort (CPUE) of the partyboat sport fishery (MacCall, Stauffer and Troadec, 1974). They found a positive relationship between this index and the upwelling indices (Bakun, 1973) off northern Baja California averaged over the March-July spawning season. Previous to 1963 no aerial surveys were available. For this period Collins and MacCall used the ratio of CPUE during a given year to the CPUE of the year previous to indicate relative recruitment success and to demonstrate a similar relationship to upwelling index as was found for the later period.

Dover sole

Many of the pleuronectids of the California current region have extended pelagic phases. Dover sole, Microstomus pacificus, which is the dominant commercial flatfish of the region, has larvae which are pelagic for up to a year; it is a late winter - early spring spawner. Off Oregon younger larvae are common both inshore, over the continental shelf, and offshore. Larger larvae are most common in waters outside of the continental shelf but during the winter there is an increase in the largest larvae over the shelf and slope where they settle (Pearcy, et. al., 1977). Hayman (1978) used fishery-based estimates of year-class size of Dover sole to determine the relationship between recruitment and oceanographic conditions. He found that recruitment was associated with reduced offshore Ekman transport during the period of maximum upwelling off Oregon (June-July) and with increased convergence during the Dover soles' settling period (December-January). It appears that increased offshore dispersal, during the period of the year when upwelling prevails off Oregon, is associated with reduced recruitment of the Dover sole and that wind-related features during the winter settling period also affects recruitment.

Rockfish

Little is known about the population fluctuations of rockfish in the California Current, but it seems useful to our discussion of drift responses to present some anecdotal information. In the California

Current region there are nearly 60 separate species of the genus Sebastes which are known by the collective term rockfish. The existence of such a variety of species in the very dispersive medium of an upwelling system may be facilitated by their livebearing mode of reproduction which produces young which may be capable of maintaining position relative to very specific ocean depths, bottom types and other conditions. Most of these species release young in the late winter when offshore surface transport is most relaxed (Parrish, et al., Ms). The larvae are pelagic for 4-6 months and the juveniles are observed to congregate in the inshore region in the summer. It is known that occasional good year-classes pass through the fishery; however, until very recently the fishery has not been regularly sampled and the relative sizes of individual year-classes is unknown.

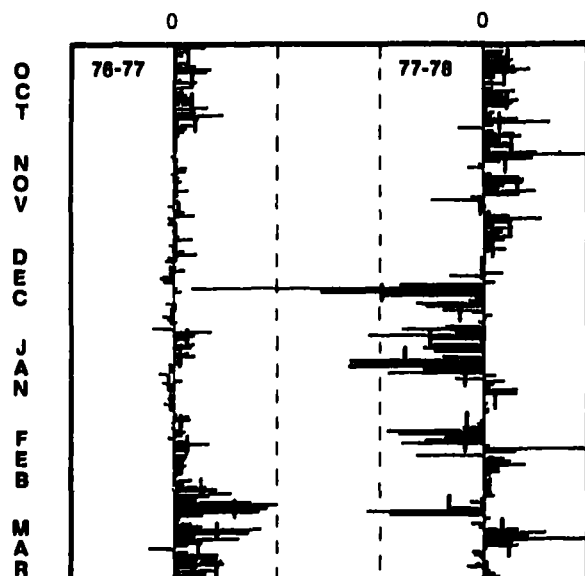


Figure 9. Daily and weekly means of 6-hourly upwelling index computations at 36 degrees N. latitude on the Central California coast. Horizontal lines indicate daily mean values. Values to the right of the zero line indicate offshore transport and upwelling; those to the left indicate onshore transport and downwelling.

Two very anomalous recent winter situations have been the winter of 1976-77, in which the near absence of storms contributed to a serious drought in California, and the winter of 1977-78 in which the drought was broken dramatically by unusually intense winter storm activity. Upwelling index computations (Figure 9) illustrate the contrasting conditions. The winter of 1976-77 is a consistently low energy situation marked by the near absence of periods of transport either toward or away from the coast. This lack of significant transport events is unique in the time series of daily indices which begins in 1967 (Bakun, 1975). During 1977-78 intense storm events followed one another in rapid succession, resulting in a highly fluctuating mixture of strong onshore and offshore transport episodes.

During the summer of 1977 extraordinary concentrations of juvenile rockfish⁶ were observed off northern⁷, central⁸, and southern California⁸. In contrast, the 1978 year-class appears to be a complete bust, judging from observations of summer juvenile concentrations⁸.

To attribute the apparent differences in larval rockfish survival to the difference in transport conditions, it seems necessary to assume that the ability of larvae to maintain a position relative to the coast throughout the pelagic period is crucial. The extent to which the larvae may be capable of maintaining such a position is undocumented. Parrish, et al. (MS) point out a pattern of correspondence between fish reproductive strategies and transport characteristics which suggest a general difficulty in maintaining resident populations in the region of intense upwelling. If the relative success of the large number of rockfish species in countering this pattern is based on their livebearing mode of reproduction, the required assumption seems the most likely mechanism. It will be interesting to note whether the present very stormy winter, 1979-80, will be followed this coming summer by a scarcity of juvenile rockfish in California coastal waters.

6. Personal communication, Jim Hank, California Dept. of Fish and Game, Monterey, California, 93940.
7. Personal communication, Kenneth Mais, California Dept. of Fish and Game, Long Beach, California, 90801.
8. Personal communication, William H. Lenarz, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Tiburon, California, 94920.

Dungeness crab

Peterson (1973) found significant correlations indicating increased Dungeness crab landings off Washington, Oregon and Northern California in years following high values of Bakun's (1973) upwelling indices averaged over the spring and summer seasons. The lag times for the correlations were 1/2 year for Washington and 1 1/2 years for Oregon and Northern California. Since the period of growth from larva to recruitment is four years, the upwelling effect on recruitment could not be acting at the larval stages. Peterson suggested that delays in molting during years of low upwelling-related productivity could be the causative mechanism. However, the data do not appear to support this mechanism. Crabs cannot delay their molts indefinitely and one would expect a pattern of increased catches in the year following as the "delayed-molting" crabs reached harvestable size. This pattern is not evident. Rather, multi-year runs of good or poor catches dominate the available time series.

Botsford and Wickham (1975) using slightly different statistical techniques confirmed Peterson's results of significant correlation at lag times near one year. Their cross correlations were positive for lags extending out to the four year growth period, but not significant at the levels required to confidently reject the null hypothesis of no relationship. They hypothesize density dependent biotic factors, such as cannibalism of adults upon juveniles, as mechanisms for the observed long period cyclic variations.

These studies were done using upwelling index data through 1971 reported by Bakun (1973). More recent upwelling index computations have indicated an unprecedented series of very high spring and summer values beginning in 1973 and continuing through 1975. The crab correlation reported by Peterson appears to be continuing to hold with northern California landings rising explosively from 160 MT during the 1973-74 season, to nearly 700 MT in 1974-75, to over 6,000 MT in 1975-76, and to over 11,000 MT in 1976-77 (Orcutt, 1978). A drop to about 6,000 MT in 1977-78 may reflect slightly lessened seasonal upwelling index values for 1976 or perhaps the density dependent biotic factors suggested by Botsford and Wickham.

The Dungeness crab fishery in central California was appreciable through the 1960's but catches dropped to a low value in 1962 and have remained near that value ever since (Orcutt, 1978). Attempts to link the collapse to pollutants derived from human activities have been inconclusive (Wild, Hauger, and Horn, 1978). Wild and Haugen (1977) have shown a significant correlation between sea level values during the fall and winter and crab landings three years later. This is the proper season and time lag for the relationship to reflect an effect on spawning success, possibly through the linkage of sea level to temperature. Laboratory studies have shown deterioration of egg masses at warmer temperatures (Wild, Hagen and Horn, 1978). The period analyzed in the regression covers the collapse of the fishery and a period of secular rise in sea level, although the authors point out that the highest correlations found are at the expected season and time lag rather than at all seasons and lags as would be expected if the correlations were controlled by the long term trends. This analysis is one in which a test of the correlation after high pass filtering of both the catches and sea level values would seem to be very helpful for interpretation.

Coho salmon

Gunsolus (1978) has indicated a relationship between seasonal upwelling index values off Oregon and both survival of juvenile coho salmon in their first year and the ultimate size of adults present that same year. Both survival rates and growth increase with indication of increased upwelling.

Further work by Zirges⁹ suggests that the date of transition from the winter situation of generally negative daily values (Bakun, 1975) off Oregon to the positive values characteristic of spring and summer may be more directly related to survival than the seasonal average of the index values. The effect of upwelling on the direction of the local alongshore current flow could be the causative factor; after transition the predominant flow switches abruptly from poleward to equatorward (Huyer, Sobey and Smith, 1979). Another possible mechanism is that early transition would allow a larger fraction of the smolts leaving the rivers to experience the higher food particle concentrations resulting from upwelling-related primary production.

9. Personal communication, Mac Zirges, Oregon Department of Fish and Wildlife, Newport, Oregon, 97365.

This result is pertinent to a controversy over the growing number of private salmon hatcheries being established in the region. If the indicated relationship reflects some sort of food-limited carrying capacity for salmon smolts in the ocean, then additional production should perhaps be discouraged. However, if the indicated relationship represents a control of the proportion of smelts surviving, rather than on the absolute numbers surviving, a limitation of production at present levels would not be warranted. Such a proportional control would be more likely if the effect of current direction were predominant or alternatively, if the linkage to upwelling were through size-dependent mortality interacting with growth rates dependent on upwelling-produced particle concentrations.

SUMMARY AND CONCLUSIONS

In defining the effect of the environment on fishery stocks we must deal with a space-time continuum of processes; the necessary coverage is generally not available from research vessel operations. Recently progress has been made using routinely collected marine and shore station data to produce indicators of variations in important environmental processes. These have led to empirical studies of recruitment variations in certain California Current fishery stocks.

The studies have shed a certain amount of light on processes controlling fish stock fluctuations but have been information-limited. The empirical models based on the studies are not expected to be extraordinarily reliable or skillful in detailed prediction and simulation. However, they at least provide some indication of the tendencies created by environmental variability; they allow simulations of management strategies to at least incorporate a realistic spectrum of environmental variance.

Fishery management science is far from an exact science at this time. Present methods to incorporate environmental effects share this lack of exactness. However, experience has shown that ignoring the problem is no answer. Certainly, it would make little sense to attempt to manage the Peruvian anchoveta fishery without reference to El Nino occurrences. Even as basic a fishery management concept as surplus production can become pretty nebulous in the face of major environmental perturbation; for example, Clark (1977) has suggested the possibility that the collapse of the anchoveta stock, which coincided with the 1972 El Nino, could have been due to insufficient fishing in 1971 as well as to excessive fishing in 1972.

The requirements for further progress are easily stated. We need more independent data points to provide additional degrees of freedom for the empirical approach and/or we need a better understanding of the processes linking fish stocks to their environment for advances via the rational approach. The two approaches are in many ways complementary. A better rational understanding would allow us to predetermine the shape and properties of the function which will be fitted to the available data points. More data points will allow a better and more detailed fit which would reveal more aspects of the functional relationship and thereby lead to increased understanding of the actual processes involved.

Since independent estimates of year-class strength of a given stock are available only once per year, increase of data points is a slow process. Substantial improvement in statistical significance comes only when degrees of freedom are at least doubled or tripled. Thus, in cases where we have several decades of information, simply waiting for more data to accumulate is not a useful response to present needs. However, where we may have only several years of data or no data at all, significant empirical advances would be possible in a reasonable time frame. In any case, when monitoring activities are needed, the best time to begin is immediately. Of course, our conception of what characteristics need to be monitored is always based on our rational understanding of the processes involved; thus substantial data accumulations are always based on a previous conception which is often altered as the data yield improved insight.

One development which may be capable of dramatically increasing the number of independent data points for larval survival processes is the technique of counting daily growth rings on larval otoliths

(Methot and Kramer, 1979). If larvae collected at sea can be effectively aged and their birthdates precisely fixed, the condition and abundance of larvae can be related to short term environmental conditions occurring between birth and collection. Thus, multiple independent data points on larval survival might be established in a single year. The technique appears to be quite labor-intensive, but expenditure in such a pertinent area may be preferable to dissipation of an equivalent amount of effort on activities which, although less tedious, may be less central to the management problem.

Substantial progress in the rational understanding sector likewise does not come easily. It is incredibly difficult to reproduce actual ocean conditions in laboratory experiments. Experiments at sea are also fraught with difficulties. The mixture of scales of motion at sea make it impossible to observe time-dependent aspects of any defined "parcel" of organisms and associated environment without artificially confining it somehow, which represents a fundamental alteration of conditions. Likewise, the actual processes tend to occur on such small space scales that it may be nearly impossible to make observations without perturbing the process being observed. However, the work of Lasker, Hunter, Thellacker and others, on larval anchovy survival processes, has shown that a well-conceived and painstakingly executed series of laboratory and field experiments can yield exciting breakthroughs.

Sometimes this process can be shortcut to yield certain limited results by simply comparing seasonal and geographic features of fish reproductive strategies with corresponding seasonality and geography of environmental processes. When a pattern is recognized, deductions can be made as to which processes appear to control reproductive success. Parrish et al (MS), for example, assembled seasonal transport and wind curl distributions on a finer scale than hitherto available and noted a striking pattern of avoidance of offshore transport in the spawning habits of the most successful coastal fish stocks of the California Current region. This provides a rational basis for empirical attempts to relate anomalous offshore transport to decreased reproductive success.

Dynamic modelling is undoubtedly useful in clarifying conceptual understanding. Mathematical models provide the necessary "bookkeeping" to test whether a given set of assumptions can lead to results which resemble reality. However they cannot generate, nor are they a substitute for, observational data. Their results can only reflect the information and assumptions which are put into their formulation. Mathematics cannot, for example, by itself inform us how far offshore larvae must be transported for their contribution to eventual recruitment to be seriously impaired.

The concept of comparative studies can perhaps be profitably extended to detailed comparisons among the major eastern boundary current regions. Similarities and differences in seasonality and geography of analogous environmental and biological features may lead to pattern recognition which will enhance our understanding of the controlling relationships. Of course such comparisons must be made with great care and be based on a commonality of data types. Because of the continuity of space-time coverage required, the environmental features must probably be defined largely by maritime and other routinely collected data. Specialized research cruises and experiments can illuminate certain aspects within limited time-space "windows". The setting of these "windows" within the larger seasonal-geographical framework is critical. For example, the recent CUEA studies need to be interpreted carefully when used to compare gross aspects of the three eastern boundary current regions in which they were made. In many ways the location off Oregon where the CUE-1 and CUE-2 experiments were made is probably an analog to the area off Portugal (Wooster, et al., 1976) rather than to Cape Blanc where JOINT-I was situated. Cap Blanc may be a better analog to Cape Mendocino (Bakun, et al., 1974) in the California Current. The JOINT-II location off Peru shares certain aspects, such as apparent nonlocal generation of upwelling characteristics (Smith, 1978), with the upwelling region in the Gulf of Guinea (Bakun, 1977). Such comparative studies can also be thought of as relieving the problem of limited degrees of freedom. Empirical models of environment - fish stock interactions among analogous stocks in the various regions can be compared for similarities and differences. If close enough analogies are indicated, statistical confidence would increase for the relationships in each of the regions; for example, in the theoretical case of perfect analogs the degrees of freedom could be considered to be directly additive.

REFERENCES

- AHLSTROM, E.H.
1966. Distribution and abundance of sardine and anchovy larvae in the California Current region off California and Baja California, 1951-64: a summary. U.S. Fish. Wildl. Ser. Spec. Rep. Fish 534, 71 p.
- BAILEY, K.M.
In press. Recent changes in the distribution of hake larvae: causes and consequences. MS. Larval transport and recruitment of Pacific hake.
- BAKUN, A.
1973. Coastal upwelling indices, west coast of North America, 1946-71. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-671, 103 p.
1975. Daily and weekly upwelling indices, west coast of North America, 1967-73. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-693, 114 p.
1978. Guinea Current upwelling. Nature, 271: 147-150.
- BAKUN, A., D.R. McLAIN, and F.V. MAYO
1974. The mean annual cycle of coastal upwelling off western North America as observed from surface measurements. Fish. Bull., U.S., 72: 843-844.
- BAKUN, A. and C.S. NELSON
1977. Climatology of upwelling related processes off Baja California. Calif. Coop. Oceanic Fish. Invest. Rept. 19: 107-127.
- BAUMGARTNER, T.R., N. CHRISTENSEN, JR., L. FOK-PUM, and W.H. QUINN
1979. Sources of interannual climatic variation in the Gulf of California and evidence for the biological response. Abstract. Annual Conference, Calif. Coop. Oceanic Fish. Invest., University of Southern California Conference Center, Idyllwild, California.
- BEARDSLEY, R.C., and B. BUTMAN
1974. Circulation on the New England continental shelf: response to strong winter storms. Geophys. Res. Letters 1 (4): 181-184.
- BEAUCHAMP, J.J. and J.S. OLSON
1973. Corrections for bias in regression estimates after logarithmic transformation. Ecology 54: 1403-1407.
- BEVERTON, R.J.H. and S.J. HOLT
1957. On the dynamics of exploited fish populations. Fishery Invest. Lond. Ser. 2 (19), 533 pp.
- BEYER J.B. and G.C. LAURENCE
In press. Modelling growth and mortality of larval herring (Clupea harengus). ICES/Early Life History Symposium 1979, Woods Hole.
- BJERKNES, J.
1969. Atmospheric teleconnections from the Equatorial Pacific. Mon. Wea. Rev., 97(3): 163-172.
- BOTSFORD, L.W. and D.E. WICKHAM
1975. Correlation of upwelling index and Dungeness crab catch. Fish. Bull., U.S., 73(4): 901-907.
- CHELTON, D.B.
1980. Low frequency sea level variability along the west coast of North America. Ph.D. Thesis. University of California, San Diego.

- CHRISTENSEN, N., JR., R. de la PAZ V., and G. GUTIERREA V.
1979. On the dynamics of coastal currents off Baja California, Mexico. Paper presented at CalCOFI Conference, Idyllwild, California, October 25, 1979.
- CLARK, COLIN W.
1974. Possible effects of schooling on the dynamics of exploited fish populations. J. Cons. Perm. Int. Explor. Mar. 36 (1): 7-14.
- CLARK, F.N.
1947. Analysis of the populations of the Pacific sardine on the basis of vertebrae counts. Calif. Dep. Fish and Game, Fish. Bull. 65, 26 p.
- CLARK, F.N. and J.C. MARR
1955. Population dynamics of the Pacific sardine. Calif. Coop. Ocean. Fish. Invest. Progress Rept: 11-48.
- COLLINS, R.A. and A.D. MACCAL
1977. California Pacific bonito resource, its status and management. Calif. Dep. Fish and Game, Mar. Res. Tech. Rep. 35, 39p.
- CUSHING, D.H.
1969. Upwelling and fish production. FAO Fish. Tech. Pap., 84, 40 p.

1971. The dependence of recruitment on parent stock in different groups of fishes. J. Cons. Perm. Int. Explor. Mar. 33: 340-362.

1975. Marine ecology and fisheries. Cambridge University Press, Cambridge-New York. 124 p.

1979. Climate variation and marine fisheries. World Climate Conference Overview Paper 22. World Meteorological Organization.
- ELSBERRY R.L., and R.W. GARWOOD, JR.
1978. Sea-surface temperature anomaly generation in relation to atmospheric storms. Bull. Amer. Meteor. Soc., 59 (7): 786-789.
- EMERY, W.J.
1975. Dynamic height from temperature profiles. J. Phys. Oceanogr., 6: 613-617.
- FAVORITE, F., and J.A. INGRAHAM
1978. Sunspot activity and oceanic conditions in the northern North Pacific Ocean. In: Ocean Variability: Effects on U.S. Marine Fishery Resources -1975. NOAA Tech. Rep. NMFS Circular 416: 191-196.
- FOFONOFF, N.P.
1963. Dynamics of ocean currents. In: M.N. Hill (editor) The Sea. Inter science Pub., N.Y., 1: 325-395.
- GREENSPAN, H.P.
1968. The theory of rotating fluids. Cambridge Univ. Press, Cambridge, 327 p.
- HAYMAN, R.A.
1978. Environmental fluctuation and cohort strength of Dover sole (Microstomus pacificus) and English sole (Parophrys vetulus). Ph.D. Thesis. Oregon State Univ.
- HICKEY, B.M.
1979. The California Current System - hypotheses and facts. Progress in Oceanography, Vol 8 (4): 191-279.

- HOLL, M.M. and B.R. MENDENHALL
1972. Fields by information blending, sea level pressure version. Fleet Numerical Weather Central Tech. Note 72-2, Monterey, California, 66 p.
- HUNTER, J.R. and S.R. GOLDBERG
1980. Spawning incidence and batch fecundity in northern anchovy, Engraulis mordax. Fish. Bull., U.S. 77 (3): 641-652.
- HUNTER, J.R. and C.A. KIMBRELL
In press. Egg cannibalism in the northern anchovy, Engraulis mordax. Fish. Bull. U.S.
- HUYER, A.
1976. A comparison of upwelling events in two locations: Oregon and Northwest Africa. J. Mar. Res. 34: 5310-546.
- HUYER, A., E.J.C. SOBEY, and R.L. SMITH
1979. The spring transition in currents over the Oregon continental Shelf. J. Geophys. Res. 84 (C11): 6995-7011.
- LAEVASTU, T. and I. HELA
1970. Fisheries Oceanography. Fishing News (Books) Ltd., London. 238 p.
- LASKER, R.
1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S., 73: 453-462.

1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors leading to recruitment failure. Rapp. P.-v. Reun. Cons. int. Explor. Mer., 173: 212-230.
- LASKER, R. and P.E. SMITH
1977. Estimation of the effects of environmental variations on the eggs and larvae of the northern anchovy. Calif. Coop. Oceanic Fish. Invest. Rept. 19: 128-137.
- LASKER, R. and J.R. ZWEIFEL.
1978. Growth and survival of first-feeding northern anchovy (Engraulis mordax) in patches containing different proportions of large and small prey, p. 329-354. In Spatial Pattern in Plankton Communities, J.S. Steele (ed.), Plenum Publ. Corp., New York, 470 p.
- LEWIS, J.M. and T.H. GRAYSON
1972. The adjustment of surface wind and pressure by Sasaki's variational matching technique. Tech. Note No. 72-1. Fleet Numerical Weather Central, Monterey, California.
- MacCALL, A.D.
1979. Population estimates for the waning years of the Pacific sardine fishery. Calif. Coop. Oceanic Fish. Invest. Rept. 20: 72-82.

In press. Population models for the northern anchovy (Engraulis mordax). Symposium on the biological basis of pelagic fish stock management, Paper No. 19.
- MacCALL, A.D., G.D. STAUFFER, and J.-P. TROADEC
1974. Stock Assessments for Southern California Recreational and commercial marine fisheries. Southwest Fisheries Center Admin. Rep. No. LJ-74-24, 144 p.
- MacGREGOR, J.S.
1959. Relation between fish condition and population size in the sardine (Sardinops caerulea). Fish. Bull., U.S. (166): 215-230.

- MADSEN, O.S.
1977. A realistic model of the wind induced Ekman boundary layer. J. Phys. Ocean. 7 (2): 248-255.
- MARTHALER, J.G.
1976. Comparison of sea level and currents off the Oregon coast using mean monthly data. MS thesis Oregon State Univ., Corvallis, Oregon. 64 p.
- McLAIN, D.R.
1978. Anomalies of coastal sea surface temperatures along the west coast of North America. In: Ocean Variability: Effects on U.S. Marine Fishery Resources - 1975. NOAA Tech. Rep. NMFS Circular 418: 127-140.
- METHOT, R.D. and D. KRAMER
1979. Growth of northern anchovy, (Engraulis mordax), larvae in the sea. Fish. Bull., U.S. 77 (2): 413-423.
- MONTGOMERY, R.B., and E.D. STROUP
1962. Equatorial waters and currents at 150°W in July - August 1952. The Johns Hopkins Press, Baltimore, 66 p.
- MOOERS, C.N.K. and J.S. ALLEN
1973. Final report of the Coastal Upwelling Ecosystems Analysis Summer 1973 Theoretical Workshop. School of Oceanography, Oregon State Univ., Corvallis, Oregon.
- MURPHY, G.I.
1966. Population biology of the Pacific sardine (Sardinops caerulea). Proc. Calif. Acad. Sciences, 34 (1): 1-84.

1972. Fisheries in upwelling region with special reference to Peruvian waters. Geoforum 11: 63-71.

1977. Clupeoids. In J.A. Gulland (ed.) Fish Population Dynamics. John Wiley & Sons, New York.
- NELSON, C.S.
1977. Wind stress and wind stress curl over the California Current. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-714, 87 p.
- NELSON, W.R., M.C. INGHAM, and W.E. SCHAAF
1977. Larval transport and year-class strength of Atlantic menhaden, Brevoortia tyrannus. Fish. Bull., U.S., 75 (1): 23-42.
- ORCUTT, H.G.
1978. Introduction. In Dungeness Crab Research Program, Report for the Year 1978. Calif. Dep. Fish. Game Admin. Rep. 78-16: 1-5.
- PARRISH, R.H., C.S. NELSON, and A. BAKUN
MS. Larval transport and reproductive success of fishes in the California Current.
- PARRISH, R.H., and A.D. MacCALL
1978. Climatic variations and exploitation in the Pacific mackerel fishery. Calif. Dep. Fish. Game, Fish. Bull. 167, 109 p.
- PAULIK, G.
1970. The anchoveta fishery of Peru. Quant. Science Paper No. 13. Center for Quant. Sci. in Forestry Fisheries and Wildlife. Univ. of Washington Seattle WA Processed 79 pp.

1971. Anchovies, birds, and fishermen in the Peru current. In W.W. Murdock (ed), Environment, Resources, Pollution and Society, Smauer Ass. Inc. Stanford Conn. 156-185 p.

- PEARCY, W.G., M.H. HOSIE, and S.L. RICHARDSON
1977. Distribution and duration of pelagic life of larvae of Dover sole, Microstomus pacificus; rex sole, Glyptocephalus zachirus; and petrale sole, Eopsetta jordani, in waters off Oregon. Fish. Bull. U.S. 75 (1): 173-183.
- PETERSON, W.T.
1973. Upwelling indices and annual catches of Dungeness crab, Cancer magister along the west coast of the United States. Fish. Bull. U.S., 71 (3): 902-910.
- PREISENDORFER, R.
1977. Empirical orthogonal functions in the diagnosis and prediction of climate fluctuations. In: Proceedings of the second Annual NOAA Climate Diagnostics Workshop. U.S. Dept. of Commerce.
- QUINN, W.H.
1978. Equatorial Pacific anomalies and El Nino. In: Ocean Variability: Effects on U.S. Marine Fishery Resources U.S. Dep. Commer. NOAA Tech. Rep. Circular 416: 179-190.
- REID, J.L., and A.W. MANTYLA
1976. The effect of the geostrophic flow upon coastal sea elevations in the northern North Pacific Ocean. J. Geophys. Res. 81 (18): 3100-3110.
- RICKER, W.E.
1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.
- ROBINSON, M.K. and R.A. BAUR
1973. Report on the production of the Baur-Robinson Northern Hemisphere numerical atlas. Fleet Numerical Weather Central, Monterey, Calif., 10 p.
- ROEDEL, P.M.
1952. A racial study of the Pacific mackerel. Calif. Dep. Fish. and Game, Fish. Bull., 84, 53 p.
- ROYER, T.C.
1979. On the effect of precipitation and runoff on coastal circulation in the Gulf of Alaska. J. Phys. Ocean. 9 (3): 555-563.
- SAUR, J.F.T.
1972. Monthly sea level differences between the Hawaiian Islands and the California coast. Fish. Bull., U.S. 70 (3): 619-636.
- SCOTT, J.T., G.E. MYER, R. STEWART, and E.G. WALTHER
1969. On the mechanism of Langmuir circulations and their role in epilimnion mixing. Limnol. Oceanog. 14 (4): 493-503.
- SISSENWINE, MICHAEL P.
1974. Variability in recruitment and equilibrium catch of the southern New England yellowtail flounder fishery. J. Cons. Int. Explor. Mer. 36 (1): 15-26.
- SMITH, P.E.
1975. Pacific hake larval distribution and abundance - 1951 to 1975. Southwest Fisheries Center Admin. Rep. No. LJ-75-83, 12 p.

1978. Biological effects of ocean variability; Time and space scales of biological response. Rapp. P.-v. Reun. Cons. int. Explor. Mer. 173: 117-127.

SMITH, P.E. and R. LASKER

1978. Position of larval fish in an ecosystem. *Rapp. R.-v. Reun. Cons. int. Explor. Mer.* 173: 77-84.

SMITH, R.L.

1974. A description of current, wind and sea level variations during coastal upwelling off the Oregon coast, July - August 1972. *J. Geophys. Res.* 79 (3): 435-443.

1978. Poleward propagating perturbations in currents and sea levels along the Peru coast. *J. Geophys. Res.*, 83 (C12): 6083-6092.

1980. A comparison of the structure and variability of the flow field in three coastal upwelling regions: Oregon, Northwest Africa, and Peru. *Abstract. IDOE International Symposium on Coastal Upwelling. University of Southern California. Los Angeles.*

STOMMEL, H.

1949. Horizontal diffusion due to oceanic turbulence. *J. Mar. Res.* 8 (3): 199-225.

SUTCLIFFE, W.R., R.H. LOUCKS, and K.F. DRINKWATER

1976. Coastal circulation and physical oceanography of the Scotian Shelf and Gulf of Maine. *J. Fish. Res. Board Can.*, 33: 98-115.

SVERDRUP, H.V., M.W. JOHNSON, and R.H. FLEMING.

1942. The oceans; their physics, chemistry, and general biology. Prentice-Hall, New York, 1087 p.

VALDIVIA, J.E.

1978. The anchoveta and El Nino. *Rapp. P.-v Reun. Cons. Int Explor mer.* 173: 196-202.

VROOMAN, A.M., and P.E. SMITH

1971. Biomass of the subpopulations of northern anchovy Engraulus mordax Girard. *Calif. Coop. Oceanic Fish. Invest., Prog. Rep.* 15: 49-51.

VLYMEN, W.J.

1977. A mathematical model of the relationship between larval anchovy. (E. mordax) growth, prey distribution and larval behavior. *Env. Biol. Fish.* 2 (3): 211-233.

WALSH, J.J.

1977. A biological sketchbook for an eastern boundary current. In: *The sea*, Vol. 6, E.D. Goldberg, I.N. McCave, J.J. O'Brien, J.H. Steele, editors. Interscience, New York: 923-968.

WEARE, B.C., A.R. NAVATO and R.E. NEWELL

1976. Empirical orthogonal analysis of Pacific sea surface temperatures. *J. Phys. Ocean.*, 6: 671-678.

WILD, P.W. and C.W. HAUGEN

1977. Crab environment project studies. In: *Dungeness Crab Research Program, Report for the year 1977.* Calif. Dep. Fish. Game Admin. Rep. 77-21: 29-48.

WILD, P.W., C.W. HAUGEN and R.P. HORN

1978. Crab environment project studies. In *Dungeness Crab Research Program, Report for the Year 1978.* Calif. Dep. Fish. Game Admin. Rep. 78-16: 1-5.

WOOSTER, W.S. and J.L. REID, JR.

1963. Eastern boundary currents. In, *The Sea*, M.N. Hill, ed. Interscience Pub., New York., 2: 253-280.

WOOSTER, W.S., A. BAKUN, and D.R. McLAIN

1976. The seasonal upwelling cycle along the eastern boundary of the North Atlantic. *J. Mar. Res.*, 34 (2): 131-141.

WYLLIE, J.G.

1966. Geostrophic flow of the California Current at the surface and at 200 m. Calif. Coop. Oceanic Fish. Invest., Atlas No. 4, xii p, 288 charts.

WYRTKI, K.

1974. Sea level and the seasonal fluctuations of the equatorial currents in the western Pacific Ocean. J. Phys. Ocean. 4 (1): 91-103.

LARVAL FISH DIVERSITY, A SUMMARY OF LABORATORY
AND FIELD RESEARCH

by

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INTRODUCTION

Good and poor year classes of fish may be determined during the larval stage by physical events that act upon larvae directly or indirectly by controlling their food supply (Hjort, 1914; 1926). The goal of this workshop is to evaluate our ability to identify and monitor these physical events, at appropriate scales, which might facilitate forecasting larval fish survival. Larval survival depends not only on environmental variables and prey availability at first feeding but also on a suite of species specific behavioural and physiological characteristics. Thus, minimum food concentrations needed to initiate feeding and promote larval fish survival will vary among species due to interspecific differences in egg size (hence development at hatching), resistance to starvation, feeding strategies, growth rates, growth efficiencies, and metabolic demands. Therefore, these food concentrations and other input parameters in models designed to predict survival and recruitment must incorporate species-specific functions. Presented here are pertinent life history, behavioural and physiological parameters of four important pelagic representatives of related species of the California and Peru Currents, as well as twelve predominantly demersal species of the north Atlantic Ocean (Table 1).

Table 1

EARLY LIFE HISTORY

Species	Range	Spawning season (peak)	Type	Egg diameter (mm)	Incubation		Hatching		Yolk absorption		Onset of feeding		Feederable starvation		Metamorphosis	
				Range	Days	°C	Size mm	dry wt µg	Days from hatching	°C	Days from hatching	°C	(a) Days from hatching	(b) Days from Yolk Abs.	Days from hatching	Length (mm)
<i>Limanda ferruginea</i> (Yellowtail flounder) 1.	Gulf of St. Lawrence to Virginia	March-June	Pelagic	0.88 0.79-1.01	5-7	10	2.0-3.5	16	4-5	10	4-5	10				14
<i>Limanda limosa</i> (h.b.) 2.	North Sea, English Channel	March-June (Feb-April)	Pelagic	0.65-0.95			2.6		Yolk absorption							
<i>Platystroctes platessa</i> (Plaice) 3.	North Sea, English Channel to Norwegian Home Skagerrak	Dec-April	Pelagic	2.0 1.7 - 2.2	18	7-11	5.0-6.7	151	6-10	7-11	4-6	7-10	6-8(b)	8-11	42-75	7-11 9-13
<i>Pleuronectes americanus</i> (Winter flounder) 4.	Northern Labrador to Oceania	Jan-May	Demersal	0.80 0.71-0.96	17-25	3	2.3-3.5	10-30	9	8	5	8	5-7(b)	8	58	8 6.5-9
<i>Paralichthys dentatus</i> (Summer flounder) 5.	Maine to Florida	Oct-April	Pelagic	1.04 0.90-1.13	2	17	2.4-2.7		3-4	16	4	16	6-7	16	47-56	16 12
<i>Solea solea</i> (Sole) 6.	North Sea, English Channel	April-June	Pelagic	1.0 - 1.5	8	10-12	3.3-3.7		7						42-56	10-12 9-10
<i>Achirus lineatus</i> (Lined sole) 7.	Florida and Gulf of Mexico to Uruguay		Pelagic		1	28		21.8	3	28	2	28	3-3.5	28	16	28 4-5
<i>Heterostichus rostratus</i> (Sole) 8.	Kona, Scotland to Eastern Florida	May-July	Pelagic	0.94 0.85-1.15	1.5	22	2.0		3	22	3					10
<i>Archaeogadus rhomboidalis</i> (Sole) 9.	New Jersey to Rio de Janeiro	Sept-May	Pelagic		1	26	1.8-3.2	27.0	2	26	1.5	28	2.5	28	9-11	23-27 2-3
<i>Gadus morhua</i> (Cod) 10.	North Atlantic Coastal Waters	Dec-April	Pelagic	1.52 1.10-1.72	12	5-5	3.3-5.7		6	7.2	-5	7	5(b)	7	52	7 10
<i>Melanogrammus aeglefinus</i> (Haddock) 11.	North Atlantic, Iceland to Arctic Sea, Newfoundland to Cape Cod	Feb-June	Pelagic	1.46 1.10-1.67	17	5-5	2.0-4.1		7	7	-5	7	5(b)	7	42-49	7 10
<i>Clupea harengus</i> (Atlantic herring) 12.	Greenland-Cape Hatteras, Iceland-Gibraltar	July-Nov.; May (Sept. & Nov.)	Demersal	1.0 - 1.4 0.35-3.0	15 (Shine, Brown)	8	4.0-10.0	90 (50-220)	6 (Birth of Clyde) 15-20 (W. Baltic)	8 15-20 (Baltic)	2-6 (Birth of Clyde) 15-20 (Baltic)		6(b) (Birth of Clyde) 12-22 (a)	8-12 8	112-168	8-12 30-40
<i>Scophthalmus maximus</i> (Pacific halibut) 13.	Southern Alaska to Gulf of California	Feb-July (May-June)	Pelagic	1.7	2.8	15	3.75	36			4-5	16			45-50	31-35

Table 1 - Cont'd.

Species	Range	Spawning season (peak)	Type	Egg diameter (µm)	Incubation		Hatching		Yolk absorption		Onset of feeding		Extraviable starvation		Metamorphosis	
					Days	°C	Size mm	dry wt µg	hatch	°C	Days from hatch	°C	(a) Days from hatch	(b) Days from Yolk Abs.	Days from hatch	Length (mm)
<i>Merluccius</i> <i>merluccius</i> (Atlantic hake)	14. Northern Baja California to Arctic Alaska and Japan	Jan.-July (March-May)	Pelagic	0.66(0.35)	2-3	16	2.9-3.2	21	4	16	4	15-16	2.5 ^(b) 4.5	16.5 15	30-60	34-40
<i>Merluccius</i> <i>langsdorfi</i> (Antarctic)	15. Coast of Peru and Chile	July-March (Sept. & Feb.)	Pelagic	0.77(0.42)	2-2.25	14-16	2.19-2.72		3	18	4-5 (3.5-6.8)	18	4-5	18		32
<i>Merluccius</i> <i>merluccius</i> (Pacific hake)	16. East-coast Alaska to Mexico Bay, Mexico	April-August (May-July)	Pelagic	1.05-1.14	3-6	16	3.1	40	3	19	2-2.5 4	19 16	2 ^(b) 3.5 ^(b)	19 16	25	15
<i>Merluccius</i> <i>merluccius</i> (Arctic hake)	17. Beringian Bay, Baja California to Southwest Alaska	Feb.-August (May-June)	Pelagic	1.0 0.90-1.02	2-3	15	2.13/ 2.6	34 ^{2/}			5	15	2.5 ^(b)	15	40	11-16

1. Martin and Brown, 1970; Gilton and Murak, 1969
2. Howell and Howell, 1963
3. Huxley and Staines, 1970; Harding, Nichols and Tansley, 1970; Hyatt, 1972, 1974
4. Martin and Brown, 1970; Lawrence, 1971; Lawrence and Brown, 1970
5. Martin and Brown, 1970
6. Huxley and Staines, 1970; Riley, 1974
7. Huxley, 1974, 1977, 1978
8. Johnson, 1970; Gilton and Murak, 1969
9. Staines, 1970; Huxley, 1974
10. Huxley, 1970; Lawrence, 1970
11. Huxley, 1970; Lawrence, 1970
12. Jones et al., 1970; Bannister and Huxley, 1969; Brown and Lawrence, 1970; Huxley and Staines, 1971; Huxley and Staines, 1971 (Notes: Values vary widely between individual stocks of Atlantic herring; values used above known)
13. Leach, 1962; Leach, 1964; Ahlstrom, 1964; Ahlstrom, 1966
14. Leach, 1964; Leach et al., 1970; Brown and Swartz, 1970; Huxley, 1976; Thelackner, unpubl.; Ahlstrom, unpubl.
15. Huxley de Witte (this volume)
16. Brown, 1970; Huxley and Huxley, 1970
17. Brown, 1970; Ahlstrom and Ball, 1974; Thelackner, 1980

2/ 0.90 mm egg

3/ 1.0 mm egg

4/ wt at yolk absorption, day 5

SPAWNING

With the exception of the cod, *Gadus morhua*, the Atlantic species discussed here form localized coastal populations and do not undertake extensive migrations. The stocks of these species are considered to be relatively distinct in their various localities for that reason. Each species has its own preference for bottom terrain, depth and temperature. All undertake at least a short migration before or during their spawning period, most of them toward shallower, inshore waters.

Peak spawning times vary with each species in each locality. Generally, in the northern hemisphere spawning begins in the southern part of the species' range and moves northward as the season advances following the advance of primary production cycles. This is reversed in the southern hemisphere. Spawning times of the four California Current species overlap. Northern anchovy, *Engraulis mordax*, and northeastern Pacific sardine, *Sardinops sagax*, spawn in early spring, and Pacific mackerel, *Scomber japonicus* and jack mackerel, *Trachurus symmetricus*, spawn later. Kramer and Smith (1970) summarized spawning from 1951-1960 in the California Current, 20-300 miles off the coast as follows: Pacific sardine spawning begins in small areas in January off both southern California and Baja California, the centers of the northern and southern subpopulations. Spawning areas continue to expand to the north and south and by May-June spawning is maximum, appearing as one area extending from Point Conception, California to mid-Baja California. Spawning of northern anchovy extends from Point Conception to southern Baja California from January to May; the spawning area decreases somewhat in June and July. Lasker and Smith (1977) could find no relation between amount or location of northern anchovy spawning and changes in temperature or zooplankton production over the spawning area between 1953 and 1960. Pacific mackerel spawning begins in the Spring off southern Baja California, moves north with warming water to southern California in May, June and July. Major spawning of jack mackerel first occurs in March off northern Baja California, and spawning gradually spreads northward off southern California in April and peaks in May and June as the water warms. Thus, between April and July, spawning of the four California Current species overlaps both temporally and spatially.

Frequency

Although little information is available on spawning frequency, some species are known to spawn at intervals during the spawning season. In cod and haddock, *Melanogrammus aeglefinus*, not all of the eggs within the ovary ripen at once; for cod there are at least three and possibly up to eight batches of eggs in a season (Hardy, 1978). Yellowtail flounder, *Limanda ferruginea*, also spawn more than once throughout a prolonged spawning season (Martin and Drewry, 1978). Hunter and Goldberg (1980) give evidence of batch spawning in the northern anchovy with a periodicity of about seven days and perhaps as many as 20 spawnings over the season. Thus, relationships between adult biomass and apparent egg abundance are complex.

EGGS

The eggs of the subject species range in size from 0.65 to 2.2 mm in diameter (Table 1) and, with the exception of anchovy, eggs are spherical. Egg buoyancy varies; most eggs are pelagic except for those of winter flounder, *Pseudopleuronectes americanus*, and herring, *Clupea harengus*. Early-stage pelagic eggs are found in the surface waters but they may descend to mid or bottom depths as development proceeds. Cod eggs are an example of this latter process (Hardy, 1978). Variations in density within the water column may "trap" eggs in their iso-density surfaces or vertical mixing may distribute them throughout the mixed water layer, but most pelagic eggs are found at or near the surface.

Size

Within species, egg size has been shown to decline from spring to summer and vary inversely with temperature (Ware, 1975). Decreasing egg size with season may be due to a shift in spawning from older to younger females (Ahlstrom, pers. comm.). Within species larger eggs are hypothesized to improve survival by producing larger larvae that are able to swim faster and search a greater volume of water for food (Hunter, in press). However, Hempel and Blaxter (1963) found that within a race of herring, the larvae hatching from large eggs did not survive longer than those from smaller eggs (no food was added), presumably because larger larvae have proportionately higher metabolic demands. But it has been shown that jack mackerel hatched from large eggs can grow twice as fast with the same feeding treatment as those hatched from small eggs (.09-.15 mm/day versus .05 mm/day; Theilacker, 1980a).

Incubation time is a function of egg size and temperature; larger eggs take more time to hatch at similar temperatures (Table 1). Egg size also affects duration of yolk-sac stage (Ware *et al.*, 1980), time to irreversible starvation (Blaxter and Hempel, 1963), and hatching size (Blaxter and Hempel, 1963; Theilacker, 1980a; Eldridge, pers. comm.). Temperature has a significant and reproducible effect on each of these parameters. However, at constant temperature, the influence of differing egg sizes on these parameters may vary; in particular, jack mackerel incubation time, yolk-sac stage, and time to irreversible starvation did not differ between egg sizes (0.9 versus 1.0 mm), yet size at hatching and growth rates did differ (Theilacker 1980a).

LARVAE

At hatching larvae range from 1.89 mm for lined sole, *Achirus lineatus*, to over 6.0 mm for the plaice, *Pleuronectes platessa*, and herring (Table 1). Larvae show varying degrees of development at hatching, but at yolk absorption, the described larvae have pigmented eyes, open guts, and functional mouths if development occurred within the species' optimal temperature range. Most larvae, with the exception of anchovy and sardine, are capable of feeding before their yolk is completely absorbed. There is evidence that when food is present the yolk is absorbed at a constant rate, but if food is not present the rate of utilization begins to decline (Ryland and Nichols, 1975).

At the time of complete utilization of the yolk reserves, larval survival is dependent upon the larva's ability to find and capture sufficient prey. The amount of time a larva can survive without food, before it is too weak to feed and death is inevitable, has been termed the time to "point of no return" (Blaxter and Hempel, 1963). Days to point of no return (irreversible starvation) are quite similar among described Atlantic species and among described California Current species (Table 1). In general, the Atlantic species have one week to capture a critical number of prey organisms for survival and subsequent development. The California Current and tropical Atlantic species have only 2-5 days until irreversible starvation, but they are generally exposed to higher temperatures than the subject Atlantic species. The time to irreversible starvation has been shown to decrease with increasing temperature (Lasker *et al.*, 1970; Hunter and Kimbrell, 1980).

Survival vs starvation

After the yolk has been absorbed, larvae must eat. The locomotory and perceptual capabilities of the larvae, the density of suitable prey and the behavioural patterns of larvae and prey are the important factors that influence feeding, and thus survival and growth. Delaying larval feeding for one or more days after yolk absorption decreases survival and growth rate. For example, starving northern anchovy for three days after they were capable of feeding decreased survival to age 13 days from 70% (for fed larvae) to 20% (for delayed-fed larvae) and decreased size from 7.1 mm standard length (SL) to 4.6 mm SL respectively. Four days of starvation decreased survival at age 13 days to 6% and size to 3.6 mm SL (Theilacker, unpubl.).

Starved northern anchovy larvae were active during the first day without food but activity decreased thereafter; larvae began to sink, head down, but they exhibited avoidance behaviour throughout the four-day starvation period. As anchovy larvae sink, reduction of activity may reduce risk of predation (Hunter, in press). The larvae may also enter an area of higher food concentration or enter cooler water, thus increasing available calories and/or decreasing metabolic demands, thereby increasing probability of survival for a longer time. At the time of irreversible starvation, Pacific mackerel, unlike anchovy and jack mackerel, continue to swim and eat but they cannot eat enough to survive (Hunter and Kimbrell, 1980).

The onset of starvation in anchovy and mackerel larvae is characterized by changes in the histological characteristics of the pancreas, liver and gut (O'Connell, 1976; Theilacker, 1978). The mackerels require two days of eating to repair tissue damaged by one day of starvation, and they do not grow during this period. The gut is the first tissue degenerated by starvation and apparently the last tissue to be repaired (Theilacker, 1980a).

The number of days to irreversible starvation increases with age. For northern anchovy, time to irreversible starvation from the onset of feeding (when the larvae had no body reserves) was 3-4 days (Table 1); at metamorphosis (when the fat level was 30%, dry weight) it was 15 days. Fat levels declined to about 12% in the 15-day starved metamorphosed fish and recovered to the original levels after 5-8 days of feeding (Hunter, 1976). Results were similar for herring larvae; time to irreversible starvation increased from six days at yolk absorption (6 days of age) to 15 days at 88 days of age (Blaxter and Erlich, 1974).

Swimming modes

The food-searching ability of larvae is a function of their swimming capabilities, activity levels, perceptive distances and their ability to successfully complete the attack sequence on a prey organism.

The dominant swimming mode of larval anchovy is a beat and glide, or intermittent swimming (Hunter, 1972). In contrast, Pacific mackerel (Hunter and Kimbrell, 1980) and jack mackerel beat continuously (Theilacker, unpubl.). Vlymen (1974) has calculated that slow, intermittent swimming is efficient for larval anchovy while Weihs (1974) shows that intermittent swimming is less efficient for mackerels of all sizes. Larval Pacific mackerel swim at more than twice the speed of northern anchovy (.46 versus .2 cm/s; Table 2), owing in part to their differences in swimming mode.. Swimming speeds for 6 mm jack mackerel are intermediate between Pacific mackerel and northern anchovy of the same size (Table 2). O'Connell (in press) suggests that the differences in swimming modes between northern anchovy and Pacific mackerel may be due to anatomical differences. The short post-anal tail (thus short flexure) of anchovy is due to their long digestive tract, and the long post-anal tail (thus long flexure) in mackerel is due to their short, compact digestive tract.

Swimming speed

Voluntary swimming (cruising) speeds for young larvae (Table 2) range between 0.1-0.5 cm/s; sardine, anchovy, sole and plaice are at the low end of the range with mackerel and herring at the high end. Variation in experimental methods has produced widely differing results. For example, in forced swimming experiments (Ryland, 1963) plaice swam about 2 to 7 times faster than during voluntary swimming experiments (Blaxter and Staines, 1971; Table 2). Swimming speeds of young larvae in experimental tanks may be comparable to, or typical of, speeds achieved in the field, but container size probably affects activity of older larvae. In particular, Hunter (pers.comm.) has seen 10 mm northern anchovies swim approximately 1 m in about two seconds (about 50 cm/s) in a large, deep tank (5 m x 10 m). This is much faster than burst speeds over short distances measured in smaller experimental tanks for northern anchovy (e.g., 15 cm/s; Hunter, 1972).

Although voluntary and sustained swimming speeds are needed to determine routine energy expenditures of larval fish, estimates of burst swimming speeds are essential to determine energy required to capture prey and avoid predators. Both burst speeds for northern anchovy larvae and distance travelled per burst (endurance) increased linearly with length (Webb and Carolla, MS; Table 2); for herring larvae the duration of single bursts decreased with length while the number of bursts per minute increased (von Westernhagen and Rosenthal, 1980). Jack mackerel burst speed and endurance is about twice that of anchovy at the same age (Table 2).

Swimming speeds appear to be inversely correlated with prey density. For example, plaice (Wyatt, 1972) and cod (Ellertsen *et al.*, 1980) increased their swimming activity in the absence of food, and northern anchovy, 4-8 days of age, swam at 0.5 cm/s outside a food patch and at 0.3 cm/s inside a patch (Hunter and Thomas, 1974). Thus, swimming speeds are apparently reduced when food organisms are encountered, and the commensurate expenditure of energy due to swimming activity could conceivably be less in high food concentrations. But it may be that within a food patch the combined energy expended in slow swimming plus attacking prey is greater than energy used outside a food patch for faster swimming (see section on Attack modes). Owing to these observed decreases in swimming speed with increasing prey density, extrapolations to calculate volume of water searched and hence prey density requirements from swimming speeds should be made with caution.

Table 2. Activity -- swimming speeds.

Species	°C	Age (d; mm; µg)	Cruising ¹		Burst		Duration of burst or distance traveled per burst	Reference
			cm/s	BL/s	cm/s	BL/s		
<u>Sardine</u> <u>Sardina pilchardus</u>	15-18 "	yolk; 3-5 mm 3 wks.	0.2 0.3					Blaxter & Staines 1971
<u>Herring</u> <u>Clupea harengus</u>	8-12 "	yolk; 6-11 mm 8 wks.	0.4 1.4					Blaxter & Staines ² 1971 Blaxter 1969
				2.3		8-10		
<u>Northern anchovy</u> <u>Engraulis mordax</u>	13 19 13 19 17	3 mm 3 mm 5 mm 5 mm 15 mm	0.1 0.2 0.3 0.5 1.5	.2 .6 .5 .9 1.0				Hunter 1972 Hunter (in press)
" "	17 17 17 17 17	35 mm ² 80 mm 150 mm 8 mm ³ 13 mm ³	3.5 12.0 50.0	1.0 1.5 3.3				Theilacker (unpubl.)
					3 8		8-16 ms 8-16 ms	Hunter 1972
" "	17 17 17	3 mm 8 mm 13 mm			7.3 ⁴ 11.4 ⁴ 15.5 ⁴	24 14 12	1.3 cm/176 ms 3.1 cm/277 ms 5.0 cm/323 ms	Webb & Carolia (MS)
<u>Whitefish</u> ⁵ <u>Coregonus clupeaformis</u>	7-15	15 mm	1.5	1.0				Hoagman 1974
<u>Jack mackerel</u> <u>Trachurus symmetricus</u>	16	6.0-6.5 mm	.36 - .72	0.8 (0.6-1.2)		4-6	2-8 cm; 2 s	Devonald (pers.comm.)
<u>Pacific mackerel</u> <u>Scomber japonicus</u>	19 "	3.6 mm 15.0 mm ²	0.46 5.6	1.3 3.8				Hunter & Kimbrell 1980
<u>Large mouth bass</u> <u>Micropterus salmoides</u>	19	2-7 d; 6-7 mm	3-4 ⁶	4-5				Laurence 1971
<u>Plaice</u> ⁷ <u>Pleuronectes platessa</u>	10-12 " " " "	yolk; 5-7 mm 9-10 mm 5-7 mm 9-10 mm 25 mm	0.2 1.0 1.5 ⁸ 2.2 ⁸ 6.5 ⁸			4-9 ¹ -10 9-15 ¹ -13	9-15 cm 12-36 cm	Blaxter & Staines 1971 Ryland 1963
<u>Sole</u> ⁷ <u>Solea solea</u>	10-12	yolk; 3-5 mm 9-10 mm	0.1 0.7					Blaxter & Staines 1971
<u>Walleye perch</u> ⁹ <u>Stizostedion vitreum vitreum</u>	13 "	7.5 mm 11.0 mm	0.5 3.5	0.6 3.0				Houde 1969
<u>Yellow perch</u> ⁹ <u>Perca flavescens</u>	13 "	7.5 mm 11.0 mm	1.5 3.5	1.8 3.0				Houde 1969

¹ voluntary swimming

² metamorphosis

³ attacking prey

⁴ mean burst speed = 8.18 L + 4.89; maximum distance traveled = 3.79 + 0.08

⁵ no effect of temp. or age

⁶ forced swimming; speed sustained for 30 m

⁷ 90% decrease in activity at metamorphosis

⁸ forced swimming; speed sustained 4-20 s

⁹ forced swimming; speed sustained for 1 h

Attack modes

At the onset of feeding there are two basically different larval feeding behaviours, "S" and "C" postures. To illustrate, as northern anchovy sight prey their sinuous body moves into an "S" posture. Then, using their pectorals to move toward the prey, they straighten their body, driving it forward to capture the prey (Hunter, 1972). "S" posture feeding behaviour is also typical for young larvae of engraulids (bay anchovy, *Anchoa mitchelli*; Houde, 1973); clupeoids (Pacific sardine; Schumann, 1965); herring (Rosenthal and Hempel, 1970); and flatfishes (Jones, 1972). In contrast to the "S" posture behaviour, larvae of Pacific mackerel stop swimming and assume a "C" posture when sighting prey, then they open their mouths and lunge toward prey by driving the tail posteriorly (Hunter and Kimbrell, 1980). This "biting-lunge" technique is also typical for larvae of jack mackerel (Theilacker, unpubl.) and cod (Ellertsen *et al.*, 1980), but cod also appear to expand their oral cavity and suck in prey. Some fishes are more energy-efficient and opportunistic. For example, *Sebastes*, the rockfishes, use the "biting-lunge" technique but are less active and wait for prey to swim nearby (Butler, pers. comm.).

Hunter (in press) stresses two other important differences in feeding between northern anchovy and Pacific mackerel: the first, anchovy strike only once at a food particle and mackerel will move backward and persist in striking until successful. The mackerel's persistent feeding strategy is advantageous because the large prey they prefer to eat are harder to capture and less abundant than the smaller prey eaten by anchovy (Hunter, in press). Larval plaice (Blaxter and Staines, 1971), cod (Ellertsen *et al.*, 1980) and jack mackerel (Devonald, pers. comm.) also have been observed moving backward and repeatedly striking at the same particle.

The second important difference in feeding between northern anchovy and Pacific mackerel is that mackerel are cannibalistic at 10 mm (20 days) and larval anchovy are never piscivorous (Hunter, in press). Sibling cannibalism is considered to be a density-dependent disadvantage of patchy spawning (Hunter, in press; Hewitt, 1980). Neither jack mackerel nor Pacific sardine are cannibalistic in the laboratory; whether this is due to behavioural differences or an inability to physically manoeuvre this sort of prey is unknown.

The difference in manoeuvrability between species probably accounts for differences in their feeding success and habits. Initial feeding success is low for herring, 2-6% (Blaxter and Staines, 1971) and northern anchovy, 10% (Hunter, 1972). Winter flounder (Laurence, 1977), bay anchovy, *Anchoa mitchelli*, lined sole (Houde and Schekter, 1980), and big-eye anchovy, *Anchoa lamproteana*, (Chitty, 1980) also require several days of feeding to establish and improve feeding success. On the other hand, larvae with greater manoeuvrability have relatively high initial feeding success; sea bream *Acanthopagrus rhomboidalis*, (Houde and Schekter, 1980), plaice (Blaxter and Staines, 1971), cod (Ellertsen *et al.*, 1980), Pacific mackerel (Hunter and Kimbrell, 1980), and jack mackerel (Theilacker, 1978) are efficient feeders at the onset of feeding.

For larvae that are ineffective feeders on the first day of feeding, the energy cost of attacking prey must be relatively great. For example, the nutritional condition of first-feeding northern anchovy (determined by histological techniques) was poorer in larvae that had been feeding for one day than in larvae which were starved. Most first feeding northern anchovy larvae were not in a healthy, robust condition until they increased their capture efficiency, usually on the third day of feeding (O'Connell, 1976). On the other hand, the same experimental situation with jack mackerel larvae had opposite results (Theilacker, 1978); fed larvae were always in better histological condition than starved larvae. Thus, jack mackerel are probably more efficient than anchovy at capturing prey on the first and second day of feeding. In addition, yolk reserves in unfed jack mackerel were greater than in fed larvae, again indicating that energy expenditure for non-feeding larvae was less than for feeding larvae (Theilacker, 1978).

Visual Perception

Most larvae are believed to be purely visual feeders. Perceptive distances may depend on prey movement, orientation in relation to the eye, contrast to the background and illumination. Perceptive ranges for herring even depended on their swimming speed; ranges were greater during slow swimming than fast swimming (Rosenthal and Hempel, 1970). At first feeding, movement of prey does not appear to be a criterion for acceptance, as larvae often eat non-motile foods such as copepod eggs. Distance to the prey and prey size probably are the important factors in prey detection. In all larval fish studies, perceptive distance, usually expressed as a function of body length (BL), has been shown to increase with age/size (Hunter, in press). For example, over an eight-week period, the perceptive distance of plaice increased from 3.5 to 5.5 mm, that of pilchard, *Sardina pilchardus*, increased from 1.0 to 2.5 mm, and of herring from 3.5 to 5.0 mm (Blaxter and Staines, 1971). Average perceptive distances summarized by Hunter (in press) are:

	BL	
herring	0.7-1.0	Rosenthal and Hempel 1970
herring	0.4	Blaxter and Staines 1971
plaice	0.5	Blaxter and Staines 1971
pilchard	0.2	Blaxter and Staines 1971
anchovy	0.4	Hunter 1972
whitefish	0.4-0.7	Hoagman 1974

Most fish larvae feed only during the day, but some larvae feed in dim light, and some may feed at night. Houde and Schekter (1980) noted limited feeding of young bay anchovy, lined sole, and sea bream, at 50 mc. Freshwater larval whitefish, *Coregonus alpeaformis*, feed at one mc (Hoagman, 1974), and Smith *et al.* (1978) mentioned four species that feed at night; rockfish, *Sebastes marinus* (Marak, 1974), sole, *Solea solea* (Blaxter, 1969), plaice (Shelbourne, 1953) and yellowtail flounder. Blaxter (1969) found that feeding became reduced in herring at a light intensity range of 10^2 - 10^{-1} mc and in plaice at 10^2 - 10^{-2} mc.

Increased visual sensitivity probably occurs in northern anchovy when rod recruitment begins at about 10-11 mm SL or 20 days of age (O'Connell, in press). Appearance of rods occurs at about the same size in Pacific hake, *Merluccius productus*, (O'Connell, pers. comm.). Thus, older fish may feed at night or in dim light. Indeed, older larvae of plaice were capable of feeding in the dark (Blaxter, 1969). Yet, young Pacific hake (before rod recruitment) and young cod (of unknown rod appearance) feed intensively after sunset (Sumida and Moser, 1980; Ellertsen *et al.*, 1980). The role of bioluminescence should be considered.

Chemical stimuli may be a factor for location of prey by larval fish. For example, herring larvae show increased activity when extracts of *Balanus*, *Artemia* or herring are added to their tank (Dempsey, 1978) and northern anchovy appear to locate dense patches of *Gymnodinium* prior to eye pigmentation (Hunter and Thomas, 1974).

Distribution

Our knowledge of larval distribution in time and space is extremely limited. Diurnal variations in larval distribution are attributed to activity, phototaxis, temperature preference, prey distribution, and current movements. Vertical distribution studies, like most field studies, suffer from the difficulty in determining the importance of net avoidance in sampling. Net avoidance results in fewer larvae collected by day, especially larger larvae; use of high-speed nets appears to decrease avoidance.

Results of vertical distribution studies of two Atlantic species, yellowtail flounder and haddock, show that young larvae may have a different distribution than older larvae. The young larvae of both species did not migrate and remained below a thermal gradient; yellowtail flounder remained at 20-24 m, between the shallow and deep thermal gradients (Smith *et al.*, 1978), and haddock seemed to occur below the thermocline (Miller *et al.*, 1963). Older haddock (8-20 mm) did not migrate and appeared to be more abundant within the limits of the temperature discontinuity layer while older yellowtail flounder (4-10 mm) migrated as much as 15-34 m, crossing two separate 5° C thermal gradients. Ahlstrom (1959), on the other hand, found that the species he studied in the California Current did not move across the thermocline, a gradient of 4-8° C; offshore, larval Pacific mackerel and jack mackerel were observed in the upper 30 m and Pacific sardine and northern anchovy ranged deeper, to 50 m. The range in temperature where the majority of larvae were collected was restricted to 2° C for jack mackerel, 14-16° C; 3° C for northern anchovy and Pacific mackerel, 14-17° C; and 4° C for Pacific sardine, 13-17° C.

Current measurements by Smith *et al.* (1978) seemed to indicate that at night the yellowtail flounder larvae would be caught in the wind-driven surface layers, and during the day, at mid-depth, they would be transported in the opposite direction, resulting in relatively localized settling of the demersal stages.

An adaptive advantage of vertical migration for larval fish would be to accompany the diel migration of prey, and some larvae (Pacific hake, Sumida and Moser, 1980; cod, Ellertsen *et al.*, 1980) do show high post-sunset peaks in feeding incidence. But Smith *et al.* (1978) analyzed larval stomach contents and concluded that the daily movements of yellowtail flounder were not related to feeding.

Vertical migration may be an energy saving device. Northern anchovy (11 mm SL) that are below 10 m during the day migrate to the surface at night to fill their swim bladders; for larvae 13.5 mm and larger, the energy saved by using the swim bladder to maintain position in the water column at night exceeds the energy used to migrate to the surface (Hunter and Sanchez, 1976). Another advantage of these nightly migrations may be that they concentrate young larvae at the surface, thus increasing visual contacts that may facilitate schooling behaviour which begins at about 12 mm SL (Hewitt, 1980; Hunter, in press).

PREY

Size

The dimensions of prey organisms relative to larval fish mouth size are important variables which require consideration in any modelling effort. The size (usually measured at maximum width) of the prey eaten by fish larvae is a function of larval mouth width; within species mouth width is related to length, but mouth widths vary between species (Arthur, 1976; Beyer, 1980; Hunter and Kimbrell, 1980; Hunter, in press). For example, mouth width of northern anchovy and Pacific mackerel at first feeding is approximately the same size, 0.20 mm. But, between 5-15 mm SL, mouth width of Pacific mackerel rapidly increases in size; northern anchovy mouth also increases in size with age, yet at the same SL, northern anchovy mouth width averages about 30 percent smaller than Pacific mackerel width (Hunter, in press).

Although mouth width limits the maximum prey size, in nature fish larvae often do not eat maximum size prey. For example, at 14 mm Pacific mackerel have a mouth width of 1 mm; particles up to 0.8 mm are found in their guts, but the mean diameter of prey eaten by larvae in the sea was only 38 percent of their mouth width (i.e. 0.34 mm, Hunter and Kimbrell, 1980). Anchovy at the same standard length have a mouth width of 0.7 mm, and the maximum size prey observed in anchovy guts was 0.3 mm (Arthur, 1956; de Ciechomsky, 1967). Deviations are greater for hake larvae. Mouth width of 5 mm Pacific hake is 0.6 mm, and the mean width of prey eaten was about 0.08 mm, 13 percent of hake-mouth width (Sumida and Moser, 1980). Beyer's (1980) model of feeding success of clupeid fish larvae shows why optimum prey size, that allows the highest feeding success, is less than the maximum potential prey size determined from mouth measurements. However, there is a tendency for larvae in the sea to feed on progressively larger prey as they grow (Marak, 1960; Shelbourne, 1953; Rojas de Mendiola, 1974; Arthur, 1956). Furthermore, the dynamic population model of Jones and Hall (1974) postulates that cohorts of cod and haddock larvae must be spawned in the proper time to grow up with a cohort of their copepod prey (*Calanus* sp.).

In the laboratory it was found that size of prey fed to larvae must increase for larvae to grow at maximum rates. Small food particles (*Gymnodinium*; Table 3) sustained northern anchovy for more than two weeks, but growth was reduced (Lasker *et al.*, 1970). Feeding northern anchovy a larger particle (*Brachionus*) increased the growth rate (Theilacker and McMaster, 1971), however copepods were soon required for anchovy to attain maximum growth and survival through metamorphosis in the laboratory (Hunter, 1976). Hunter and Kimbrell (1980) described a similar increase in required particle size for rearing Pacific mackerel, as has Stepien (1976) for sea bream, Ware *et al.* (1980) for the anchoveta, *Engraulis ringens*, Jones *et al.* (1974) for turbot, *Scophthalmus maximus*, and Houde (1978) for three species of sub-tropical marine fish.

It should be stressed that both large- and small-mouth larvae eat small, more ubiquitous prey and that it is possible that fish larvae can eat enough small prey to meet metabolic demands for several days. This is the case with larval jack mackerel in the laboratory. Jack mackerel (large-mouth larvae) fed *Gymnodinium* from the onset of feeding (day 5) to age 12 days were the same size and as "healthy" (determined by histological assessment) as larvae eating *Gymnodinium*, *Brachionus* and copepods (Theilacker, unpubl.). However, northern anchovy fed on a *Gymnodinium* diet grew at maximum rate for three days only (Lasker *et al.*, 1970).

Beyer and Laurence (1980) conclude from their model of growth and mortality of larval herring that as larva reach certain sizes the energetic cost of each attack exceeds the gain from ingesting smaller food particles; this size depends upon the larva's metabolic requirements, which are both genetically and environmentally imposed.

Table 3. Prey size and caloric content.

Particle	Width (μ m)	Dry wt. (μ g)	Calories	Reference
<u>Gymnodinium splendens</u> naked dinoflagellate	50	-	0.00005	Hunter 1977
<u>Brachionus plicatilis</u> rotifer	133	0.16	.00085	Theilacker and McMaster 1971
Copepods ¹ nauplii	200	0.80	.0042	Laurence 1977
nauplii	250	1.30	.0068	"
copepodid	600	15.40	.0809	"
nauplii		0.15		Houde and Schekter 1980
<u>Artemia</u> nauplii	236		.0096	Hunter 1977

¹ Copepod weight and fat varies seasonally causing caloric variations.

Selection

There is evidence for selection by food type. Gut analyses indicate that field-collected jack mackerel less than 10 days of age may select brightly coloured harpacticoid copepods (*Microsetella*, *Oncaea*, *Corycaeus*) (Arthur, 1976), and laboratory-reared jack mackerel may be unable to catch or may reject *Labidocera* nauplii in favour of *Acartia* and *Paracalanus* (Devonald, pers. comm.). Although naupliar body size, .06-.09 mm diameter, of *Labidocera* and *Acartia* is similar, *Labidocera*'s appendages are 2-3 times longer than *Acartia*'s appendages; hence, *Labidocera* nauplii may be too large to ingest, or, owing to larger appendages, simply too fast to catch. However, most evidence points to selection related to particle size (Stepien, 1976; Uotani *et al.*, 1978; Hunter, in press). It is reasonable that larval fish exhibit little selectivity for food type; if food particles are rejected, selectivity costs energy. Something must be gained by being selective; selection of large food particles offers a gain, i.e. more calories ingested per energy expended (as particle diameter increases 2.5 times, calories increase by a factor of 10; Hunter, in press; Table 3). In the field, large-mouth larval Pacific hake, 3-8 mm contained large numbers of small organisms; however the large adult copepods that they ate accounted for 74 percent of the volume (hence, 74 percent of the calories) of food eaten (see table below, from Sumida and Moser, 1980).

	Range max.width (μm)	Mean food volume ($10^6 \mu\text{m}^3$)	Standard deviation ($10^6 \mu\text{m}^3$)	Frequency	Frequency x volume ($10^9 \mu\text{m}^3$)	% of total volume
Copepod eggs	50-100	0.364	0.083	674	0.24534	0.7
Copepod nauplii	40-300	4.013	5.148	441	1.76973	5.3
Copepodites	80-450	14.698	24.308	393	5.77631	17.4
Adult copepods	110-600	57.418	54.850	426	24.46007	73.8
Other	40-550	49.401	107.783	18	0.88922	2.7
					$\Sigma = 33.14067$	

Density

Critical prey density, the food concentration required for first-feeding larvae to initiate feeding, is a component of larval survival which has caused great controversy among scientists involved with larval fish research. Laboratory experiments to date have usually been done with somewhat uniform and high concentrations of prey and a relatively high density of larvae. Prior to 1970, threshold food-density experiments in the laboratory were considered "successful" when there was high survival and fast growth of larvae. Fishery biologists accepted that field-mortality rates in excess of 90 percent during the egg and larval stages produced healthy year-classes, but in the laboratory biologists demanded high survival rates. The critical prey densities determined by these experiments were higher than densities measured in the integrated natural larval habitats. Lowest survival rates in laboratory feeding experiments (Table 4) were usually at particle densities reported to be common in the field (Table 5); thus, these experiments may represent levels characteristic to the field. Houde's (1974; 1978) work on three species of subtropical fish reported significant survival at low prey densities; sea bream required 50 plankters/l and lined sole required 100/l (Table 4). These food levels are common in coastal and partly enclosed areas (Table 5; from Hunter, in press, and Houde, 1978).

Critical prey densities determined in the laboratory and presented in Table 4 are constant prey concentrations required for optimum survival from first feeding to 2-7 weeks of age (with the exception of the herring experiment that was conducted with older larvae). These densities vary among species and will also vary with life stages within species. For example, Laurence (1977) showed that the initial required prey density for winter flounder to meet metabolic requirements (including growth) was 800 nauplii/l; after successful feeding behaviour was established, the critical density decreased to 300 nauplii/l. Then as growth and metabolic demands increased, critical density increased to 600 nauplii/l. Laurence also showed that at the onset of feeding, winter flounder started feeding at 10 and 100 nauplii/l but did not survive longer than two weeks. Thus, threshold densities for first feeding (Table 4) are not indicative of particle concentrations required for survival during all life stages.

Laboratory experiments reveal that variations in prey density affect larval fish feeding rates, ration, activity, evacuation time, growth rates (time to metamorphosis), and gross growth efficiencies (Werner and Blaxter, 1980; Houde and Schekter, 1980; Wyatt, 1972; Laurence, 1977; Hunter and Thomas, 1974). Generally, as prey density increases, feeding rates, ration and growth rates increase (Table 6); gross growth efficiencies may increase or decrease (Table 9) and activity, evacuation time (Table 10) and time to metamorphosis decrease. Due to differences in experimental technique, comparisons of studies that depend on controlled prey levels need some qualifications. These restrictions are discussed in the final section of this review, wherein laboratory techniques and facilities for obtaining relevant physiological data are described, and comparative observations are tabled.

Table 4. Food density thresholds for 8 species of marine fish larvae

Species and common name	Container volume (liters)	Duration (days)	Food type	Stock density No./L	Survival at various food densities		Reference
					Density No./L	Percent survival	
PLAICE <u>Pleuronectes platessa</u> s	5	14	<u>Artemia</u> nauplii	50 (larvae)	1,000 500 200 100	72 ¹ 72 54 32	Wyatt 1972
NORTHERN ANCHOVY <u>Engraulis mordax</u> s	10.8	12	Wild zoo- plankton (nauplii)	10 (eggs)	4,000 900 90 9	51 12 0.5 0	O'Connell & Raymond 1970
BAY ANCHOVY <u>Anchoa mitchilli</u> s	76	16	Wild zoo- plankton (nauplii- copepodites) ³	0.5 - 2 (eggs)	5,000 1,000 100 50	64 48 5 0-12	Houde 1978
SEA BREAM <u>Archosargus rhomboidalis</u> s	76	16	"	0.5 - 2 (eggs)	500 100 50 25 10	72 37 13 7 4	" "
LINED SOLE <u>Achirus lineatus</u> s	38	16	"	0.5 - 2 (eggs)	1,000 100 50	54 13 1	" "
HADDOCK <u>Melanogrammus aeglefinus</u> s	37.8	42	Wild zoo- plankton (nauplii)	9 ⁴ (larvae)	3,000 1,000 500 100 10	39 22 3 0 0	Laurence 1974
HERRING <u>Clupea harengus</u>	20	21-63 58-84	<u>Artemia</u>	8	3,000 1,000 300 100 30	4-8 3-12 0-8 0-12 0-1	Werner & Blaxter 1980
WINTER FLOUNDER <u>Pseudopleuronectes americanus</u>	64	49	Wild zoo- plankton (nauplii)	9 ⁴ (larvae)	3,000 1,000 500 100 10	34 4 3 1 0	Laurence 1977

¹ Survival was 100% at 50/L for first 7 days without a decrement in length; see also Riley (1966).

² Estimated food density for indicated survival levels.

³ Plankton blooms of *Chlorella* sp. and *Anacystis* sp. maintained in rearing tanks.

⁴ Estimated by adjusting for hatching success.

s Hunter, in press.

Table 5. Average¹ densities of microcopepods in the sea

	Average density of microcopepods (number per liter)			Location	Reference
	nauplii	copepodites	total		
OPEN SEA	13	2	15	Southeast Coast of Kyushu	Yokota <u>et al.</u> 1961
	22	36	58 ²	California Current	Beers and Stewart 1967
	40	5	45 ²	Southern California near shore	Beers and Stewart 1970
	27	7	34 ³	Eastern Tropical Pacific	Beers and Stewart 1971
	36	1	37	California Current	Arthur 1977
PARTLY CLOSED	76	19	95	Azov Sea	Duka 1969
	-	-	223 ⁴	Gulf of Taganrog	Mikhman 1969
	40	-	40	North Sea (0-10 m)	Ellertsen <u>et al.</u> 1980
	20-30	-	25	North Sea (10-20 m)	"

¹ Mean for all stations and years given in publication listed in table (Hunter, in press).

² Includes all copepods passing 202 μ m mesh net.

³ Includes all copepods passing 202 μ m mesh net and caught on 35 μ m mesh.

⁴ Defined as food of Clupeonella delicatula; microcopepods account for over 90% of items eaten (Mikhman 1969).

Reported concentrations of some potential larval fish food organisms from coastal and estuarine areas.
(Table 10 from Houde 1978)

Reference	Place	Organisms	Concentration
Burdick (1969, cited in May, 1974)	Kaneohe Bay, Hawaii	copepod nauplii	50-100/l common 200/l sometimes present
Duka (1969)	Sea of Azov	<u>Acartia clausi</u> nauplii Other copepod nauplii and copepodids Total	62-65/l > 30/l > 90/l
Mikhman (1969)	Gulf of Taganrog, Sea of Azov	Early stages of copepoda	39-546/l
Hargrave and Green (1970)	Two eastern Canada estuaries	Copepod nauplii and copepodids	> 60/l
Reeve and Cosper (1973)	Card Sound, South Florida	Copepod stages 20-200 μ m in breadth Tintinnids	range 23-209/l mean for 28 collections 72/l range 40-369/l
Heinle and Flemer (1975)	Patuxent River estuary	<u>Eurytemora affinis</u> nauplii & copepodids	>100/l frequently >2,000/l occasionally
Houde (unpublished data)	Biscayne Bay, South Florida	Copepod nauplii and copepodids <100 μ m in breadth Tintinnids	usually 50-100/l frequently >100/l

Table 6. Feeding rates at various prey concentration.

Species	°C	Age (d; mm; µg)	Container volume (liters)	Prey type	Prey con- centration (#/l)	Feeding rate (#/h)	% body wt. eaten per day	Reference
YOUNG LARVAE								
Pacific sardine <i>Sardinops sagax</i>	16	first-feeding 15-17 mm	500	nauplii ¹ <i>Artemia</i>	max. max.	2 60 ²		Schumann 1965
Northern anchovy ³ <i>Engraulis mordax</i>	17	4 d; 20 µg 10 d; 70 µg	500	Rotifer ⁴	10,000- 20,000	15.0 46.0	144 126	Hunter 1972
Bigeye anchovy ⁶ <i>Anchoa mitchilli</i>	26	2 d; 3.6 mm 8 d; 5.5 mm	9.5	nauplii ¹⁻⁵	100	43.0 70.0	440 197	Chitty 1980
Bay anchovy ⁶ <i>Anchoa mitchilli</i>	26-28	4 d; 4.8 µg 4 d; 13.4 µg 4 d; 17.4 µg	76	nauplii ¹⁻⁵	50 100 1000	0.5 2.4 19.3	20 39 221	Houde & Schekter 1980
Sea bream ⁶ <i>Archosargus rhomboidalis</i>	26-28	4 d; 13 µg 4 d; 12.7 µg 4 d; 18.2 µg	76	nauplii ¹⁻⁵	50 100 1000	0.9 1.3 9.0	21 28 158	Houde & Schekter 1980
" "	23-26 29	2-3 d 2-3 d	75	nauplii ¹⁻⁵	1000	8.0 18.0	199	Stepien 1976
" "	23 26-29	16 d 16 d	75	nauplii ¹⁻⁵	1000	54.0 150.0		"
Pacific mackerel <i>Scomber japonicus</i>	19	3 d; 38 µg 4 d; 43 µg 5 d; 85 µg	200	Rotifers ⁴	157,000 47,000 198,000	14 20 45	70 89 102	Hunter and Kimbrell 1980
Striped knifejaw ⁷ <i>Oplegnathus fasciatus</i>	22	7 d 3.9 mm 13 d; 5.2 mm	-	Rotifers	5,000	6 44		Fukusho 1979
Lined sole ⁶ <i>Achirus lineatus</i>	26-28	4 d; 8.7 µg 4 d; 11.4 µg 4 d; 13.5 µg	76	nauplii ¹⁻⁵	50 100 1000	0.2 1.1 12.0	6 21 80	Houde & Schekter 1980
Plaice <i>Pleuronectes platessa</i>	7			Rotifers		35		Howell 1973
OLDER LARVAE								
Herring ⁶ <i>Clupea harengus</i>	9	4 wks.	20	<i>Artemia</i>	30 100 300 1000 3000	5 4.5 4 6 5		Werner and Blaxter 1980
" "	9	5 wks.	20	<i>Artemia</i>	30 100 300 1000 3000	6 6 8 8 7		"
Winter flounder <i>Pseudopleuronectes americanus</i>	8	2 wks.	64	nauplii ¹	100 500 1000 3000	1 2 1 2		Laurence 1977
" "	8	5 wks.	64		100 500 1000 3000	11 19 25 23		"

¹ Wild plankton - copepod nauplii

² 3.5 strikes/min for 10 min until gut full; then 1/min

³ estimated from number strikes and adjusted for percent successful capture

⁴ dry wt = 0.16 µg (fresh material)

⁵ dry wt = 0.15 µg (fresh material)

⁶ larval dry wts determined for preserved samples

⁷ hatch at 2.2 mm; gut length intermediate between Pacific mackerel and jack mackerel; growth rate begins at 0.2 mm/d and increases to 0.5 mm/d (similar to anchovy, Table 2).

Houde and Schekter (1980) compared feeding rates, ration and growth among three marine fish, bay anchovy, sea bream and lined sole, fed at several low but constant prey concentrations (Table 6). Feeding rates of the three species increased with increasing prey density; however, at the onset of feeding, the sea bream, a sparid, was more effective at capturing prey at the lowest density, 50 prey/l, than anchovy or sole. But, anchovy had the highest feeding capability at 50 and 100 prey/l after the first few feeding days when anchovy had increased their prey-capturing efficiency. Sea bream had the best potential to increase growth rates at higher food levels, 500-1 000/l, and were capable of higher survival at low prey densities, 100/l (37 percent survival) than anchovy or sole (5-13 percent survival; Table 4). Thus, although ration increased with increasing prey density, the feeding abilities of these three species, that differ in morphology and behaviour, varied at the different prey densities.

Feeding rates of older herring larvae (Werner and Blaxter, 1980) and older winter flounder (Laurence, 1977) fed at several prey levels also increased with increasing prey density until a maximum ration was achieved. This maximum ration was achieved in both cases at 1 000 prey/l. Growth rates within species were the same at prey densities from 300 to 3 000 prey/l, but were significantly less at 100/l. Laurence (1977) found that survival of winter flounder increased with increasing prey levels, but Werner and Blaxter (1980) did not find this with herring larvae. Perhaps, suitability of prey type was a factor affecting survival; winter flounder were eating copepods, a natural prey, and herring were eating *Artemia*.

In addition to depending on prey density, feeding rates also depend on life stage and temperature. A 3-6°C increase in temperature may triple feeding rates (Stepien, 1976), and a 5-6 day increase in age of young larvae raises feeding rate 2-7 times (Table 6).

At high prey densities of *Artemia* nauplii (5 000/l), herring larvae exhibited reduced ingestion of the prey; furthermore, the prey were evacuated faster from the stomach and were not completely digested or assimilated (Werner and Blaxter, 1980). Houde and Schekter (1980) also recorded a decrease in gross growth efficiency at the highest prey concentrations for the three species they tested (Table 9).

Distribution

One of the major questions arising from the evaluation of laboratory feeding experiments, such as those mentioned in the preceding sections, is where areas exist in the field with the necessary concentrations of esculent food for larval fish. The sampling gear most often employed (pumps and plankton nets) sample large volumes of water and gives results that average numbers of organisms over depths or distances. Despite these sampling difficulties, Lasker (1975) found natural occurrences of the high prey densities (20 000-40 000/ml) that are needed by northern anchovy to initiate feeding. The prey particles, a dinoflagellate, *Gymnodinium splendens*, occurred in water taken from the chlorophyll maximum layer. Similar bioassay experiments with cod larvae showed feeding at 30-40 nauplii/l. The maximum naupliar biomass was found at 0-15 m and 60-80 percent of the larvae sampled from these depths had 2-3 nauplii in their guts (Ellertson *et al.*, 1980). Owens (this volume), and Mackas (1976) have attempted to apply more sensitive and discrete sampling techniques. They have found micro-stratification of esculent food particles in appropriate numbers to support larval fish survival. Further use of these techniques should lead to more information on prey distribution on the scale relevant to a larval fish.

Vlymen (1977) used an empirically based mathematical model to demonstrate the importance of food microstructure (geometry) and behaviour, and how they affect growth of northern anchovy larvae. He found that the critical habitat of an anchovy larva should contain between 14 and 32 particles/ml. Within this range the numbers represent a structured environment with 14 particles/ml in the interpatch areas and 32 particles/ml in the critically dense regions of contagion.

Lasker and Zweifel (1978), using a modified version of Vlymen's model (1977) for northern anchovy larval growth, determined that "it is not the absolute concentration of the large particles that govern their capture by the larva, but rather their concentration relative to the larger number of small particles in the larval environment." In this simulation, large particles made very little contribution to survival when the immediate environment of the first-feeding larva contained 40 small particles/ml. Because it is more likely that there will be aggregations of small particles than large ones, survival of first-feeding larvae would be enhanced by a favourable number of patches of that density within their habitat.

In the laboratory, it has been shown that larval survival is increased by exposure to a food patch; however, larval behaviour to patch situations differ. Houde and Schekter (1978) found that during a 13 hour feeding day a short, 2-3 hour patch exposure increased survival of larval sea bream from 7.5 percent (on day 16) to 20 or 30 percent. On the other hand, bay anchovy larvae needed a 9 hour exposure for 10 percent survival. Thus, larval sea bream appear to be more capable of taking advantage of periodic patch conditions than bay anchovy.

LARVAL MODEL PARAMETERS AND REQUISITE LABORATORY RESEARCH

Existing larval survival models were developed from basic energetic principles based on laboratory and field studies. These models consist of conjectures concerning the manner in which excess energy (i.e. the difference between the energy expended in capturing and processing food and energy gained) results in growth and/or survival. Thus, basic physiological data are the bases for the models. In spite of the sophisticated mathematics of the models, the results can be worthless if the physiological data is gathered through inaccurate or biasing techniques. This discussion describes some parameters used in models and the techniques used to measure these parameters.

Rearing containers

Container size may be a critical variable in larval fish studies. Size of container affected results in jack mackerel rearing experiments; larvae grew faster and were in better nutritional condition in 100 l than in 10 l containers (Theilacker, 1980c). Size of container also affects swimming speed. For example, swimming speed of laboratory-held larval herring was less than *in situ* contained herring—0.9 cm as compared to 1.59 cm (von Westernhagen and Rosenthal, 1980). Likewise, northern anchovy swim 3-4 times faster in large than in small containers (Hunter, pers. comm.; see Swimming speed).

Metabolic rates

The sensitivity of the techniques used to determine oxygen consumption is limited by experimental container volume. Volumes need to be small in the case where oxygen consumption rates are low and very small total changes are expected; hence fish larvae are definitely confined and movement is probably restricted. Experimentalists that use Warburg (10 ml) or Winkler (40-60 ml) techniques (Table 7) usually assume that the respiration estimates are somewhere between "resting" and "active". Vlymen (1974), in his estimate of swimming energetics of northern anchovy, suggested that activity in the confines of a small container would be inhibited and below natural levels. However, it has been shown that average respiration rates (determined by Warburg) of groups of early stage Pacific sardine eggs were the same as rates determined for single, late stage eggs housing "active" larvae (Lasker and Theilacker, 1962). Because fish eggs probably are not affected by restrictive containers, this observations shows that shaking Warburg flasks, required to equilibrate oxygen between water and air, may induce "active" metabolism.

Variation in "resting" (standard) metabolic rates among poikilotherm species can sometimes be explained by differences in experimental temperature. The temperature coefficient of respiration (Q_{10} , a measure of the increase in rate of an activity for a 10°C temperature difference) is typically about 2-4 (Giese, 1962). The Q_{10} of respiration for Pacific mackerel (at unknown activity) between 18° and 22°C is about 5 (Table 7). But, differences in metabolic rates between anchovy and mackerel (Table 7) cannot be explained by differences in temperature and must be caused by differences in activity and metabolic demands. Hence, knowledge of activity is needed to make meaningful comparisons of metabolic rates among species. Activity has been shown to increase respiration rates up to 3.5 times for Pacific sardine larvae (Lasker and Theilacker, 1962) and 5-10 times for larval herring (Holliday *et al.*, 1964).

Because activity increases respiration rates, extrapolations of laboratory-determined respiration rates to the field conditions are difficult due to our inability to accurately measure activity in the field. Ware (1975) suggests using a value of 2.5 times "standard" ("resting") metabolic rate to estimate "active" field metabolism. However one value will not likely account for interspecific differences in metabolic demands, i.e. such as differences in activity at first feeding of "beat" and "glide" swimmers like Pacific sardine and

Table 7. Respiration rates.

Species	°C	Age (d; mm; µg)	ul/mg/hr						Reference	
			Egg			Larva				
			Rest- ing	Activity unknown	Act- ive	Rest- ing	Activity unknown	Act- ive		
Pacific sardine ¹ <u>Sardinops sagax</u>	14	-	0.8		1.8		1.3		2.7	Lasker and Theilacker 1962
Northern anchovy ^{2 3} <u>Engraulis mordax</u>	17			1-1.5						Theilacker (unpubl.)
	17	1-3 d					3.5			
	17	4-30 d ⁴					4.1(3.1-6.9)			
	17	15 mm; 30 d ⁵					6.7			
Herring <u>Clupea harengus</u>	8	1-10 d					2.3		10-23	Holliday <u>et al.</u> 1964
Pacific mackerel ^{1 3 6} <u>Scomber japonicus</u>	18	3.7-17.9 mm 3.2-10.5 mm						5.1 11.4		Hunter and Kimbrell 1980
Rockfish ⁶ <u>Sebastes rhodochloris</u>	11	Late		1.8						Moser 1967
<u>Sebastes eos</u>	11	Late		2.0						
Winter flounder ⁶ <u>Pseudopleuronectes americanus</u>	5	7 d; 12 µg						5.5 ⁷		Laurence 1975
	5	7 wk; 250 µg						4.8 ⁷		
	5	7 d; 12 µg						6.0 ⁸ (2.8-8.8)		
	5	7 wk; 250 µg						6.5 ⁸ (3.4-9.7)		
Pollock ³ <u>Theragra chalcogramma</u>	4	11-14 d; 90-120 µg					1.4- 3.0			Clarke (pers. comm.)
Striped bass ⁶ <u>Morone saxatilis</u>	18	0 d 5 d 10 d 15 d		7.5				5.4 ⁷ 4.6 4.2		Eldridge (pers. comm.)

¹ determined for individual eggs and larvae

² Winklers; 40-60 ml

³ weight-specific rates; slope = 1

⁴ N = 43

⁵ 230 ml, no agitation; n = 2

⁶ Warburgs; <10 ml

⁷ weight-specific rates decreased; these rates taken from weight-specific metabolism regression

⁸ median rates taken from actual data points and range

northern anchovy that rest 50-60 percent of the time (Schumann, 1965; Hunter, 1972) and the continuous swimming Pacific mackerel and jack mackerel (Hunter and Kimbrell, 1980; Theilacker, unpubl.). These species-specific behaviours point to large differences in required calories at the onset of feeding.

Growth

A comparison of laboratory growth of the California Current species illustrates species-specific differences in growth rates (Figure 1; Table 8). At similar temperatures, Pacific mackerel reach metamorphosis twice as fast as Pacific sardine and northern anchovy. Sardine and anchovy reach metamorphosis at about the same size, but initially larval sardines grow faster than larval anchovies, hence sardines reach metamorphosis at an earlier age. Growth rates of larval jack mackerel are slow; although jack mackerel transform at the same size and probably similar weight as Pacific mackerel, metamorphosis occurs about two weeks later than in Pacific mackerel. Zweifel and Lasker (1976) have shown that the Laird-Gompertz growth function may be used to define the genetically determined and dynamically changing growth rates in the early life stages of many fish.

Measuring changes in length is convenient for estimating growth, but it has been shown that shrinkage in length of laboratory-preserved larvae differs from shrinkage of field-collected larvae (Theilacker, 1980b); hence, to compare animals at the same developmental stage there is a need to intercalibrate laboratory and field measurements. For northern anchovy larvae, difference in shrinkage between laboratory-preserved larvae (pipetted directly into Formalin) and netted and preserved larvae (simulated field-collected) of the same initial size decreased with age. For example, 3 mm larvae that were netted and preserved in Formalin shrank 15 percent more than 3 mm larvae that were laboratory preserved, but shrinkage of 20 mm larvae was the same for both treatments (Theilacker, 1980b). Thus, for estimates of larval growth, shrinkage calibration is important for small larvae. Shrinkage appears to be species specific; shrinkage of body parts is not the same among larvae with similar body forms (e.g. compare mackerels in table below).

	Laboratory formalin			10 min. net treatment			Formalin preservation after net treatment		
	SL	HL	BD	SL	HL	BD	SL	HL	BD
Northern anchovy	.92	.91	.90	.81	.91	.70	.78	.88	.67
Jack mackerel	.92	.91	.80	.90	.91	.84	.87	.88	.81
Pacific mackerel	.92	--	--	.90	.90	.98	.86	.86	.94

Ratio = treated size/live size; 1.00 = no shrinkage

-- = no data

SL = standard length; HL = head length; BD = body depth measured at anus

A better estimate of growth than the change in larval length is the change in dry weight. Measuring changes in dry weight allows estimates of energy incorporated during growth and is more suitable for interspecific comparisons of growth. For example, at 20 days of age, northern anchovy raised at 17°C and Pacific mackerel raised at 16.8°C are about the same length, 10 mm SL, but their weights differ by a factor of 6, anchovy weigh 0.3 mg and mackerel 1.9 mg (Hunter, in press). Thus, feeding of Pacific mackerel during this 2-3 week period must be more intense and/or the size of the food eaten must be greater (hence more calories/food item) than food eaten by northern anchovy.

Table 8. Growth.

Species	°C	Growth rate (mm/d)				Reference	Metamorphosis		Reference	1 year	
		Days					Size (mm SL)	Age (days)		Size (mm SL)	Reference
		4-15 ¹	16-30	31-40	41-50						
Pacific sardine, <u>Sardinops sagax</u>	16-19	1.0	0.5	0.5	0.5	(4)	31-35	45-50	(4) (8)	120	(8)
Northern anchovy, <u>Engraulis mordax</u>	17	0.2	0.5	0.5	0.5	(5)	34-40	50-60 90	(9) (11)	95-115 ²	(11)
Jack mackerel ³ , <u>Trachurus symmetricus</u>	15	0.1	0.2	0.5	1.0	(6)	11-16	40	(10)	200	(12)
Pacific mackerel, <u>Scomber japonicus</u>	16.8	0.1	1.0	-	-	(7)	15	25	(7)	272	(13)

¹ Hatching = day 0

² Size at 1 year = 115 mm at low anchovy biomass; high-biomass size = 95 mm

³ Large-egg larvae

⁴ Kimura 1970

⁵ Kramer and Zweifel 1970

⁶ Theilacker 1978

⁷ Hunter and Krimbrell 1980

⁸ Ahlstrom 1966

⁹ Hunter 1976; lab

¹⁰ Ahlstrom and Ball 1954; Theilacker (unpubl.)

¹¹ Methot (pers. comm.); field, age estimated from daily otolith increments

¹² Wine and Knaggs 1975

¹³ Knaggs and Parrish 1973

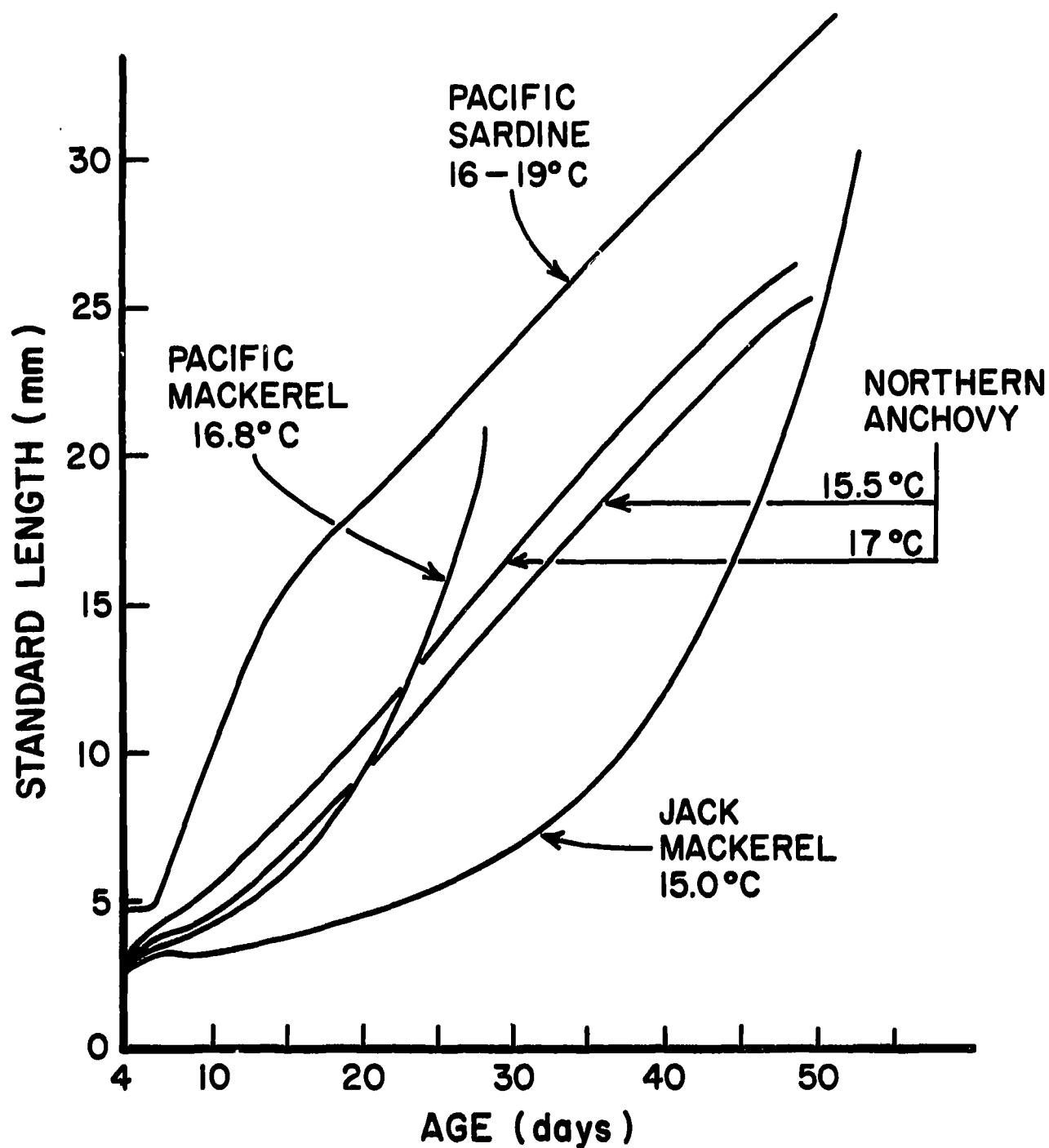


Figure 1.

LABORATORY REARED FISH

It is important that dry weights be determined with fresh samples. Formalin preservation caused a 30 percent decrease in dry weight of larval sardines, and preservation in ethyl alcohol decreased dry weights of Pacific mackerel by 50 percent (30-80 percent) (Theilacker, unpubl.). These determinations were for young, 4-6 mm SL larvae. Methot (pers. comm.) weighed field-collected, alcohol-preserved anchovy to determine weight at age, estimated by increase in otolith increments. His weights for 15-30 mm SL larvae were 30-40 percent less than the fresh dry weights determined by Hunter (1977). Thus, weight loss in alcohol preservative does not appear to decrease with increasing larval size.

Laurence (1978) measured unpreserved dry weights for seven species of larval fish common to the American east coast. He presented his data as linear regressions, $\log_{10}$ weight on $\log_{10}$ length. The species were from different taxonomic families (Clupeidae, Gadidae, Sparidae, Bothidae and Pleuronectidae) but there were no obvious species-specific correlations with the length-weight regressions. The length exponents ranged between 3.78-4.77 and averaged 4.15, thus weight was proportional to length to the fourth power. Length-weight relations for northern anchovy and Pacific mackerel are curvilinear (Hunter, 1976; Hunter and Kimbrell, 1980), therefore extrapolations of linear regressions of length-weight measurements are probably inappropriate.

Prey density

Because variations in prey density affect larval fish feeding rates, ration, activity, evacuation time, growth rates, and gross growth efficiencies, accurate estimates of prey levels are needed for comparisons of experimental results. Many young larvae are delicate, and extremely susceptible to mechanical injury; thus, experimental rearing containers are not mixed to randomize prey distribution until larvae are older. As a result, in experiments that control prey levels, the effective density available to larvae must vary; at low prey levels, food patches may form and thereby elevate the actual density of food encountered by some larvae. In addition, some larval rearing techniques include use of high algal concentrations ("green" water) in rearing containers with invertebrate prey and fish larvae (Stepien, 1976; Houde and Schekter, 1980). In these experiments, it is difficult to assess whether consumed algae directly provided calories to fish in addition to the prey calories; this is particularly important at low prey levels. Inter-experimental comparisons of life functions that may be affected by prey concentration and media differences (i.e. algal content) are difficult and lead to uncertainties regarding their general comparability.

Growth efficiencies

Because it is presently impossible to accurately measure metabolic rates during various swimming and feeding behaviours and to describe behaviour and activity in the field, a comparison of interspecific growth efficiencies may elucidate those species that maximize their growth relative to others in similar environments and feeding regimes. A high growth efficiency (calories of growth/calories consumed) indicates efficient assimilation of food energy for growth, with little being lost by excretion or used in respiration, thus conservative expenditure of energy for swimming and feeding. Calories of growth can be estimated from daily increases in dry weight, and calories consumed can be estimated from the daily ration. Meaningful estimates of growth calories depend on whether energy expenditure for swimming and feeding is the same in the laboratory and the field. Laboratory and field age-length measurements are also needed.

Procedures used to estimate ration (calories consumed) for larval fish vary. Ration has been estimated by (1) feeding rate x weight of prey x hours feeding (Houde and Schekter, 1980; Stepien, 1976), (2) weight of stomach at capture x hours feeding/hours to clear gut (Laurence, 1977), or (3) weight of mean stomach contents x gastric evacuation rate x hours feeding + weight of mean stomach contents (Hunter and Kimbrell, 1980). Daily ration estimates in percent of body weight eaten per day range from 70-300 percent for larvae fed 1 000 or more prey/l (Table 9).

Table 9. Gross growth efficiencies.

	°C	Age (d; µg)	Prey density (#/L)	Container volume (liters)	Daily ration		Gross efficiency (%)	Reference
					ug	% body wt.		
Bay anchovy ¹ <u>Anchoa mitchilli</u>	26	17 d; 200 µg	50	10	19	31	57	Houde & Schekter 1980
	"	15 d; 200 µg	100		37	51	32	
	"	11 d; 200 µg	1000 nauplii (wild plankton)		115	140	14	
Herring <u>Clupea harengus pallasii</u>	-	12-22 d; 100-150 µg	14,000- 20,000 rotifers	8			71	Eldridge et al. 1977
Sea bream ¹ <u>Archosargus rhomboidalis</u>	26	17 d; 200 µg	50	10	12	-	83	Houde & Schekter 1980
	"	15 d; 200 µg	100		31	42	38	
	"	10 d; 200 µg	500 nauplii (wild)		45	-	38	
" "	23-26	2-3 d	1000	75	14	68-147	33	Stepien 1976
	29	2-3 d	1000		32	199	16	
	23	10 d	1000		-	69	31	
Pacific mackerel ² <u>Scomber japonicus</u>	19	3 d; 38 µg	157,000	200	27	70	20	Hunter & Kimbrell 1980
	"	4 d; 43 µg	47,000		38	89	37	
	"	5 d; 85 µg	198,000 rotifers		86	102	44	
Striped bass <u>Morone saxatilis</u>	18	15 d; 400 µg	10				13	Eldridge (unpubl.)
	"		100				15	
	"		500				20	
	"		1000				21	
	"		5000				50	
			<u>Artemia</u>					
	18	29 d	10				20	
	"		100				14	
	"		500				17	
	"		1000				19	
	"		5000				32	
			<u>Artemia</u>					
Lined sole <u>Achirus lineatus</u>	26	21 d; 200 µg	50	10	14	-	63	Houde & Schekter 1980
	"	17 d; 200 µg	100		20	29	52	
	"	12 d; 200 µg	1000 nauplii (wild)		74	~90	20	
Winter flounder ^{3,4} <u>Pseudopleuronectes americanus</u>	8	2 wks.	500				10	Laurence 1977
	8	7 wks.	nauplii-				20	
	8	2 wks.	copepods		300		15	
	8	7 wks.	3000		30		33	

¹ Daily ration estimated from grazing experiments; dry weights determined with preserved larvae; wild plankton nauplii 0.15 µg, fresh dry wt.

² Ration from stomach contents and evacuation rate (discontinuous feeding).

³ Ration from stomach contents and evacuation rate (active feeding).

⁴ Net growth efficiencies.

Gut clearance times depend on feeding history; the time to a clear gut depends on the amount of food in the stomach (Werner and Blaxter, 1980) and it is more rapid at high food densities. Hence, gut clearance rates should probably be estimated from actively-feeding larvae. The technique used to avoid evacuation-time biases that may occur from discontinuous feeding (transferring larvae with full guts into tanks without food and subsequently noting the time taken to evacuate gut contents), is first to present larvae with natural prey to fill guts and then with dyed prey and note time to first dyed fecal material. Most experimentally-determined evacuation times (Table 10) are for discontinuous feeding.

From Table 10, the observed evacuation times ranged from 3-9 hours; time decreased with (1) increasing prey density (herring, Werner and Blaxter, 1980), (2) age (knifejaw, Fukushima, 1979; Pacific sardine, Arthur, 1956), and (3) temperature (herring, Blaxter, 1965; Table 9). Larvae of two *Anchoa* species (Chitty, 1980) deviate greatly from the "average", having evacuation times measured in minutes, 7-13, instead of hours. Schumann (1965) also noted a fast time, 3 minutes, for anchovy larvae fed *Artemia* nauplii to form a food plug at the anus in 15 mm northern anchovy (Table 10).

Some fish larvae are more capable of digesting certain prey types than other fish larvae. Although *Artemia* nauplii allow survival of herring and plaice, *Artemia* are an inferior food for northern anchovy; anchovy do not appear to digest *Artemia* until after gut differentiation (Hunter, 1976). Jack mackerel also may be unable to digest *Artemia*; mackerel defecate profusely when fed a diet of *Artemia* (Theilacker, unpubl.).

Gross growth efficiencies are not dependent on digestive efficiencies. Only Laurence's (1977) growth estimates in Table 9 are for net efficiency (assimilated calories/calories consumed); he assumed the coefficient of utilization to be 0.7.

It is well known that growth efficiencies of the young are higher than in older animals. Efficiency of yolk utilization (conversion of yolk to tissues) of fish embryos ranges between 50-79 percent (Pacific sardine 79 percent, Lasker, 1962; herring 50-74 percent, Blaxter and Hempel, 1966; herring 74 percent, Eldridge *et al.*, 1977). Growth efficiencies for exogenous feeding, on food not as well suited for assimilation as yolk, are lower (Table 9). Results from the few measurements of larval growth efficiencies in Table 9 are inconsistent. Efficiencies apparently decrease with (1) increasing prey density (Houde and Schekter, 1980), (2) age (Eldridge, unpubl.), and (3) increasing temperature (Stepien, 1976); apparent efficiencies may also increase with (1) increasing prey density (Laurence, 1977; Eldridge, unpubl.) and (2) age (Hunter and Kimbrell, 1980; Laurence, 1977). As a result, it is impractical to try to make interspecific comparisons.

The growth efficiencies for larvae fed 1 000 or more prey/l are fairly high, 14-41 percent. It seems reasonable that most of the food energy would be used in growth in larval fish. Faster growing individuals develop more quickly, hence rapidly growing larvae will become faster swimmers and more able to avoid predators at an earlier age.

Temperature

Many abiotic factors (temperature, light, salinity, currents) may influence growth of fish larvae. Because temperature is relatively easy to measure, there is more information on effects of temperature than on other factors. Temperature may affect larval fish by influencing (1) oxygen content of sea water, (2) nutrients that control algal blooms, (3) time, place and duration of spawning, (4) incubation time, (5) size at hatching, (6) efficiency of yolk utilization, (7) growth, feeding rates and time to metamorphosis, (8) behaviour and swimming speed, (9) digestion and evacuation, (10) metabolic demand, and (11) distribution (Table 11). Thus, in laboratory experiments designed to test any of the above eleven parameters, temperature must be rigidly controlled.

Table 10. Evacuation; time to empty gut.

	°C	Age (d; mm; µg)	Prey density (#/L)	Time to fill gut (hr)	Time to empty gut (hr)	Reference
Pacific sardine <u>Sardinops sagax</u>	-	5.5 mm	field	0.15 ¹	11	Arthur 1956
	-	6-9.5 mm	"	-	6	
	-	10-25 mm	"	-	3	
Herring ² <u>Clupea harengus</u>	9	3-9 wks.	3,000- 30,000 <u>Artemia</u>	1-3	3-4	Werner & Blaxter 1980
	"	3-9 wks.	30-300 <u>Artemia</u>	-	7+ ³	
" "	7	12d; 9 mm	-	-	8	Blaxter 1965
	15	12 d; 9 mm	-	-	4	
Northern anchovy <u>Engraulis mordax</u>	17	4-5 d	20,000 rotifers;	0.5	-	Hunter 1972
	17	15 mm	<u>Artemia</u> ; field	-	5-6 <.05 ⁴ 1-3	Moffatt, pers. comm. Schumann 1965 Arthur 1956
Big eye anchovy ² <u>Anchoa lamprotaenia</u>	26	2 d 8 d	100 ⁶ nauplii	0.15 ⁵	0.15 ⁴ 0.12 ⁴	Chitty 1980
Bay anchovy ² <u>Anchoa mitchilli</u>	26	2 d 8 d	100 ⁶ nauplii	- -	0.22 ⁴ 0.18 ⁴	Chitty 1980
Whitefish ⁷ <u>Corygonus clupeaformis</u>	14	19-20 mm	max ⁶ ; nauplii	-	16 ½ in 6	Hoagman 1974
Striped knifejaw ⁷ <u>Oplegnathus fasciatus</u>	22	7-11 d; 3-4 mm	4,000- 10,000 rotifers	0.5	6.5-9.4	Fukusho 1979
	"	13-18 d; 5-8 mm	-	-	2-2.5	
Pacific mackerel ⁷ <u>Scomber japonicus</u>	19	3-5 d	30,000 rotifers	<1.0	½ in 2	Hunter & Kimbrell 1980
Pacific hake <u>Merluccius productus</u>	-	3-11 mm	field	-	~11	Sumida & Moser 1980
Plaice <u>Pleuronectes platessa</u>	-	-	field	3	6	Ryland 1964
Winter flounder ² <u>Pseudopleuronectes americanus</u>	8	-	1,000- 2,000 ⁶ nauplii	-	6.6	Laurence 1977

¹ Schumann 1965; 15 mm; Artemia

² evacuation determined during active feeding

³ complete digestion; little-no evacuation

⁴ incomplete digestion

⁵ to 50% fullness

⁶ wild plankton-copepod nauplii

⁷ evacuation determined during discontinuous feeding

Table 11. Effect of temperature.

HATCHING TIME	1) At 13° Northern anchovy hatch about 1 day earlier than Pacific sardine	Lasker 1964
	2) Pacific sardine do not develop normally below 13°C	Lasker 1964
	3) Pacific mackerel do not hatch below 14°C	Hunter & Kimbrell 1980
HATCHING SIZE	4) Herring; decreases with increasing temperature	Blaxter & Hempel 1963
	5) Pacific sardine and Northern anchovy; no temperature effect	Lasker 1964
DEVELOPMENT: YOLK-SAC STAGE	6) Pacific sardine; $Q_{10}^1 = 4$ for yolk absorption, and development of pigmented eyes and functional jaw (14-21°C)	Lasker 1964
EFFICIENCY OF YOLK ABSORPTION	7) Plaice; more efficient at 6.5° than at 8.0°C; larvae 10% larger	Ryland & Nichols 1967
TIME TO EXOGENOUS FEEDING (FROM SPAWNING AT 15°C)	8) Pacific sardine; 8 d Northern anchovy; 6-7 d Jack mackerel; 8-9 d Pacific mackerel; 7 d	Lasker 1964 Theilacker (unpubl.)
POINT OF NO RETURN (TABLE 1)	9) Time to starvation decreases with increasing temp.	
FEEDING RATES (TABLE 6)	10) Northern anchovy; 6-12 d, 6° (13-16°C) increased rate 4 times (<2→8 acts/min)	Hunter (in press)
	11) Sea bream; 16 d, 3° (26-29°C) increased rate 2 times (8→18 acts/h)	Stepien 1976
GROWTH	12) Pacific mackerel, 17-22°C; 7-15 mm; $Q_{10} = 3$ no effect of temp. 12 d	Hunter & Kimbrell 1980
	13) Northern anchovy; 17-22°; 7-15 mm; $Q_{10} = 2.7$	Kramer & Zweifel 1970
ACTIVITY (TABLE 2)	14) Northern anchovy, 6-12 d, 4° increase (13-17°C) increased swimming speed 2 times (0.4→0.9 BL/s)	Hunter (in press)
RESPIRATION RATES (TABLE 7)	15) Pacific mackerel, 18-22°C; $Q_{10} = 4.8$	Hunter & Kimbrell 1980
	16) Herring; $Q_{10} = 2$	Holliday, <u>et al.</u> 1964
GROSS GROWTH EFFICIENCIES (TABLE 9)	17) Sea bream, 2-3 d, 3-6° increase (23-26 to 29°C) decreased K; 33% to 16%	Stepien 1976

$$^1 \log Q_{10} = \frac{10}{t_2 - t_1} \log \frac{k_2}{k_1}$$

Responses to the same temperature may differ among species (Table 11). For California Current species at 15°C, time to the onset of feeding from spawning is earliest in northern anchovy, 6-7 days, and latest in jack mackerel, 8-9 days; at 15°C, northern anchovy can withstand starvation one day longer than Pacific mackerel and two days longer than jack mackerel. Northern anchovy have a greater tolerance for cooler temperatures than Pacific mackerel or Pacific sardine; anchovy will hatch and develop at 11°C, sardine do not develop below 12°C, and Pacific mackerel will not hatch below 14°C. Miscellaneous temperature responses are outlined in Table 11.

In conclusion, it is hoped that this information on the species-specific behavioural and physiological characteristics of fish larvae may lead to the identification of critical factors needed to predict larval fish survival. This summary of physiological laboratory research and field behaviour describes differences among fish species in spawning times, resistance to starvation, feeding rates, growth rates, feeding behaviour, swimming activity, and metabolic demands. Monitoring methods and models designed to predict larval fish survival must incorporate these species-specific functions. Clearly, more comparable standardized research techniques need to be used in producing descriptions of early life histories, and far more behavioural observations are needed to fully elucidate the diverse groups of larvae.

REFERENCES

- AHLSTROM, E.H. 1943. Studies on the Pacific pilchard or sardine (*Sardinops caerulea*). Influence of temperature on the rate of development of pilchard eggs in nature. U.S. Fish Wildl.Serv., Spec.Sci.Rept.23:1-2
- _____. 1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S.Fish Wildl.Serv., Fish.Bull., 60:107-146
- _____. 1966. Distribution and abundance of sardine and anchovy larvae in the California Current region off California and Baja California, 1951-1964: a summary. U.S.Fish Wildl.Serv., Spec.Sci.Rept.Fish.No.534, 71 p.
- AHLSTROM, E.H. and O.P. BALL. 1954. Description of eggs and larvae of jack mackerel (*Trachurus symmetricus*) and distribution and abundance of larvae in 1950 and 1951. Fish.Bull.U.S., 56:209-245
- ARTHUR, D.K. 1956. The particulate food and food resources of the larvae of three pelagic fishes, especially the Pacific sardine *Sardinops caerulea*. Ph.D. Thesis, University of California, Scripps Institution of Oceanography, 231 p. (type-written).
- _____. 1976. Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax* and *Trachurus symmetricus*. Fish.Bull. U.S., 74:517-530
- BEYER, J.E. 1980. Feeding success of clupeoid fish larvae and stochastic thinking. Dana, 1:65-91
- BEYER, J.E. and G.C. LAURENCE. 1980. In press. Modelling growth and mortality of larval herring (*Clupea harengus*). Symposium on Early Life History of Fish, Woods Hole, Massachusetts, April 1979. Rapp.P.-v.Réun.Cons.int.Explor.Mer, 178:in press
- BLAXTER, J.H.S. 1965. The feeding of herring larvae and their ecology in relation to feeding. Calif.Coop.Oceanic Fish.Invest.Rep., 10:79-88
- _____. 1969. Development: eggs and larvae, p. 177-252. In W.S. Hoar and D.J. Randall (eds), Fish Physiology, Vol. 3, Academic Press, New York
- BLAXTER, J.H.S. and K.F. EHRLICH. 1974. Changes in behavior during starvation of herring and plaice larvae, p. 277-285. In J.H.S. Blaxter (ed), The Early Life History of Fish. Springer-Verlag, Berlin
- BLAXTER, J.H.S. and G. HEMPEL. 1963. The influence of egg size on herring larvae. J.Cons. perm.int.Explor.Mer, 28:211-240
- _____. 1966. Utilization of yolk by herring larvae. J.Mar.Biol.Ass.U.K., 46:219-234
- BLAXTER, J.H.S. and M.E. STAINES. 1971. Food searching potential in marine fish larvae, p. 467-481. In D.J. Crisp (ed), 4th European Marine Biology Symposium. Cambridge University Press, Cambridge
- de CIECHOMSKI, J.D. 1967. Investigations of food and feeding habits of larvae and juveniles of the Argentine anchovy, *Engraulis anchoita*. Calif.Coop.Oceanic Fish.Invest. Rept., 11:72-81

- CHITTY, N. 1980. In press. Behavioural observations of feeding bigeye anchovy larvae, *Anchoa lamprotaenia*. Symposium on Early Life History of Fish, Woods Hole, Massachusetts, April 1979. Rapp.P.-v.Réun.Cons.Int.Explor.Mer, 178
- COLTON, J.B. and R.R. MARAK. 1969. Guide for identifying the common planktonic fish eggs and larvae of continental shelf waters, Cape Sable to Block Island. Bureau of Commercial Fisheries Biological Laboratory, Woods Hole, Massachusetts. Laboratory Reference Number 69-9
- DEMPSEY, C.H. 1978. Chemical stimuli as a factor in feeding and intraspecific behavior of herring larvae. J.Mar.Biol.Ass.U.K., 58:739-747
- DUKA, L.A., 1969. Feeding of larvae of the anchovy *Engraulis encrasicolus maeoticus* Pusanov, in the Azov Sea. Prob.Ichthyol, 9:223-230 (transl. from Vopr.Ikhtiol.)
- EINARSSON, H. and B. ROJAS DE MENDIOLA. 1963. Descripción de huevos y larvas de anchoveta peruana (*Engraulis ringens* J.). Bol.Inst.Invest.Recurs.Mar, 1(1):1-23
- ELDRIDGE, M., T. ECHEVERRIA and J.A. WHIPPLE. 1977. Energetics of Pacific herring (*Clupea harengus pallasi*) embryos and larvae exposed to low concentrations of benzene, a monoaromatic component of crude oil. Trans.Amer.Fish.Soc., 106(5):452-461
- ELLERTSEN, B., P. SOLEMDAL, S. SUNDBY, S. TILSETH, T. WESTGARD and V. ØIESTAD. 1980. In press Feeding and vertical distribution of cod larvae in relation to availability of prey organisms. Symposium on Early Life History of Fish, Woods Hole, Massachusetts, April 1979. Rapp.P.-v.Réun.Cons.int.Explor.Mer, 178
- FUKUSHO, K. 1979. Studies on fry production of Japanese striped knifejaw *Oplegnathus fasciatus*, with special reference to feeding ecology and mass culture of food organisms. Spec.Rept. of Nagasaka Prefectural Inst. of Fisheries, No. 6, 173 p.
- GIESE, A.C. 1962. Cell physiology. W.B. Saunders Co., Philadelphia, Pa.
- HARDING, D., J.H. NICHOLS and D.S. TUNGATE. 1978. The spawning of plaice (*Pleuronectes platessa* L.) in the southern North Sea and English Channel. Rapp.P.-v.Réun. Cons.int.Explor.Mer, 172:102-113
- HARDY, J.D. JR. 1978. Development of fishes of the mid-Atlantic bight. Vol. II Anguillidae through Syngathidae. U.S. Dept. of Interior, Fish and Wildlife Service
- HEMPEL, G. and J.H.S. BLAXTER. 1963. On the condition of herring larvae. Rapp.P.-v.Réun. Cons.int.Explor.Mer, 154:35-40
- HEWITT, R. 1980. In press. The value of pattern in the distribution of young fish. Symposium on the Early Life History of Fish, Woods Hole, Massachusetts, April 1979. Rapp.P.-v.Réun.Cons.int.Explor.Mer, 178
- HILDEBRAND, S.F. 1946. A descriptive catalog of the shore fishes of Peru. Smithsonian Institution, U.S. Nat.Mus.Bull. 189
- HJORT, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp.P.-v.Réun.Cons.int.Explor.Mer, 20:1-228
- HJORT, J. 1926. Fluctuations in the year classes of important food fishes. J.du Conseil, 1(1):5-38
- HOAGMAN, W.J. 1974. Vital activity parameters as related to the early life history of larval and post-larval lake whitefish (*Coregonus clupeaformis*), p. 547-558. In J.H.S. Blaxter (ed), The Early Life History of Fish, Springer-Verlag, Berlin

- HOLLIDAY, F.G.T., J.H.S. BLAXTER and R. LASKER. 1964. Oxygen uptake of developing eggs and larvae of the herring (*Clupea harengus*). J.Mar.Biol.Ass.U.K., 44:711-723
- HOUDE, E.D. 1969. Sustained swimming ability of larvae of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*). J.Fish.Res.Bd Can., 26:1647-1659
- _____. 1974. Effects of temperature and delayed feeding on growth and survival of larvae of three species of subtropical marine fishes. Mar.Biol., 26:271-285
- _____. 1975. Effects of stocking density and food density on survival, growth and yield of laboratory-reared larvae of sea bream *Arochosargus rhomboidalis* (L) (Sparidae). J.Fish.Biol.7:115-127
- _____. 1978. Critical food concentrations for larvae of three species of subtropical marine fishes. Bull.Mar.Sci., 28:395-411
- HOUDE, E.D. and R.C. SCHEKTER. 1978. Simulated food patches and survival of larval bay anchovy, *Anchoa mitchilli*, and sea bream *Arochosargus rhomboidalis*. Fish.Bull. U.S., 76:483-486
- _____. 1980. In press. Functional and developmental responses of fish larvae to varying prey concentrations. Symposium on Early Life History of Fish, Woods Hole, Massachusetts, April 1979. Rapp.P.-v.Reun.Cons.int.Explor.Mer, 178
- HOWELL, B.R. 1973. Marine fish culture in Britain. VIII A marine notifer, *Brachionus plicatilis* Muller, and the larvae of the mussel, *Mytilus edulis* L. as foods for larval flatfish. J.Cons.int.Explor.Mer, 35:1-6
- HUNTER, J.R. 1972. Swimming and feeding behavior of larval anchovy, *Engraulis mordax*. Fish.Bull.U.S., 70:821-838
- _____. 1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. Fish.Bull.U.S., 74:81-88
- _____. 1977. Behavior and survival of northern anchovy, *Engraulis mordax*, larvae. Calif.Coop.Oceanic Fish.Invest.Rept., 19:138-146
- _____. In press. The feeding ecology of marine fish larvae. In J.E. Bardach (ed), The Physiological and Behavioral Manipulation of Food Fish as Production and Management Tools. International Center for Living Aquatic Resources Management, Manila.
- HUNTER, J.R. and S.R. GOLDBERG. 1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish.Bull.U.S., 77:641-652
- HUNTER, J.R. and C. KIMBRELL. 1980. Early life history of Pacific mackerel, *Scomber japonicus*. Fish.Bull.U.S., 78:89-101
- HUNTER, J.R. and C. SANCHEZ. 1976. Diel changes in swim bladder inflation of the larvae of the northern anchovy, *Engraulis mordax*. Fish.Bull.U.S., 74:847-855
- HUNTER, J.R. and G.L. THOMAS. 1974. Effect of prey distribution and density on the searching and feeding behavior of larval anchovy *Engraulis mordax* Girard, p. 559-574. In J.H.S. Blaxter (ed.), The Early Life History of Fish. Springer-Verlag, Berlin
- JOHNSON, G.D. 1978. Development of fishes of the mid-Atlantic bight. Vol. IV. Carangidae through Ephippidae. U.S. Department of Interior, Fish and Wildlife Service

- JONES, A. 1972. Studies on egg development and larval rearing of turbot, *Scophthalmus maximus* L., and brill, *Scophthalmus rhombus* L., in the laboratory. J.Mar.Biol. Ass.U.K., 52:965-986
- JONES, A., R. ALDERSON and B.R. HOWELL. 1974. Progress toward development of a successful rearing technique for larvae of the turbot, *Scophthalmus maximus* L. In Early Life History of Fish, J.H.S. Blaxter (ed.). Springer-Verlag, Berlin, p. 731-737
- JONES, P.W., F.D. MARTIN, J.D. HARDY, JR. 1978. Development of fishes of the mid-Atlantic bight. Vol. I. Acipenseridae through Ictaluridae. Fish and Wildlife Service, U.S. Department of the Interior
- JONES, R. and W.B. HALL. 1974. Some observations on the population dynamics of the larval stage in the common gadoids. In Early Life History of Fish, J.H.S. Blaxter (ed.). Springer-Verlag, Berlin, p. 87-102
- KIMURA, M. 1970. Formation of a false annulus on scales of Pacific sardines of known age. Calif.Coop.Oceanic Fish.Invest.Rept., 13:73-75
- KNAGGS, E.H. and R.H. PARRISH. 1973. Maturation and growth of Pacific mackerel *Scomber japonicus* Houttuyn. Calif.Dept.Fish Game, Mar.Res.Tech.Rept.No.3, 19 p.
- KRAMER, D. 1960. Development of eggs and larvae of Pacific mackerel and distribution and abundance of larvae 1952-1956. U.S. Fish.Wildl.Serv., Fish.Bull., 60:393-438
- _____. 1969. Synopsis of the biological data on the Pacific mackerel, *Scomber japonicus* Houttuyn (Northeast Pacific). FAO Fisheries Synopsis No. 40
- KRAMER, D. and J.R. ZWEIFEL. 1970. Growth of anchovy larvae (*Engraulis mordax* Girard) in the laboratory as influenced by temperature. Calif.Coop.Oceanic Fish.Invest. Rept., 14:84-87
- KRAMER, D. and P.E. SMITH. 1970. Seasonal and geographic characteristics of fishery resources. California Current Region. Commer.Fish.Rev., 32:27-49
- LASKER, R. 1962. Efficiency and rate of yolk utilization by developing embryos and larvae of the Pacific sardine *Sardinops caerulea* (Girard). J.Fish.Res.Bd Can., 19:867-875
- _____. 1964. An experimental study of the effect of temperature on the incubation time, development and growth of Pacific sardine embryos and larvae. Copeia, No.2:399-405
- _____. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish.Bull.U.S., 73:453-462
- LASKER, R. and G.H. THEILACKER. 1962. Oxygen consumption and osmoregulation by single Pacific sardine eggs and larvae (*Sardinops caerulea* Girard). Journ.du Cons. XXVII(1)
- LASKER, R., H.M. FEDER, G.H. THEILACKER and R.C. MAY. 1970. Feeding, growth and survival of *Engraulis mordax* larvae reared in the laboratory. Mar.Biol., 5:345-353
- LASKER, R. and P.E. SMITH. 1977. Estimation of the effects of environmental variations of the eggs and larvae of the northern anchovy. Calif.Coop.Oceanic Fish.Invest. Rept., 19:128-137

- LASKER, R. and J.R. Zweifel. 1978. Growth and survival of first-feeding northern anchovy larvae (*Engraulis mordax*) in patches containing different proportions of large and small prey, p. 329-354. In J.H. Steele (ed.), Spatial Pattern in Plankton Communities.
- LAURENCE, G.C. 1971. Digestion rate of larval largemouth bass. New York, Fish and Game Journal, 18(1):52-6
- _____. 1974. Growth and survival of haddock (*Melanogrammus aeglefinus*) larvae in relation to planktonic prey concentration. J.Fish.Res.Bd Can., 31:1415-1419
- _____. 1975. Laboratory growth and metabolism of the winter flounder *Pseudopleuronectes americanus* from hatching through metamorphosis at three temperatures. Mar.Biol., 32:223-229
- _____. 1977. A bioenergetic model for the analysis of feeding and survival potential of winter flounder, *Pseudopleuronectes americanus*, larvae during the period from hatching to metamorphosis. Fish.Bull.U.S., 74:529-546
- _____. 1978. Larval length-weight relations for seven species of northwest Atlantic fishes reared in the laboratory. Fish.Bull.U.S., 76:890-5
- LAURENCE, G.C. and J.E. BEYER. 1980. A stochastic dynamic model of growth and mortality in winter flounder larvae (*Pseudopleuronectes americanus*) reared in the laboratory under experimental conditions. Symposium on Early Life History of Fish, Woods Hole, Massachusetts, April 1979. Rapp.P.-v.Réun.Cons.int.Explor.Mer, 178: in press
- MACKAS, D. 1976. Horizontal spatial heterogeneity of zooplankton on the Fladen Ground. Prepared for presentation to the Plankton Committee at the 64th Statutory Meeting of the International Council for the Exploration of the Sea, Copenhagen, Denmark, October 1976.
- MARAK, R.R. 1960. Food habits of larval cod, haddock and coalfish in the Gulf of Maine and George's Bank area. J.Cons.Perm.int.Explor.Mer, 25(2):147-157
- _____. 1974. Food and feeding of larval redfish in the Gulf of Maine. In The Early Life History of Fish, J.H.S. Blaxter (ed.). Springer-Verlag, Berlin, p. 267-275
- MARTIN, F.D. and G.D. DREWRY. 1978. Development of fishes of the mid-Atlantic bight. Vol. VI. Stromateidae through Ocyrocephalidae. U.S. Department of Interior, Fish and Wildlife Service
- MILLER, D., J.B. COLTON and R.R. MARAK. 1963. A study of the vertical distribution of larval haddock. J.Cons.int.Explor.Mer, 28(1):37-49
- MOSER, H.G. 1967. Reproduction and development of *Sebastes paucispinis* and comparison with other rockfishes off southern California. Copeia No. 4:773-797
- NEWELL, G.E. and R.C. NEWELL. 1963. Marine plankton. Hutchinson Educational Ltd., 243 p.
- O'CONNELL, C.P. 1976. Histological criteria for diagnosing the starving condition in early post yolk sac larvae of the northern anchovy, *Engraulis mordax* Girard. J.Exp.Mar.Biol.Ecol., 25:285-312
- _____. In press. Development of organ systems in the northern anchovy, *Engraulis mordax* and other teleosts

- O'CONNELL, C.P. and L.P. RAYMOND. 1970. The effect of food density on survival and growth of early post yolk-sac larvae of the northern anchovy (*Engraulis mordax* Girard) in the laboratory. *J.Exp.Mar.Biol.Ecol.*, 5:187-197
- RILEY, J.D. 1966. Marine fish culture in Britain. VII. Plaice (*Pleuroneotes platessa* L.) post-larval feeding on *Artemia salina* nauplii and the effects of varying feeding levels. *J.Cons.Perm.int.Explor.Mer.*, 30(2):204-221
- _____. 1974. The distribution and mortality of sole eggs (*Solea solea* L.) in inshore areas. In *The Early Life History of Fish*, J.H.S. Blaxter (ed.). Springer-Verlag, Berlin, p. 39-52
- ROJAS DE MENDIOLA, B. 1974. Food of the larval anchoveta, *Engraulis ringens* J. In J.H.S. Blaxter (ed.), *The Early Life History of Fish*. Springer-Verlag, Berlin, p.227-285
- ROSENTHAL, H. and G. HEMPEL. 1970. Experimental studies in feeding and food requirements of herring larvae (*Clupea harengus* L.). In J.H. Steele (ed.), *Marine Food Chains*. University of California Press, Berkeley, p. 344-364
- RYLAND, J.S. 1963. The swimming speeds of plaice larvae. *J.Exp.Biol.*, 40:285-299
- _____. 1964. The feeding condition of plaice and sand-eel larvae in the southern North Sea. *J.Mar.Biol.Ass.U.K.*, 44:343-364
- RYLAND, J.S. and J.H. NICHOLS. 1975. Effect of temperature on the embryonic development of the plaice *Pleuroneotes platessa* L. *J.Exp.Mar.Biol.Ecol.*, 18:121-137
- SANTANDER, H. and O.S. DE CASTILLO. 1977. Variaciones en la intensidad del desove de la sardina *Sardinops sagax sagax* (J.) en la costa peruana en los años 1966-1973. *Bol.Inst.Mar Perú*, 3(3):73-94
- _____. 1977a. Ichthyoplankton from the Peruvian coast. In *Proceedings of the Symposium on Warm Water Zooplankton*, National Institute of Oceanography, EDA. UNESCO
- SHELBOURNE, J.E. 1953. The feeding habits of plaice post-larva in the Southern Bight. *J.Mar.Biol.Assoc.U.K.*, 32:149-159
- SCHUMANN, G.O. 1965. Some aspects of behavior in clupeoid larvae. *Calif.Coop.Oceanic Fish Invest.Rept.*, 10:71-78
- SMITH, W.G., J.D. SIBUNKA and A. WELLS. 1978. Diel movements of larval yellowtail flounder, *Limanda ferruginea*, determined from discrete, depth sampling. *Fish.Bull.U.S.* 76: 167-178
- STEPIEN, W.P., Jr. 1976. Feeding of laboratory-reared larvae of the sea bream *Archosargus rhomboidalis* (Sparidae). *Mar.Biol.*, 38:1-16
- SUMIDA, B.Y. and H.G. Moser. 1980. In press. Food and feeding of Pacific hake larvae, *Merluccius productus*, off southern California and northern Baja California. *Calif.Coop.Oceanic Fish.Invest.Rept.* 21
- THEILACKER, G.H. 1978. Effect of starvation on the histological and morphological characteristics of jack mackerel, *Trachurus symmetricus*, larvae. *Fish.Bull.U.S.*, 76:403-414

- _____. 1980. In press. Effect of feeding history and egg size on the morphology of jack mackerel, *Trachurus symmetricus*, larvae. Symposium on the Early Life History of Fish, Woods Hole, Massachusetts, April 1979. Rapp.P.-v.Reun.Cons.int.Explor.Mer, 178
- _____. 1980a. In press. Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due handling and preservation. Fish.Bull.U.S.
- _____. 1980b. In press. Rearing container size affects morphology and nutritional condition of larval jack mackerel, *Trachurus symmetricus*. Fish.Bull.U.S., 78
- THEILACKER, G.H. and M.F. McMASTER. 1971. Mass culture of the rotifer, *Brachionus plicatilis*, and its evaluation as a food for larval anchovies. Mar.Biol., 10: 183-188
- UOTANI, I., A. IZUKA and K. ASAI. 1978. Food habits and selective feeding of anchovy larvae (*Engraulis japonicus*). Nihon Suisan-Gakkai Shi, 44(5):427-434
- VLIMEN, W.J. 1974. Swimming energetics of the larval anchovy, *Engraulis mordax*. Fish.Bull. U.S., 72:885-899
- _____. 1977. A mathematical model of the relationship between larval anchovy (*E. mordax*), growth, prey microdistribution and larval behavior. Environ.Biol. Fishes, 2:211-233
- VON WESTERNHAGEN, H. and H. ROSENTHAL. 1980. In press. Laboratory and *in situ* studies on larval development and swimming performance of Pacific herring, *Clupea harengus pallasii*. Symposium on Early Life History of Fish, Woods Hole, Massachusetts, April 1979. Rapp.P.-v.Reun.Cons.int.Explor.Mer, 178
- WARE, D.M. 1975. Relation between egg size, growth and natural mortality of larval fish. J.Fish.Res.Bd Can., 32:2503-2512
- WARE, D.M., B. ROJAS DE MENDIOLA and D.S. NEWHOUSE. 1980. In press. Behavior of first-feeding anchoveta larvae, *Engraulis ringens* J. Symposium on Early Life History of Fish, Woods Hole, Massachusetts, April 1979. Rapp.P.-v.Reun.Cons.int.Explor.Mer, 178
- WEBB, P.W. and R.T. COROLLA. MS. Burst swimming performance of anchovy larvae, *Engraulis mordax*. Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038
- WEIHS, D. 1974. Energetic advantages of burst swimming of fish. J.Theor.Biol., 38:215-229
- WERNER, R.G. and J.H.S. BLAXTER. 1980. In press. The effect of prey density on mortality, growth and food consumption in larval herring (*Clupea harengus* L.). Symposium on the Early Life History of Fish, Woods Hole, Massachusetts, April 1979. Rapp. P.-v.Reun.Cons.int.Explor.Mer, 178
- WINE, V.L. and E.H. KNAGGS. 1975. Maturation and growth of jack mackerel, *Trachurus symmetricus*. Mar.Res.Tech.Rept.32
- WYATT, T. 1972. Some effects of food density on the growth and behavior of plaice larvae. Mar.Biol., 14:210-216
- YOKOTA, T., M. TORIYAMA, F. KANAI and S. NOMURA. 1961. Studies on the feeding habit of fish. Rep.Naukai Reg.Fish.Res.Lab.14, 243 p. (in Japanese, English summary)
- ZWEIFEL, J.R. and R. LASKER. 1976. Prehatch and posthatch growth of fishes - a general model. Fish.Bull.U.S., 74:609-621

COLONIZATION: MODES OF OPPORTUNISM IN THE OCEAN

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INTRODUCTION

In the life history of fishes there are numerous processes which determine the reproductive contribution realized by each individual in a population. These processes can be considered to be "critical" if they are irreversible and result in either death, loss of fertility, or isolation of the individual from the appropriate reproductive requirements. In "sub-critical" processes the individual's development and subsequent reproduction may only be retarded, resulting in a contribution below that individual's optimal potential.

A sizable array of empirical and modelling investigations into these processes has developed. The majority of recent studies has covered one or more of the following: effects of pre-spawning condition of the adults on egg quality; subsequent egg dispersion; percent hatch; larval development and transformation processes; survival of eggs, larvae, post-larvae, on through maturity; predation (including fishery effects); species interactions; geographic and temporal variations; and most important, spatial geometries of food for survival of fishes throughout their lives.

From a survey of the literature it is apparent that most studies have concentrated on the various life history stages which are presumed to have some bearings on the subsequent status of adults or exploited stocks. Some studies have taken an alternate approach by using estimates of distribution and abundance of eggs and larvae to estimate the parent stock size. One of the common denominators of most of these studies based on at-sea sampling has been the use of integrative sampling techniques (e.g. net tows, pumps). A parallel and persistent problem area in extracting information about natural limiting processes in fish biology is measurement of ambient physical-biological interactions on appropriate scales. Definition of the relevant scales is important.

The scales of events which determine survival of individual fish larvae range from the visual perception range of larval fish for feeding (mm) upward to large scale wind-driven turbulence (km). The mobilities of the larvae, the densities and geometries of occurrence of their prey, and temperature are the major features which have been used to describe the "immediate" requirements, behaviour, and developmental processes of fish larvae (Hunter 1972, Vlymen 1977, and Hunter 1977). A problem area which appears to have attracted the least attention to date in regard to the available early life history information is the distribution and availability of appropriate larval fish habitat and the means various species of marine fish have evolved to cope with the seasonal, local, and open ocean variation in availability of these "requirements" for reproductive success. Given present knowledge and interest, these are significant considerations which should be evaluated comparatively to provide useful insights.

More recently Beyer (1980) and Beyer and Laurence (1979) have extended the "immediate requirements" concepts into time in their modelled quantifications, including the effects of food particle selection, size dependent feeding success, and inherent energetic strategies which result in differential survival of larval fishes in different ambient systems. Such side issues as the beneficial effects of intermediate temperatures to fish larvae (within their tolerance range) in a food-scarce system, as predicted by Vlymen's growth-energetics model and also apparent in Beyer's model, are also clarified, confounding the intuitive assumption made by many that higher ambient temperatures promote faster growth through the period of high predation thereby yielding greater proportional survival. Their studies, based on empirical data from laboratory and field studies, also show why the approach of employing "average" estimates of "fishery-wide mortality constants" over even relatively concise stages (e.g. egg to larvae, larvae to transformation, juvenile to recruit, etc.) provides so little insight beyond verbal, intuitive speculations into recruitment variations. The use of "average" mortalities without regard to local phenomena merely increases the abundant computer output and familiar graphics produced by the classical theoretical-quantitative models. These products, however, only rarely exhibit conformity to empirical observations or lend firm support to presumed mechanisms which are proposed to control abundance of aquatic populations.

Detailed evaluation of quantified "recruitment" models which ignore the fundamental availability of appropriate larval fish food particle distributions and/or behavioural characteristics of both the fish larvae and their prey, in favour of competitive and predation interactions also makes little sense at present. The approach to the multi-faceted system analysis provided by Riffenburgh (1969), when fleshed out by employing sequential, stochastic evaluations of all of these processes, will certainly improve our ability to comprehend the lack of stability inherent in aquatic populations. The approach of Lett and Kohler (1976), and in subsequent studies by Lett (1978, MS) wherein all processes in a species-pair interaction are assumed to be stable, simple variables, from which effects of species interactions are "resolved" leave much to be desired, considering the significant variation in realization of recruitment potential between year classes of species as functions of primarily environmental-ambient variation. The literature is abundant on the implicit mechanics of variation in commercial fish catches and environmental fluctuations, and there is a growing body of information showing how reproduction potential is constrained by short-term physical-environmental effects. Ignoring any of these processes can only generate a series of semi-realistic or hypothetical cases which support (or not) preconceptions, the basic assumptions of which are surreal at best and often just facilitative tautologies (e.g. "Year class size should tend toward some central [level] such that an equilibrium can be struck between recruitment and mortality.").

Each step in the development of oviparous fish, from egg to egg, needs to be critically analyzed and sources of mortality or reduced reproductive potential identified and evaluated with respect to properties of the ambient which can be readily monitored. In this light it is only logical to start with the early mobile stages, their behaviour and developmental patterns, limitations and facilitations; rather than at any intermediate stages prior to recruitment. A simultaneous evaluation of the appropriate scale ambient properties and definition of truly limiting or "critical" characteristics, based on energetic and thermodynamic principles, will provide a firm basis for hypothesis structuring and determination of cause-and-effect relationships useful in constructing useful survival models, and then perhaps even synoptic simulators for monitoring and forecasting on the short-term.

It is clear that "traditional" sampling methods used for studies of primary production and subsequent ecological processes are too integrative to be of more than cursory value in locating or defining appropriate larval fish habitat. They are insensitive to variations on distance scales which are "critical" to the early life history processes. They may also be insensitive to productivity parameters relevant to the subsequent stage which ultimately determines the numbers of adults (or fishery recruits). For example, Fasham (1978) concluded from his review of statistical and mathematical treatments of plankton patchiness, that only the gross scale events (on the order of hundred to thousands of metres) can be evaluated from available data because the typical sampling interval is greater than the common dimensions of individual plankton patches. It follows from these conclusions that analysis of plankton patchiness as it relates to fish reproduction has also been accomplished predominantly on too gross a scale for direct links between patches and larval requirements to be defined. This should not be "news" to anyone at this time.

Neither here do I intend to press the problems of our ignorance regarding predation upon fish larvae by their own species, other fishes, or the sea full of invertebrate predators. Let us at once accept that the necessary conditions for survival are physical processes, resulting over evolutionary history in biological responses by predators and prey alike, such that some of each always gets through to provide for the next generations. It is the initial physical events which set the stage for the subsequent, and hopefully persistent life-giving processes in the evolutionary play.

THE STOCK RECRUITMENT QUESTION

In light of the developments in information about early life history of fishes in the last decade or so, there are few if any reasons to persist in the search for relations between "The Stock" and "Recruitment", as if there were some "real" dependence of one or the other beyond the obvious "too few" cycle which generally accompanies the decline of populations (e.g., "too few" adults result in "too few" recruits result in "too few" adults, etc.). More important issues are "how few" adults can saturate the available larval habitat, and how does the behaviour of the adults promote full or optimum utilization of the variations in larval habitat distribution and availability?

A brief hypothetical example, using the kind of observations which are available from any fisheries, but extending the time frame and numbers of observations beyond any available data, can be used to illustrate an important point. Figure 1 shows that there are three conceptual axes in the stock recruitment question, not two as is the typical portrayal. The two axes commonly portrayed are 1) Spawning Biomass (or less useful Stock Size) and 2) Recruitment. In Figure 1 the three axes are: 1) Spawning Stock Size (year N), 2) Ratio of Biomass ($\frac{\text{year N} + \text{M}}{\text{year N}}$) and 3) Frequency of Occurrence. I have chosen this third axis to give insights into the "expected" trajectories of recruitment at any given spawning stock size, but any measure of variance would do better than none. The figure includes some purely arbitrary probability density functions at various spawning stock sizes, which reflect typical recruitment trajectories. The concepts of most relevance are that very large stock sizes rarely "reproduce themselves" ($\text{Ratio Stock Size } \frac{\text{year N} + \text{M}}{\text{year N}} = 1$, where M is the time to maturity from spawning), and very small stock sizes tend to increase the subsequent biomass more often than not. The reasons for this should be obvious if extinction or "runaway" populations are excluded. There is no reason at the intermediate stock sizes for implied "normal" expectations at any time, given only information on spawning stock size.

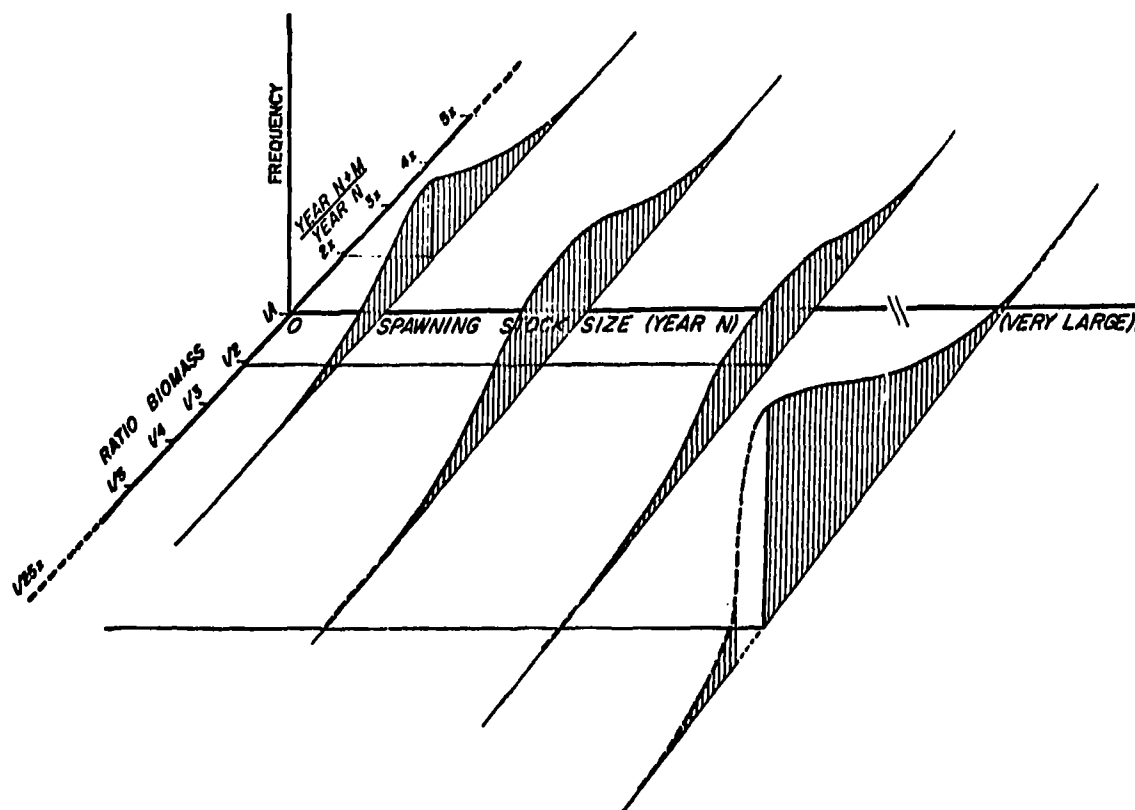


Figure 1

The major differences in this conceptualization of the recruitment process in contrast to the standard S/R approach is that the variations which occur in recruitment at any given Spawning Stock Size are accountable. There is no inherent equilibrium assumed to exist in the population. The numbers of adults or recruits at year $N + M$ is that figure presumed by some to be proportional to Spawning Biomass in Year N . Given the opportunistic nature of biological systems, equilibrium is rarely (virtually never) observed. Therefore, it does not follow that there should be any relation between these two "variables" unless there are some very constant limiting features. In the case of marine fishes this would have to include constant larval habitat conditions, including predators and species interactions. This is most unlikely scenario. I believe that this is the basis of the failure to observe S/R relations which provide anything but fodder for "post mortems" in marine situations.

It should not be forgotten that there are examples where habitat "constants" are closely approximated and the spawning biomass is proportional to recruitment, up until the egg-larva habitat is saturated, but these conditions are rarely observed in open ocean or pelagic situations. This is primarily due to the climate-environment interactions which result in the kaleidoscopic variations to which the various pelagic and oceanic species must adapt, or become extinct. How to measure these environmental characteristics seems to be a more important question than how to better fit S/R data. That is, if the goal is to succeed in *a priori* recruitment estimations and relevant stock evaluation.

COLONIZATION OF EGGS AND LARVAE

Realistically it is important to recognize that once viable eggs are expelled into the open environment the adults of most or all pelagics and oceanics have no further involvement with the developmental process. This is not to say that the adults cannot turn right around and prey on the eggs or larval stages, resulting in significant early stage mortality, but there is virtually no change in expectation for the surviving egg or larval development due to the presence of the adults. This points to a rather interesting logical premise. Namely, that if one concludes that the egg to larval transformation period is the single greatest probable "bottleneck" period for each fish year class, then one can conclude that the complexities of the life history stages to follow are the evolutionarily successful egg's way of getting itself reproduced and redeposited in an appropriate environment for survival. It could be considered that each successful year class is the result of effective "colonization" of the eggs and larval stages.

From this viewpoint I would like to discuss some important questions that cannot be directly answered from available information, which arise from consideration of the scales of events and requirements of early life history stages of fish, and the fact that they are similar for most oviparous fishes.

From the studies of Lasker, Feder, Theilacker and May (1970); Hunter and Thomas (1974); Laurence (1974); Houde (1976, 1977); Beyer (1976a and b); Vlymen (1977); Lasker and Zweifel (1978); and Hunter and Kimbrell (MS), and many others, it is clear that fish larvae must have available to them in close proximity a relatively high density of appropriate sized food organisms for survival and development. These densities are only observed in smaller scale patches, on the order of metres or less in narrowest dimension (Owen, this volume and MS). These patches are themselves part of larger patches or production systems, whose upper dimensions may be on the order of tens of metres to hundreds of kilometres. A scenario which must be appreciated is the dynamic scale changes which must be considered in any discussion of life history events and their effectors.

For example, effective primary production is localized to regions where nutrients are injected into the photic layer of the ocean. The critical situation in regards to fish reproduction is the timing and geometries of these events. Even in the densest productive "soup" the patches form lamina on the order of centimetres in thickness. The distributions of primary herbivores (e.g. copepods, euphausiids, etc.) reflect these laminae in their fine scale distribution, and the entire patch system in their gross scale occurrences, with appropriate lags in response to changes in primary production.

The primary predators (e.g., herrings, clupeids and other small fishes) are patchy on the same gross scale as the primary herbivores, but with even greater lags in response to variations in primary production due to their second order dependence in the chain of events. Primary predators often move between gross scale patches of primary production, but are typically part of the array that I define here as the "primary patch" (on the gross scale). Larval fish survival is determined by fine scale events within these primary patches.

Secondary predators (e.g., jacks, scads, mackerels, etc.) move from primary patch to primary patch, in their own "patches" or schools. Tertiary predators can either be 1) solitary and/or relatively stationary (e.g., bass, barracudas, wahoo, etc.) with respect to the continuously moving primary patches or schools of their prey; 2) very mobile, ranging over their habitat in schools or solitarily (e.g., tunas, billfishes, dolphin and lamnid sharks) so as to encounter herbivores, or primary and secondary predators; or 3) semi-mobile and dispersely distributed, and able to take advantage of any smaller food entities moving into their range of perception, including their own species (e.g., gadoids, flatfishes, and many sharks).

The tertiary predators typically graduate from primary through the secondary predator levels as they grow and change behaviour. Some species maintain continuous participation within the three predator levels depending on the local characteristics of the habitat which they are sampling. For example, tunas can and do filter feed. The size of euphausiids and crustaceans found in the stomachs of tunas varies with gillraker gap which is a function of species and size of fish (Magnuson and Heitz 1972). Large (>100 cm) tunas are commonly observed to have their stomachs packed with small cephalopods and/or larval and post-larval fishes which it would be difficult to imagine having been consumed one at a time. Of course the bulk of tuna stomach contents are larger particulate items.

Nomadic opportunists

The tunas and other apex predators have evolved the complex life styles of the supreme opportunists because they are dependent upon a long chain of events over varying temporal and distance scales. The initial events which determine their success are no different from the other trophic levels, the primary production-nutrient cycle must provide for them all.

The events triggering or sustaining nutrient injection cycles in upwelling areas or along current boundaries are fairly well recognized. There is seasonality in most areas, particularly in the temperate zones (Cushing, 1971), although in other systems the production is nearly continuous on the lines of a grand scale chemostat, with perturbations emanating from ocean scale climatic events acting to displace and damp the production. The Peruvian system is a familiar example, and the perturbations are the well-known El Niño phenomena (Wyrteki, submitted).

There must be analogous non-coastal or surface current boundary production processes which play important roles in maintaining productivity and ecosystem integrity in the open ocean. The more obvious systems are characterized by broad surface temperature regimes. For example, the boundaries of the tropical Pacific Ocean vary seasonally, including over the year all the ocean between 30° North and 30° South. Within this broad zone are currents and disparate thermal regime interfaces which are characterized by temperature-salinity gradients. These resulting "cells" or water masses have average characteristic distinctions from neighbouring "cells". The combined effects of geography, hemisphere, thermal budgets, subsurface water motion, and wind field structure yield numerous "edge" effects. These include upwelling, downwelling, eddy formation, and their correlates: convergence, divergence and smaller scale cyclonic and anticyclonic cells.

The very obvious "nutrient injection" processes occurring at sites of upwelling have understandably occupied much of marine research. There must be analogous processes in the open-ocean which are less accessible for study and perhaps even less overt than the effects of the well-known "edge" phenomena. I say there must be analogues because the general availability of tertiary predators throughout the tropical and temperate seas, including the central gyres which have been declared to be biological deserts by the community of biological oceanographers, implies productivity levels which are unaccounted for from available sampling technology. Recent studies (Gieskes, Kraay and Baars, 1979; and Tijssen, 1979) may have shed light on these processes.

The relative apparent abundance (e.g., visibility and vulnerability) of some tertiary predators increases with the shoaling of their habitats (Sharp, 1978), a correlate of divergence and convergence zones in the open ocean. The abundant food organisms and relatively high production in these zones is evidence of nutrient injection processes. Also, large scale weather phenomena such as typhoons probably contribute to "local" production anomalies which maybe only some months later result in aggregation of the mobile oceanic predators.

In effect, the thermocline represents the depth extension of the "edge" phenomena between water mass types. Although turbulent eddies and other nutrient injection processes associated with surface phenomena would be on a smaller scale in the thermocline system. These along with wind driven mixing and subsurface current shear processes must account for

far more productivity than we think. The fact that many of the tertiary predators in the open ocean live and feed within the thermocline itself (e.g. adult *T. obesus*, *T. alalunga*, and *T. albacares*) indicates the presence of a long-term availability of food organisms and the supporting production to maintain them.

Another reason for presuming this unaccounted-for oceanic productivity is that reproductive adults of cosmopolitan tuna species are typically nearly unavailable to the surface fisheries in the world ocean. Considering the added nutritional requirements for reproduction and the general energetic requirements of these species, the spawners must be located in very productive, mature ecosystems for successful reproduction to occur. Many, and in fact most, of the islands, banks and geographic "edge" areas are exploitation centres for only the juvenile and inter-reproductive adults of these fishes. Ripe, reproductive tunas are only rarely observed in commercial catches from these areas. The reproductive individuals apparently adopt their "cryptic" behaviour in concert with their pursuit of "hospitable" larval habitats. Obviously there must be some remarkable conditions available in the open ocean which provide for these requirements. These conditions are probably not uniformly distributed in the tropical ocean as both location and season of tuna spawning are diverse, but they must occur frequently and in sufficient localities to provide for the observed continuous availabilities of these higher predators throughout the warm areas and contingent seas.

One of the more significant observations in tuna biology, for example, is that the *Thunnus* species all reproduce in relatively tropical situations (where water temperatures are warmer than 23°C), even though several of the species have juvenile and inter-reproductive distributions which include temperate seas with temperatures encountered as low as 5°C (Sharp 1978). The morphological adaptations which provide the resistance to such low temperatures develop with maturity in these fish. The genetic adaptations of the larvae are still primarily "tropical", and limit the successful spawning of tunas to warm ocean zones. This has not, however, limited the distributions of the species in any sense, due to the continuous swimming behaviour, the remarkable morphological adaptations and highly nomadic nature at various life stages of many of the species. The peak of larval tuna occurrences is observed at about 26°C in the tropical oceans, and a decline in apparent abundance occurs in warmer surface waters. This decline in the warmer surface waters may, however, indicate a submergence of the optimum zone of spawning in the areas where sea surface temperatures rarely or never are as low as 26°C. It is general that there are typically large quantities of tropical tunas found in warmer temperature (>26°C) areas, some of which have shown little tendency to stray from these waters.

Tuna larvae have been collected in open ocean areas, as well as near islands and shoals. It is unclear if there is a specific spawning area character, or if the tunas lose a great portion of their reproductive potential to indiscriminant "sowing" of their gametes into areas, such as the ocean surface, which might be inimical to development. I suspect that the successful spawnings are those which are "placed" into the small scale open ocean primary patches, or nearshore (and/or) shoal systems resulting from well developed patches which are downstream from the mixing or nutrient injection sites.

There is little question that the cosmopolitan fishes have successfully colonized the world ocean by stepwise increments. This certainly implies that larval habitat is available over much of the ocean, and that the cosmopolitan species can identify these zones. They must be able to respond relatively rapidly if these patches are rare, or perhaps they have access to numerous appropriate opportunities and take advantage of them as their reproductive state provides. This is not an either/or situation since it is probable that both cases can occur.

For example, tuna larvae have local requirements far exceeding those of clupeids and other pelagic species, due to the larval tunas' high activity levels and metabolic rates. Why is it that the tunas, not the pelagics, have colonized the areas which are characterized by the erratic production processes occurring in the open ocean? The fundamental differences in the two ways of life are the levels of nomadism in the two groups. Another great difference is the investment in trophic opportunism with increased size in the broad ranging tunas,

even in contrast to their scombrid relatives with pelagic distributions (e.g., bonitos, seerfishes, mackerels). The fast growth and large size attained by the large tunas have afforded them reserves for exploring the oceanic "deserts" for both feeding and spawning areas, which are quite obviously available to them (Sharp, 1978; Sharp and Dotson, 1977; Kawasaki, 1979).

An interesting correlate to the sporadic occurrence of larval habitat is the complex racial structure of some of the cosmopolitan tunas. For example, biochemical genetic studies of yellowfin and skipjack tunas have shown complicated racial differentiation within oceans resulting in regional differences, as well as complex subregional differentiations (Fujino, 1970; Sharp, 1978; Sharp, MS; Sharp and Kane, MS).

In the nearly 100 schools sampled for my own studies there are numerous examples from both species where the rare phenotypes occur in size similar clumps within large samples with broad size distributions (Figures 2 and 3). This data indicates persistence of groups within schools of nomadic tunas for up to and over two years. These individuals derive from the same parents and the same larval patch. These are not trivial observations in that the implications are formidable.

Not only is there apparently cohesion among individuals in schools but the size similarity and common history help provide the next most important requirement for opportunistic colonization and subsequent range extension toward cosmopolitan status. Namely, sexual parity (similar developmental state and reproductive condition) is required if there is to be successful reproduction. The incremental expansion of species ranges does not necessarily mean uniformity of reproductive success in each area, but persistent sampling for potential larval habitat could provide for optimum utilization of any development of larval habitat. Once a region has been colonized, the continuity of the colony depends upon the regularity of occurrence of larval habitat. Failure of appropriate habitat to develop results in instability of the local population, no matter whether in the open ocean or in the pelagic zone. In the open ocean these instabilities often result in disparities in the range and spawning areas of species. For example, albacore tuna have a cosmopolitan distribution, but they reproduce only in restricted sub-areas within their range. Only the juveniles are highly migratory, hence the adults exhibit a typical regional distribution comparable to adult yellowfin or skipjack tunas. Yellowfin or skipjack may not migrate as extensively as the young albacore, but their reproduction is spread over larger portions of the ocean. This results in the complex population differentiation in these species in contrast with albacore.

It is also germane that schooling behaviour has an early onset in the post larval stages of many fishes. These small aggregations may represent at least two recognized positive advantages to the early life histories. The first being a decrease in general availability of larvae to predation in that these "patches" yield rarer encounters between predators and prey of near-size scale, and second, the optimum feeding strategy for sparse resources results from aggregation of this sort (Cody, 1969). Other values derived from early schooling lead right back to my earlier comments on oceanic schooling species. The "grouping" at this stage is obvious from genetic sampling. The occurrence of siblings in schools of one, two and three-year-old tuna speaks for the relative compactness of the original larval patches. There is no better mechanism for providing similar history which promotes both sexual parity and conformity of individuals to optimal search strategies for locating either feeding grounds or the comparably important hospitable larval nursery patches.

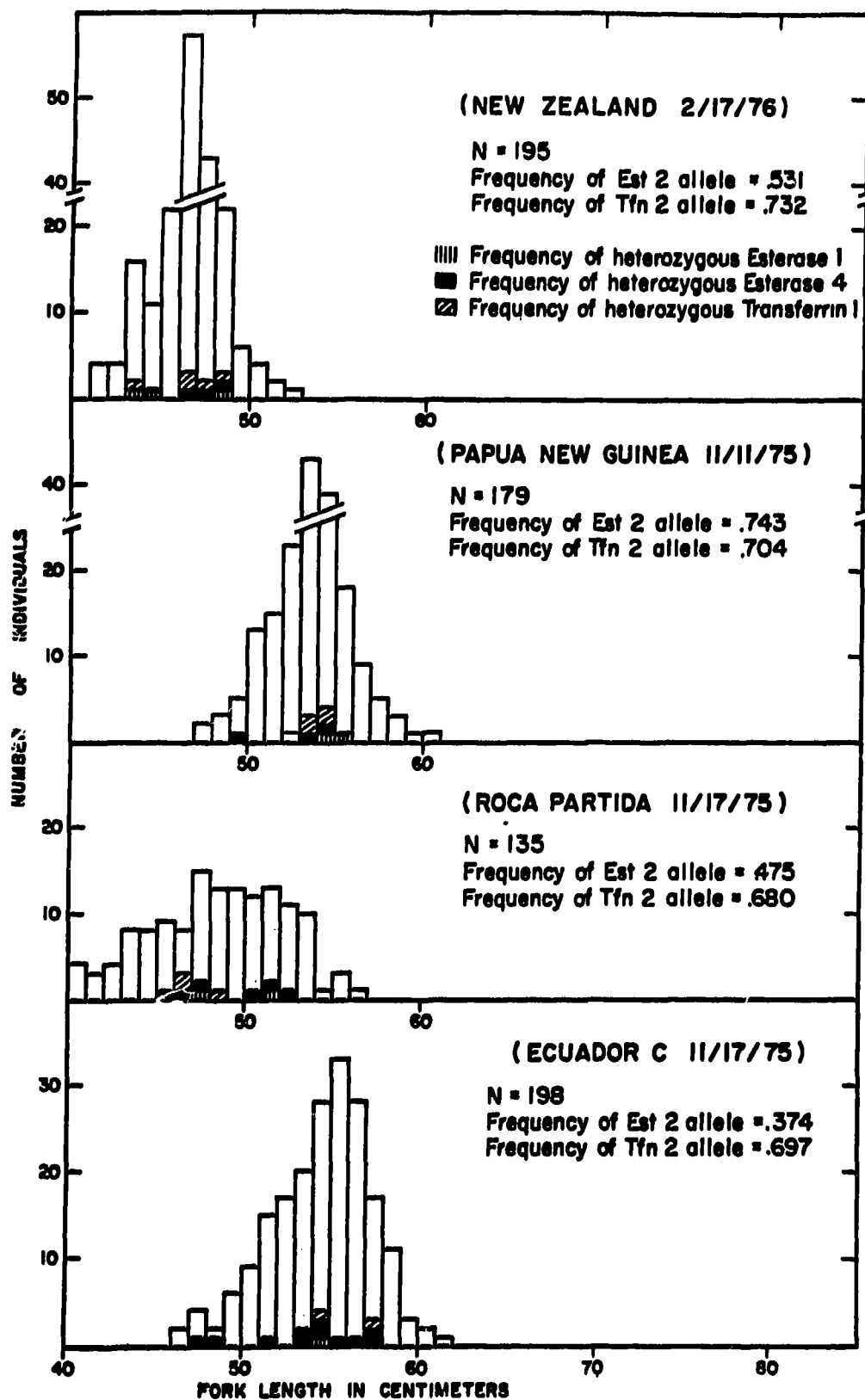


Figure 2

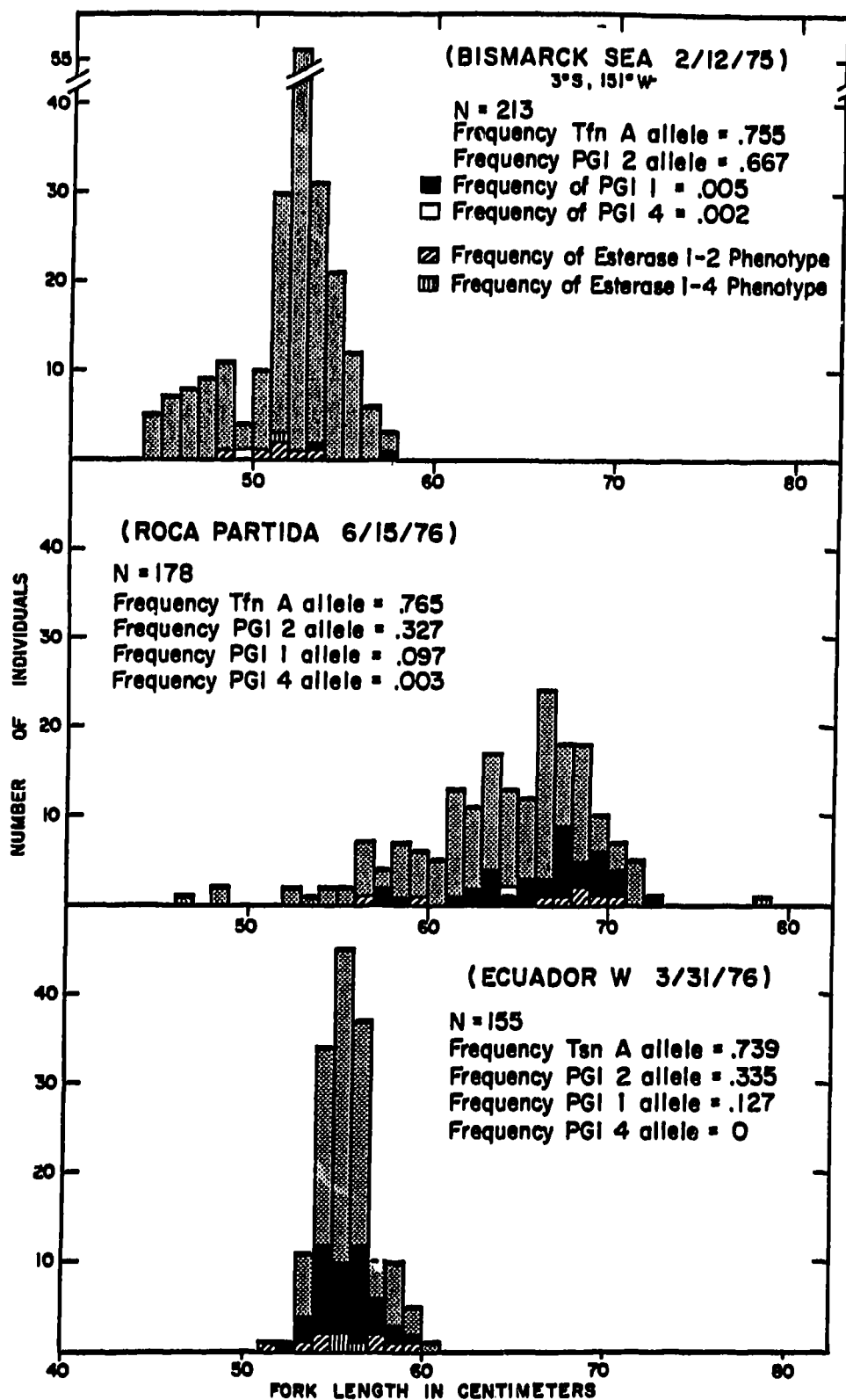


Figure 3

LOCAL OR HOMING POPULATIONS

It is not necessarily true that every individual of a cosmopolitan species will exhibit dispersive behaviour during development. Scombrid populations as well as other species appear to comprise both local and nomadic components. The proportion of nomadic individuals may be density dependent, perhaps depending upon local food abundance. This could account for the multiple component overlap and school "mixing" which is observed in tropical tunas in areas of high apparent abundance (Sharp, MS). The sporadic occurrence of unexpected cohorts or components in fisheries can often be attributed to immigration. Examination of abundance estimators from peripheral regions will usually show that any unexpected component was abundant and dominant in one or more regions, "spilling over" into the others. This behaviour has been observed in many fisheries for species with "local" population differentiation.

If the contiguous areas into which the spillover occurs are not fully occupied the opportunity for colonization is evident. Minor overlap of the population components does not necessarily imply genetic mixing will occur, particularly if the schools comprise unrelated core units in differing reproductive states.

These events can be graded from local to regional levels and beyond. They are representative of the processes which lead from local colonies onward to regional and cosmopolitan distributions.

We have numerous examples of local or "homing" populations whose entire lives may be confined to small areas (e.g. the North Sea), and whose reproduction may be limited to even smaller but very "dependable" areas. In this case the dependability of the system is absolutely required as it is clearly possible to lose the entire reproductive potential of a population if the larval habitat does not develop within the "schedule" which fish adopt in response to "local" environmental cycles.

Recent studies by Lasker (1975, 1978) have related poor year class strength in anchovies to destruction (by destratification) or later development of their larval habitat. Parrish, Nelson and Bakun (MS) have described the variation of long term characteristics affecting the California Current System which have accompanied the recent changes in species composition and biomass. They have logically developed an interesting model of biogeographic demography in the California Current System as well. Their most important point is that it is clearly possible that the larval habitat availability can restrict population size sufficiently in the early stages so that little or no strain on the carrying capacity of the system occurs by the time they become juveniles. This is likely to be a common situation and is supported by similar conclusions from modelling studies of tuna energetic requirements in comparison to food availability (Sharp and Francis, 1976).

Another aspect, perhaps too often ignored, is the decline in genetic and/or behavioural diversity which results from elimination of peripheral, localized populations by exploitation of environmentally stressed portions of populations. The California sardine was known to have at least three independent racial components before its decline (Vrooman, 1964). Of the three unique components only the Gulf of California stock has recovered to exploitable levels. Similarly, the northern anchovy in the California Current system contains at least three genetic components. Only the southernmost two have grown to exploitable levels since their biomass increase began in the early 1950's (Vrooman and Smith, 1971). It is quite difficult to imagine rapid re-establishment once these genetically characteristic population components have been eliminated due to environmental effects and/or exploitation. The subsequent recolonization of the peripheral habitats depends on numerical growth and concomitant recombination of genotypes to provide "fit" individuals, and a reversal of the stressful environmental trends.

RELATIVE STABILITY OF MARINE POPULATIONS

The Japanese sardine (*Sardinops melanosticta*) is a classic example of a complex, broadly distributed population which collapsed, resulting in a dramatic spawning area and range reduction. I have selected example material from the studies of Kondo (MS) showing the trends in catch since 1905 to 1977 of the Japanese sardine in the waters surrounding Japan. The distribution of the Japanese sardine during four stages in the decline and subsequent rise in abundance are shown in Figures 4, 5, 6 and 7. In the peak production years 1936-1937 the distribution was broad, when the entire Sea of Japan and pelagic zone of eastern Japan were occupied. Four spawning components were recognized around Japan's coastal zone. The decline in abundance was accompanied by a parallel decrease in their range. By 1940 the range had contracted to include only the pelagic zone around Japan. By 1960, there were only two spawning areas, both off eastern Japan. In 1973 the population showed the first signs of recovery which is still in progress. The range of the Japanese sardine is back to the 1940 level, including re-established spawning in the southern and western Japanese pelagic areas. This remarkable example is apparently analogous to the situation in the California Current System where Soutar and Isaacs (1974) have found evidence that both the California anchovy (*Engraulis mordax*) and the sardine (*Sardinops caerulea*) appear to go through massive population density and/or distribution changes.

The sheer numbers of recruits which are observed from the spawning biomass of these fishes during their increase phase must represent to some degree their true reproduction potential. The fact that this production rate is not "typical" but rather an extreme situation on one side of apparent cycles is proof enough that there is more to recruitment than biomass and fishery influences.

In the case of even more localized populations than those used in previous examples it is even more critical that the local spawning or "home" habitat be very stable in occurrence. Species whose reproduction is limited to small, restricted "home" habitats are seriously affected if the home habitat has shifted or ceased to be appropriate for larval survival. For any local or homing population when the habitat boundaries shift there is generally an effective increase or reduction in the potential larval habitat which directly influences reproductive potential and the subsequent changes in population size and distribution. Where the adult population habitat is shrinking it is easy to predict a decrease in reproductive potential due to "crowding" of larval habitat. Where the adult habitat is expanding, if the adult population is not relatively nomadic, it is possible to under-utilize the potential larval habitat, perhaps yielding slower population growth than one could expect. In the non-nomadic species, active transport by currents, wind stress effects, diffusion (Parrish, Nelson and Bakun, in press) and sheer luck ultimately determine their rates of increase in both numbers and area of distribution. The relative longevity of species with this mode of colonization is probably a fair indication of the relative variation in the available larval habitat. Those homing species with long life cycles (e.g. North Sea herring) occupy the more variable zones in comparison to those with shorter lives (e.g., Peruvian anchoveta). An important consideration in comparing expectation in population stability of nomadic and homing species is the probability of collapse of a stressed population. I cannot but conclude that the broad ranging nomadic species, considered as a whole, go through far smaller relative biomass changes than do homing species, or even local populations within the nomadic species. If one can use catches of commercial species to draw inferences about population abundance, then the three examples to follow support these conclusions.

The previously described changes in Japanese sardine range and spawning distribution parallel the catch records (Figure 8). Also in the northwest Pacific Ocean, there has been a relative stability in the skipjack tuna catch (Figure 9), except for the period when fishing effort was limited due to the Second World War (1939-1950). The changes in ratios of apparent abundance of these two regional examples are more than 250X in the case of the Japanese sardine, and only about 3X in the skipjack.

Figure 4

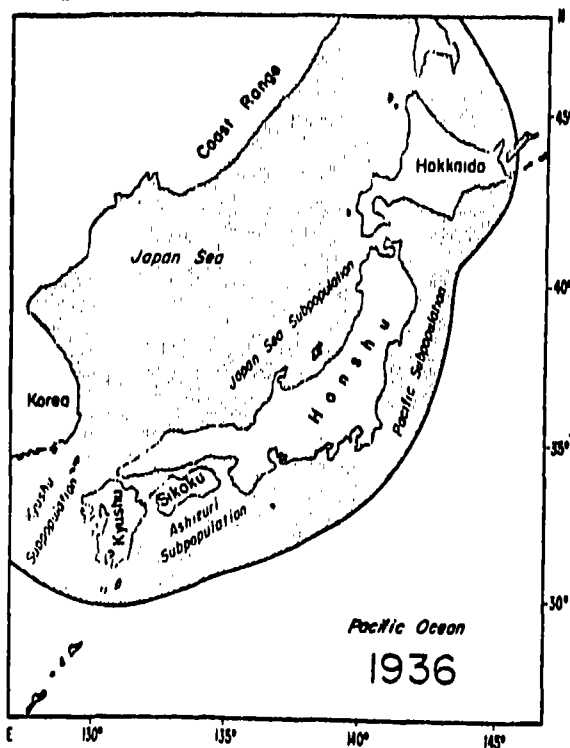


Figure 5

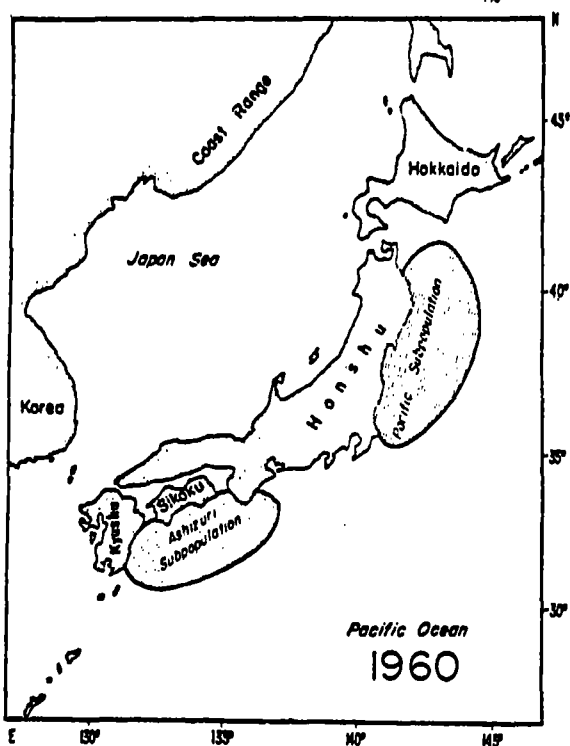
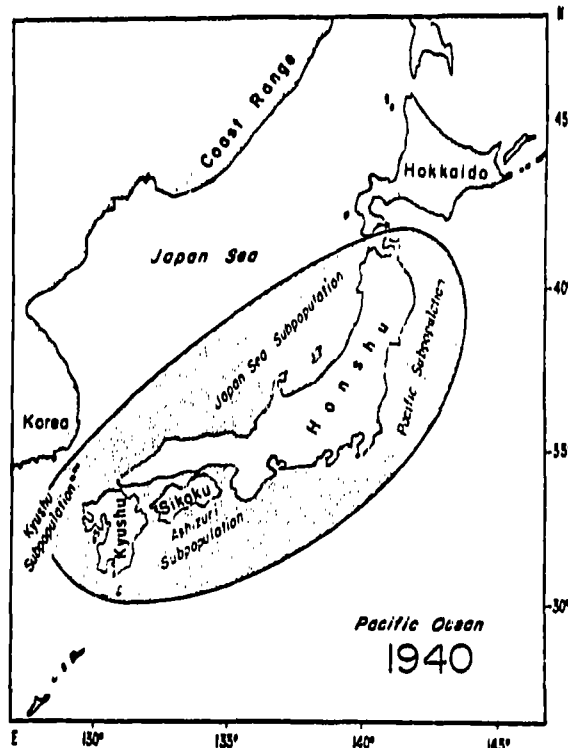


Figure 6

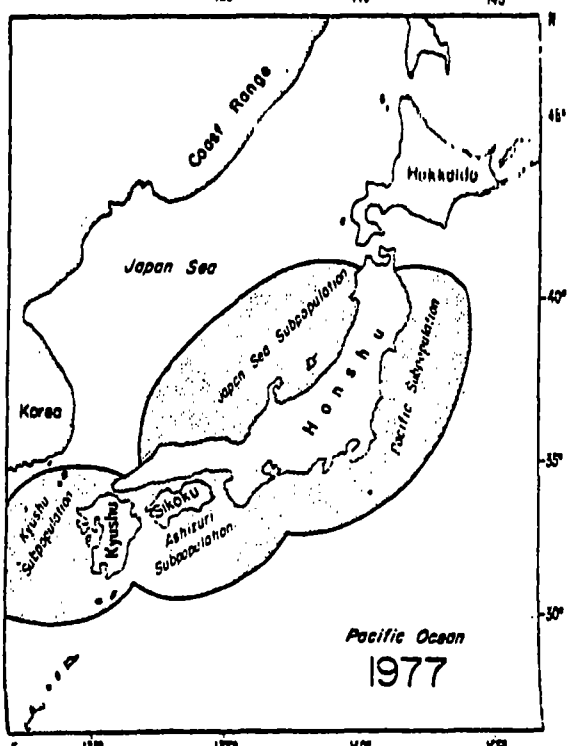


Figure 7

Figure 8

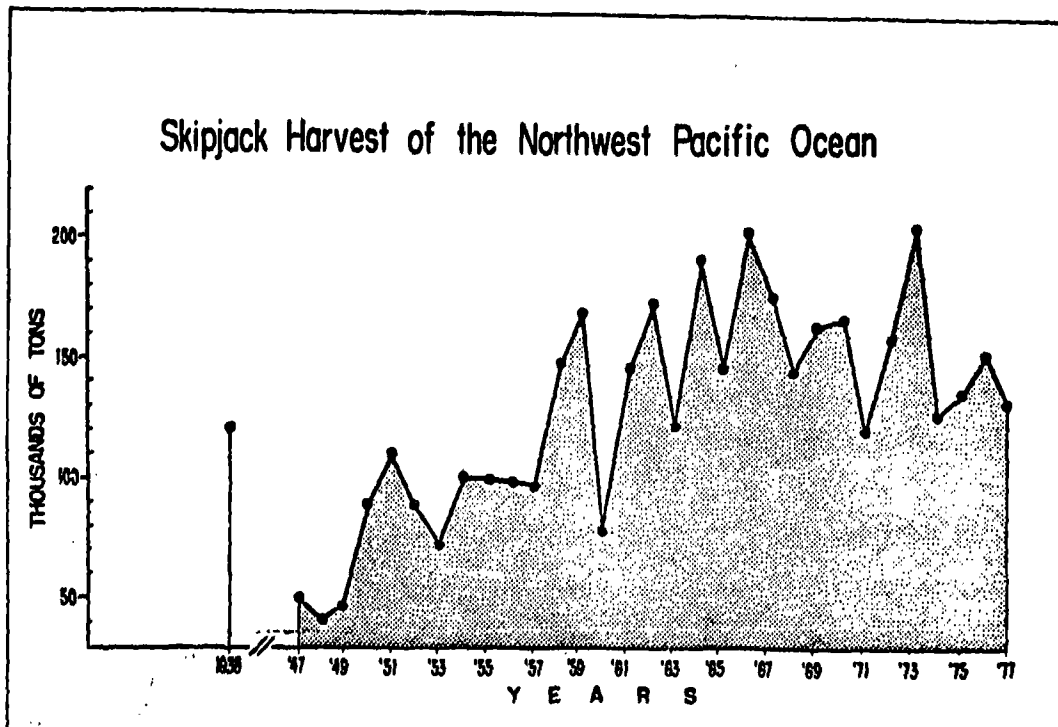
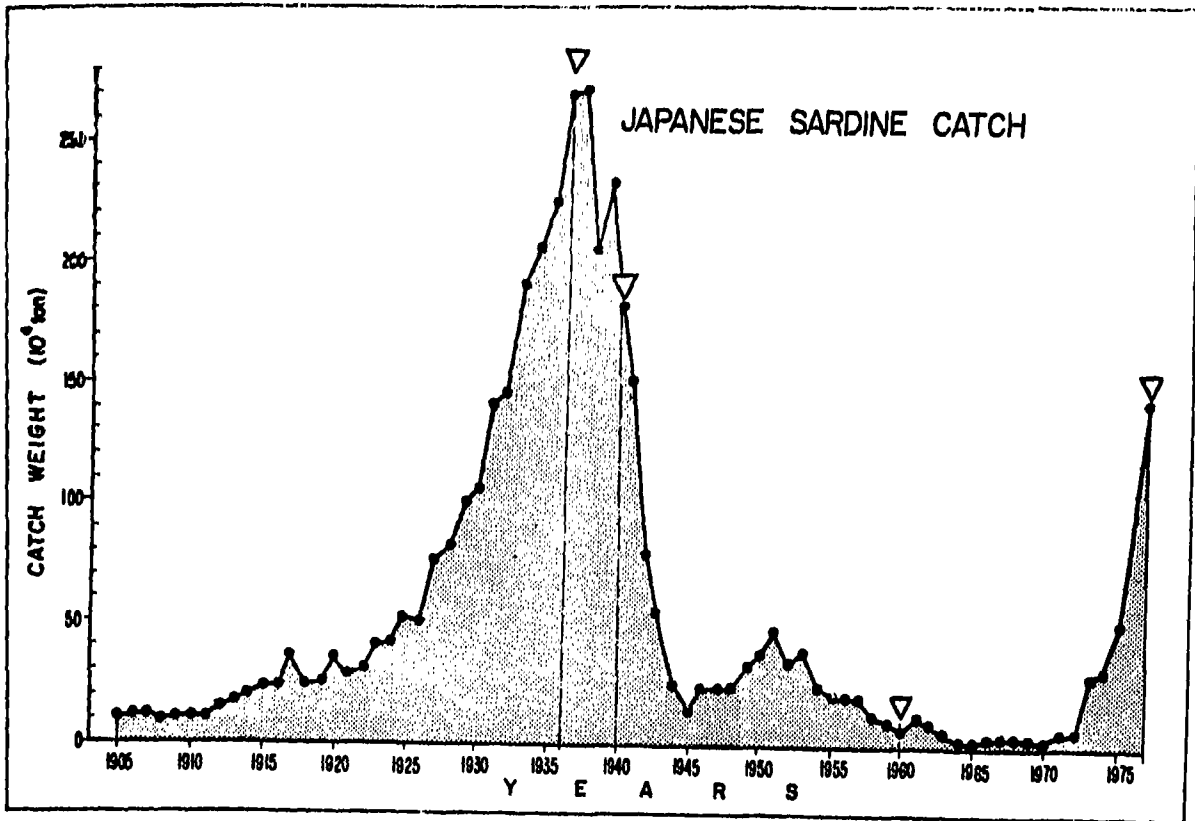


Figure 9

In the eastern Pacific Ocean yellowfin tuna fishery there are regions which appear to comprise primarily "local" populations in some years, and mixtures of various independent cohorts in others comprising both local and nomadic yellowfin from peripheral areas (Sharp, MS). In Table 1, taken from p. 38 of Sharp and Francis (1976), there is a description of annual variations in cohort catches within the three sub-regional areas which can be considered to include "local" and nomadic components of the eastern Pacific Ocean yellowfin population. The largest ratio between catches from any single recruitment semestral cohort (fish recruited in the same 6-month period, any years) within any of the three sub-regions is about 5X, whereas between sub-regions for the same recruitment period the variation approaches 19X. The catches of yellowfin tuna along the entire coastal zone of the eastern Pacific have been relatively stable since the full development of exploitation of this zone in 1961. Figure 10 shows the catch of yellowfin within 200 miles of the coast from 1961 to 1976. The ratio of greatest to smallest catch is less than 3X. This shows the regional stability characteristic of populations with large nomadic components in contrast to local or sub-regional variations.

TABLE 1.—For the years 1964-71 the data are presented for the catch in short tons by semestral cohort in the three areas (N, S, B) within the CYRA. Also given are the percent of the total catch ($S_A + S_B + B_B$) by cohort within the areas. The category, B_B , represents the fish of length $\bar{l}$ greater than 145 cm which we feel are not ageable under the present system. The percent of the individual semestral cohorts (S_A or S_B) caught in the three areas is also given. Note the erratic shifting of the cohort dominance (S_A or S_B) in the catch as well as the distribution of the cohorts between areas.

Year	North A	S A	South A	Total A	North B	S B	South B	Total B	Total A + B	B_B
1964	27,452	9,401	5,209	42,062	33,561	5,881	17,515	56,957	99,019	2,921
% total A + B	28.9	9.2	5.1	41.2	32.9	5.8	17.2	55.9		2.9
% total A or B	65.3	22.4	12.4		58.9	10.3	30.8			
1965	18,987	13,512	6,406	38,885	24,064	14,164	8,386	46,614	85,499	4,543
	21.1	15.0	7.1	43.2	26.7	15.7	9.3	51.6		5.0
	48.8	34.7	16.5		51.6	30.4	18.0			
1966	7,769	23,128	20,176	51,073	10,292	11,394	14,771	36,457	87,530	3,626
	8.5	25.4	22.1	56.0	11.3	12.5	16.2	40.0		4.0
	15.2	45.3	39.5		28.2	31.3	40.8			
1967	20,899	9,864	7,664	37,927	29,482	8,572	11,867	49,921	87,848	1,802
	23.1	10.7	8.5	42.3	32.9	9.6	13.2	55.7		2.0
	54.6	25.2	20.2		59.1	17.2	23.8			
1968	16,361	23,921	13,552	53,834	33,917	22,132	3,126	59,177	113,011	1,802
	14.3	20.9	11.8	47.0	29.6	19.3	2.7	51.6		1.4
	30.4	44.4	25.2		57.3	37.4	5.3			
1969	22,437	20,034	9,030	51,501	34,887	29,587	5,848	70,122	121,623	4,888
	17.7	15.8	7.1	40.7	27.8	23.4	4.5	55.4		3.9
	43.8	38.9	17.5		49.8	42.2	6.1			
1970	39,197	15,942	10,529	65,668	43,476	13,257	11,125	67,858	133,526	9,176
	27.5	11.2	7.3	46.0	30.5	9.3	7.8	47.6		6.4
	59.7	24.3	16.0		64.1	19.5	16.4			
1971	12,372	18,719	14,453	45,544	17,357	25,283	15,712	58,352	103,896	9,277
	10.9	16.5	12.6	40.2	15.3	22.3	13.9	51.6		8.2
	27.2	41.1	31.7		29.7	43.3	26.9			

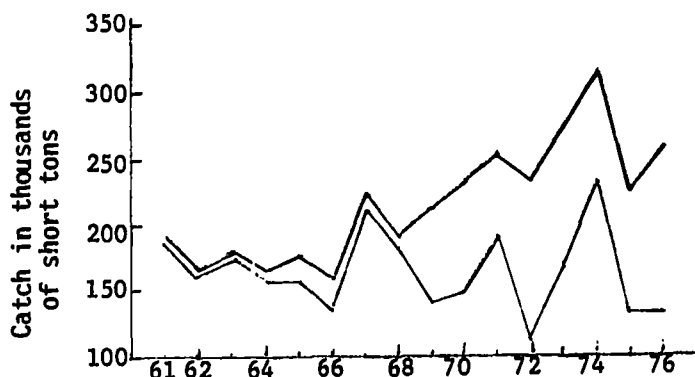


Figure 10.
Upper line: annual total catch by the eastern Pacific yellowfin surface fishery.
Lower line: catch within 200-mile economic zones in the eastern Pacific.

Examples of pelagic fisheries, which have had annual catch peaks of more than 5X the lowest catches during the period 1970 to 1977 are tabled below. It is expected that some of these catch variations are due to changes other than just population-environmental interactions (e.g., fishing effort, unreported catches). However, many reflect real recruitment and biomass effects which stem to some degree to local habitat variation, particularly those with very large increases in catch during this period.

TRAJECTORIES OF CATCH TRENDS FROM 1970-77

Species	Area	(A) Peak Catch	(B) Low catch	Ratio (A/B)	
<i>Caranx hippos</i>	West Africa	28 221	1 036	27.	+
<i>Oreynopsis unicolor</i>	West Africa	2 600	100	26.	-
<i>Trachurus capensis</i>	Southwest Africa	690 164	62 300	11.	+
<i>Trichoturus lepturus</i>	Southwest Africa	28 545	3 800	7.5	+
<i>Trachurus trachurus</i>	Southwest Africa	273 700	31 298	8.7	-
<i>Sardinella spp.</i>	Southwest Africa	142 200	20 986	6.8	- +
<i>Scorpaenopsis japonicus</i>	Peru	65 000	8 700	7.5	+
<i>Scorpaenopsis japonicus</i>	Northeast Atlantic	39 000	6 262	6.2	-
<i>Rastrelliger spp.</i>	Eastern Indian Ocean	16 300	2 000	8.2	+
<i>Rastrelliger kanagurta</i>	Eastern Indian Ocean	203 100	35 403	5.7	
Anchovies	Western Indian Ocean	118 062	16 900	7.0	+
<i>Peenopsis anomala</i>	Northwest Pacific Ocean	13 000	1 994	7.0	-
<i>Sardinops melanosticta</i>	Northwest Pacific Ocean	1 420 512	16 900	84.	+
<i>Engraulis mordax</i>	Eastern Pacific Ocean	289 002	44 600	6.4	+
<i>Cetengraulis mysticetus</i>	Eastern Tropical Pacific	168 081	15 551	10.8	+
<i>Trachurus symmetricus</i>	Eastern Pacific Ocean	50 149	9 400	5.3	+
<i>Sarda chilensis</i>	Southeastern Pacific Ocean	74 700	4 341	17.2	-
<i>Scorpaenopsis sierra</i>	Peru	2 279	400	5.7	+
<i>Engraulis ringens</i>	Peru	13 059 900	807 175	16.	-
<i>Sardinops sagax</i>	Peru-Chile	1 467 555	68 600	21.	+
<i>Trachurus trachurus</i>	Peru-Chile	839 805	111 300	7.6	+
<i>Thysitops lapidopodes</i>	Chile	7 200	630	11.6	-
<i>Cetengraulis edentulus</i>	Venezuela	4 96	850	5.8	- +
<i>Decapterus russelli</i>	Malaysia-Thailand	109 337	9 800	11.2	+
<i>Scorpaenoides spp.</i>	Indonesia-Philippines	5 186	500	10.	+

Plus and minus signs in the Table represent directions of trends during the reference period. The indication - + implies sharp changes in both directions in the order indicated.

These data illustrate the local or sub-regional variations in catch from pelagic populations on the short term (1970-1977). Even greater changes are expected on the long-term as previously described in the case of the Japanese sardine. The trends in catches and relative abundances of the oceanic opportunist species such as the tropical tunas, large billfishes and other cosmopolitan types vary on the order of 2 to 3X, but rarely as much as 5X. Where records indicate changes of such magnitude for the cosmopolitan oceanic species, they usually correspond with changes in either economic or effort distribution patterns, rather than representing relative abundance changes.

From an examination of the available information on relative abundance changes on the short and medium-term, the entire concept of population stability is questionable. The long-term and very short-term trends tend to be under emphasized in resource assessment in a "trade-off" with the simplifying "equilibrium in the medium-term" concept. The importance of multispecies interactions and their perturbation by non-man mediated processes is another complication in the application of single species equilibrium methods in stock evaluation studies. Careful examination of parallel changes in biomass composition in productive localized or regional fisheries often shows a relatively stable total biomass, with compensatory changes among the various species components. This nearly constant condition is only likely to occur in most marine systems as long as the primary production cycle remains relatively stable, and where the replacement species are ecologically equivalent. Both are unlikely events.

I have offered several observations, criticisms and re-evaluations of concepts in this discussion. I hope that they will stimulate progress rather than negate the past. Although marine fisheries have been the primary topics of my efforts, I would like to clarify a few points regarding the state of understanding of reproductive processes and adaptations to environmental processes in floodplain riverine systems and estuaries, in comparison to the available information about oviparous marine species.

Because the dynamics of floodplain systems are so great, few species in these systems produce pelagic, or free drifting eggs. Welcomme (1979) surveyed the various modes or classifications of spawning behaviour in the floodplain systems and he concluded that "Generally, the reproductive strategies are aimed at securing: 1) safe and protected places for laying and rearing eggs; 2) maximum feeding and growing time for the young fish; and 3) freedom from predation." Biological parameters of individual species respond directly to levels of flooding, drought and other short-term phenomena. For example, in many species breeding success and subsequent recruitment are much better in years with extensive flooding. Many species "stunt" in growth in response to severe habitat recession during dry years, but they tend to mature and breed earlier in response. In other species (channel breeders) floods are anathema, and their populations bloom during years of little flooding. The basic production of these complex riverine systems appears to directly respond to volume and duration of the flood cycle, and the reproductive potential of the spawning biomass.

I wonder at the complexity of the various adaptations and solutions to the barrage of environmental variation in these systems. Certainly in comparison the oceanic and pelagic resources have far fewer dynamic environmental changes in their habitats. The variations in adaptations, behavioural and physiological, are apparent, as documented in the zoogeographic implications of the Bakun and Parrish (MS) study of the California Current System, and other literature. The transition states between riverine, estuarine and tidal systems, in contrast to open ocean processes, also warrant a few words in comparison.

Legget and Carscadden (1978) showed that five separate populations of American shad (*Alosa sapidissima*) on the Atlantic coast have developed separate behavioural and physiological responses to the variable physical regimes of their spawning grounds. The northern populations allocate more of their energy reserves to upstream migration to "secure" their reproduction by increasing postspawning survival of their young. Fecundity is lower in the northern populations, and repeat spawning of individuals increases in contrast to the higher (3 to 5X more eggs per kg) fecundity and semelparous nature of the southerly populations.

Garcia and Le Reste (in press) have synthesized available literature and observations on penaeid shrimp production in the world. They describe the variations in geographic and climatic conditions for various fisheries, primarily because recruitment, hence production appears to be directly responsive to rainfall patterns and estuarine flushing dynamics, and little dependent upon adult biomass beyond the obvious "too few" cycle described earlier. Apparently "very few" penaeid shrimp can generate the same recruitment as "a large number", given the physical-climatic patterns are appropriate. This implies that more of the "potential" is realized, while the absolute abundance of adults may not be relevant in most cases. There are also direct effects of tidal flow and rainfall and ground-water flushing patterns in the estuarine systems which influence patterns of size at recruitment as well as abundance. These observations imply differential transport of various life history stages and groups of individuals. Rather than variable growth patterns, more variation in survival is implied.

Caddy (in press) examined the problem of cyclic recruitment in the Bay of Fundy scallop fishery. After evaluating many hypothetical cause and effect relations involving fishing pressure, spawner-recruitment relations and others, the regular periodicity in recruitment (9 years) could best be ascribed to similar environmental cycles associated with tides. The Bay of Fundy has the greatest tidal flux known on earth (15.4 m at the head of the Bay), and as such provides a milieu including an anti-clockwise gyre in the centre of the Bay which appears to be influenced by the tide. The gyre is hypothesized to effect larval scallop retention in the Bay, and in this fashion influences scallop harvests in a cyclic fashion tied to the tidal flux cycles.

These three examples show three separate modes of colonization: 1) direct deposition of eggs into amicable larval habitat which is not conducive to survival in the adults; 2) the independent transport and development of larvae via physical current flow into estuarine systems which may be fresh, hypersaline, or stratified, depending upon geographic location and seasonal events, to which the larvae and juveniles are adapted, but not the adults; and 3) the completely independent, physical transport system dependent redeposition of larvae or spat into the preferred range of the adult biomass. Each form of colonization portrayed is highly dependent upon physical ambient processes as much or more than on the adult behaviour. The exceptional case of the high energy expenditure in the northern shad populations can be matched by similar diversification in behaviour in and among the various species of shrimp. The Bay of Fundy scallops have certainly developed reproductive strategies which, although they are highly susceptible to the long-term trends in non-biological physical processes in a very dynamic system, make them successful in this extreme habitat.

All of these examples and the preceding discussion point to the importance of plasticity of behaviour and reproductive potential in facing the problems imposed by highly variable ambient systems. The maximization of spawning potential may best be in expending energy in search of amicable larval habitats (e.g. as in the shads and tunas), whereas homing behaviour seems to suit coastal pelagics more, although it apparently leads to greater overall biomass fluctuations. The "migratory shad" appear to be a precursor stage to the more famous, but highly specific behaviour of salmonids. Generalizations on the topic seem to be superfluous given the incredible array of extant variation from which to choose.

CONCLUSIONS

The critically important facts that larval fishes require finite densities and corresponding geometries of appropriate sized food for survival, and that these requirements are not constant in the world ocean, or even in local habitats, has only relatively recently become the focus of attention in fishery science. Since the germinal studies of Hjort (1914) and Hardy (1936) the concepts of "critical" life stages and plankton patchiness have been argued. Again, only recently have the important scales of interaction of these two concepts been clearly identified (Beyer, 1976; Vlymen, 1977; Beyer and Laurence, 1978; Lasker MS; Owen MS). Perhaps after a few years of application of finer scale sampling and correlation studies with gross scale climatic and oceanographic events, we will be able to retrieve some of the information of interest from the historical data base and extend our understanding of what has happened; however, this should not be the main thrust of fishery science today.

The crucial processes to be immediately emphasized in fishery research as it relates to project of abundance and distribution of fish populations are 1) definition of appropriate larval habitats for each resource species; 2) the monitoring of numbers, condition and distribution of spawning adults in relation to appropriate larval fish habitats; and 3) determination of the variation in appropriate larval fish habitats as affected by environmental processes. Further development of concepts, appropriate tools and sampling schemes for specific ecological conditions is required. Recent research has begun to define the appropriate scales and types and magnitudes of variation which are to be expected in localized or homing species habitats. These important resource components experience large natural population fluctuations. For this reason they are specifically vulnerable to the mortalities resulting from man's activities, particularly on the downward trend portion of typical bloom-recession cycles. The populations with broad ranging, nomadic reproductive components, such as the cosmopolitan opportunist species, are less sensitive to man's activities under present exploitation patterns. Also their overall or regional natural population abundance fluctuations are relatively smaller. This combination of events provides some measure of protection to their population status, but where local populations are exploited, even these resources can be adversely affected.

The apparent relative stability of the biomass of the broad ranging opportunist populations is due to both contributions of local populations, and the shared risks taken by the large nomadic portions of these populations in coarsing over their ranges in search of feeding grounds and hospitable spawning habitats. The dependence of local populations of oviparous fish, on the stability or continuity of local processes conducive to larval survival is well recognized. Our ability to identify many of the "critical" characteristics is developing. Until these characteristics are identified and monitored there is little hope that it will be possible to logically predict recruitment trends.

It is perhaps redundant, but I feel it has not been stressed enough that both spawning potential and the realization of this potential (via development phase-survival challenges) are directly effected by ambient events which reflect variable physical-climatic processes. The relative importance of individual processes and their interactions, which might either promote or challenge the continuity of resource populations, should certainly not be viewed as a series of equilibria, but more as a series of hurdles. Through the implied severe selection of a hurdle, one can appreciate more the remarkable variations and elegantly achieved singularities (solutions) each of these populations represents. The relative sensitivity of biological systems to physical-climatic variations should be given maximum attention if we are ever to resolve man's role as an informed, self-regulating, opportunistic predator of these resources.

SUGGESTIONS

Morphological indices have been successfully formulated in limnology which are used to classify various habitats. Ecological diversity indices are also constructed which are subsequently used to classify sub-groups of ecosystems within each habitat. The responses of each of these complexly defined "eco-types" to climatic variation is predicted by analogy with some degree of success. Similar indices need to be developed for use in the marine environment, along with appropriate climatologic characterizations. The important environmental variations which occur as patterns, trends or anomalies in seasonal or longer time scales are the events which need to be integrated into population evaluations. The development of adequate sampling programmes and long-term data bases are of paramount importance to these characterizations, if there is ever to be a means for forecasting fishery behaviour in any meaningful and practical sense.

Considering the previous discussions, the immediately important task to be faced is the development of sampling methods on appropriate scales or monitoring the many "defined" processes which effect subsequent local fishery expectation and behaviour. The necessary integration of data from the smallest up to the largest scales should follow careful analyses which are needed for evaluation of each key process to be monitored on individually appropriate scales. It is obvious in historical retrospect that it is not very effective to proceed from the alternate, disintegrative course. The levels of variation which determine population status are local, small-scale events, which when summed prematurely yield a most obscure picture. Today's dependence on monitoring techniques which neither reflect closely, or even approximately, the true status of populations before they have collapsed or seriously declined is exemplary of the problems resulting from placing too much emphasis on integrated data collection and analysis. Also, too little attention has been paid to linked cause and effect processes in the biological segments of the models or concepts used in resource monitoring. This has resulted in the relatively poor performance of predictive or forecasting schemes whose underlying principles are deduced from correlation or regression analyses rather than from derivations based on biophysical or similar theoretically sound and empirically testable bases.

REFERENCES

- BEYER, J.E. 1976a. FISH I. Survival of fish larvae - a single server queue approach. Inst.of Math.Stat.Oper.Res. Technical University of Denmark, Lyngby, 244 p.
- . 1976b. FISH II. Survival of fish larvae - a single server queue approach. Inst. of Math.Stat.Oper.Res. Technical University of Denmark, Lyngby, 68 p.
- BEYER, J.E. and G.F. LAURENCE. A stochastic model of larval fish growth. ICES C.M. 1978/L. 28. Biological Oceanography Committee
- CADDY, J.F. (in press). Long term trends and evidence for production cycles in the Bay of Fundy scallop fishery. Proc.ICES Meeting on Population Assessment of Shellfish Stocks
- CODY, M.L. 1971. Finch flocks in the Mojave desert. Theo.Pop.Bio., 2(2):142-158
- CUSHING, D.H. 1971. A comparison of production in temperate areas and the upwelling areas. Trans.Roy.Soc.South Africa, 40(1):17-33
- FUJINO, K. 1970. Immunological and biochemical genetics of tunas. Trans.Amer.Fish.Soc., Vol.99, No. 1, 152-178
- FASHAM, M.J.R. 1978. The statistical and mathematical analysis of plankton patchiness. Oceanogr.Mar.Biol.Ann.Rev., 16:43-79
- GARCIA, S. et L. Le Reste (in press). Cycles vitaux, dynamique, exploitation et aménagement des stocks de crevettes penaeides côtières. FAO Tech.Pap. series
- GIESKE, W.W.C., G.W. KRAAY and M.A. BAARS. 1979. Current ¹⁴C methods for measuring primary production: gross underestimates in oceanic waters. Netherlands J. of Sea Res., 13(1):58-78
- HARDY, A.C. 1936. Observations on the uneven distribution of the oceanic plankton. Discovery Reports 11:511-538
- HJORT, J. 1914. Fluctuations in the year classes of important food fishes. J.du Conseil 1(1):5-38
- HOUDE, E.D. 1976. Critical food levels for growth and survival of laboratory-reared larvae of three species of subtropical marine fishes. Contribution presented at Joint Oceanographic Assembly, Edinburgh, September 1976.
- . 1977. Food concentration and stocking density effects on survival and growth of laboratory-reared larvae of bay anchovy *Anchoa mitchilli* and lined sole *Achirus lineatus*. Mar.Biol., 43:333-341
- HUNTER, J.R. 1972. Behavior and survival of northern anchovy *Engraulis mordax* larvae. Fish.Bull., U.S., 70(3):821-838
- . 1977. The feeding behavior and ecology of marine fish larvae. Prepared for the Conference "The Physiological and Behavioural Manipulation of Food Fish as Production and Management Tools". Bellagio, Italy, 3-8 November 1977.
- HUNTER, J.R. and C. KIMBRELL. MS. Growth, starvation, yolk absorption, and oxygen consumption of larvae of the mackerel *Scomber japonicus* Houttyn with notes on laboratory rearing through metamorphosis

- HUNTER, J.R. and G.L. THOMAS. 1974. Effect of prey distribution and density on searching and feeding behaviour of larval anchovy *Engraulis mordax* Girard, pp. 559-574. In J.H.S. Blaxter (ed.), The Early Life History of Fish. Proc.Int.Symp. Dunstaffnage Mar.Res.Lab., Scottish Mar.Biol.Assoc., Oban, Scotland, May 17-23, 1973. Springer-Verlag, Berlin, Heidelberg, New York
- KONDO, K. MS. How has the stock of the Japanese sardine recovered? Biological basis of stock size fluctuations. ICES Symposium on the Biological Basis of Pelagic Fish Stock Management. Aberdeen, Scotland, 3-7 July 1978.
- LASKER, R. 1975. Environmental studies of the feeding regime of the larval anchovy in the Los Angeles Bight. Southwest Fisheries Center Admin.Rep.No.LJ-75. 29 p.
- _____. 1978. The relation between oceanographic conditions and larval anchovy in the California Current: identification of factors contributing to recruitment failure. Rapp.P.-v.Réun.Cons.Int.Explor.Mer 173:212-230
- _____. MS. Identification of factors contributing to variable recruitment of the northern anchovy in the California Current: contrasting years 1975 and 1978. ICES, Early Life History of Fish Symposium, Woods Hole, Massachusetts, April 2-5, 1979
- LASKER, R., H.M. FEDER, C.H. THEILACKER and R.C. MAY. 1970. Feeding, growth and survival of *Engraulis mordax* larvae reared in the laboratory. Mar.Biol.5:345-353
- LASKER, R. and J.R. ZWEIFEL. 1978. In press. Growth and survival of first-feeding northern anchovy larvae (*Engraulis mordax*) in patches containing different proportions of large and small prey. Spatial Pattern in Plankton Communities (ed. J.H. Steele), Plenum Press, New York.
- LAURENCE, G.C. 1974. Growth and survival of haddock (*Melanogrammus aeglefinus*) larvae in relation to planktonic prey concentration. J.Fish.Res.Bd Can., 31(8):1415-1419
- LETT, P.F. and A.C. KOHLER. 1976. Recruitment. J.Fish.Res.Bd Can.33:1353-1371
- OWEN, R.W. MS. Midwater microlayering of biological particles in ocean waters
- _____. Patterning of flow and organisms in the larval anchovy environment. This volume.
- PARRISH, R.H., C.S. NELSON and A. BAKUN. MS. Larval transport mechanisms and reproductive success of fishes in the California Current. Submitted to Fish.Bull., U.S.
- RIFFENBURGH, R.H. 1969. A stochastic model. J.Fish.Res.Bd Can.26:2843-2880
- SHARP, G.D. 1978. Behavioral and physiological properties of tuna and their effects on vulnerability to fishing gear; pp. 397-450. In G.D. Sharp and A.E. Dizon (eds), The Physiological Ecology of Tunas. Academic Press, New York, San Francisco, London
- _____. MS. In review. A population study of some tropical Pacific tunas with emphasis on evolutionary implications inferred from distribution, morphological, age frequency, and biochemical genetic data.
- SHARP, G.D. and R.C. DOTSON. 1977. Energy for migration in albacore, *Thunnus alalunga*. Fish.Bull., U.S. 75(2):447-450
- SHARP, G.D. and R.C. FRANCIS. 1976. An energetics model for the exploited yellowfin tuna, *Thunnus albacares*, population in the eastern Pacific Ocean. 74(1):36-50

- SHARP, G.D. and W.P. KANE. MS. In review. Biochemical genetic comparison and differentiation among some eastern Atlantic and Pacific Ocean tunas.
- SUZUKI, Y., M. NAKAHARA, R. NAKAMURA and T. VEDA. 1979. Roles of food and sea water in the accumulation of radionuclides by marine fish. Bull.Jap.Soc.Sci.Fish.45(11):1409-1416
- TIJJSSEN, S.B. 1979. Diurnal oxygen rhythm and primary production in the mixed layer of the Atlantic Ocean at 20°C. Netherlands J.of Sea Res. 13(1):79-84
- VLYMEN, W.J. 1977. A mathematical model of the relationship between larval anchovy (*Engraulis mordax*) growth, prey microdistribution and larval behaviour. Env.Biol.Fish. 2(3):211-233
- VROOMAN, A.M. 1964. Serologically differentiated subpopulations of the Pacific sardine, *Sardinops caerulea*. J.Fish.Res.Bd Can.21(4):691-701
- VROOMAN, A.M. and P.E. SMITH. 1971. Biomass of the subpopulations of northern anchovy, *Engraulis mordax* Girard. Cah.Coop.Oceanic Fish.Invest.Rep.15:49-51
- WELCOMME, R.L. 1979. Fisheries ecology of floodplain rivers. Longman Group Limited (Publishers), London, 317 p.

**PATTERNING OF FLOW AND ORGANISMS IN THE LARVAL
ANCHOVY ENVIRONMENT**

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INTRODUCTION

This work reviews patterning of plankton populations and communities by their interaction with physical processes, with special reference to eastern boundary regions and their capacity to support early stages of engraulid fish populations. It describes patterning mechanisms and effects documented by case studies appropriate to a large range of scales and restates some old hypotheses. Coastal upwelling and its biological effects are treated in only a general way. The literature is extensive and is covered elsewhere in this volume (cf Bakun and Parrish).

By the time its yolk-sac is gone, an anchovy larva is a seeing animal with a functioning digestive system and an immediate need for food. It feeds by the hunt-and-peck tactic (Hunter, in press), selecting at first for rather specific particle types from the wide variety of organisms and detritus that it encounters. Favoured food particles are single, rounded plant cells or animals 20-120 μ m in width which lack long spines (Arthur, 1976; de Mendiola, 1974). On the average, even in upwelling zones, it is unlikely to encounter enough particles to meet its metabolic needs (e.g., Lasker, *et al.*, 1970). This average, however, is known from methods that sample inappropriate volumes of water at inappropriate intervals. The interval immediately appropriate to a larva is the volume it searches in a day, and the path it takes to search this volume. These are as small as a litre and a few metres, respectively, as derived from Hunter's (1972) laboratory experiments, Smith's (1978) observations on plankton variability, and Vlymen's (1977) theoretical treatment of food concentration geometry and larval fish energetics. It is evident from work on inappropriately large intervals that larval food must occur in patterns in space and time to exceed concentrations larvae require, and that systematic approaches need to be taken to estimate the scale and degree of food patterning in the larval habitat in areas and at times of spawning if fishery models are to be realistically expected to specify recruitment under any particular measurable regime.

There is a considerable body of evidence that patchiness of plankton frequently and widely arises from patterned circulation. Environmental circumstances under which such patterns arise are often rather unexceptional, and thus may be more widespread than isolated case studies describe. There is also some promise of prediction of patterning and depatterning circulations, which would be of inestimable value in forecasting yield of fish stocks as affected by patterning of their food supply. Accounting for patterning of organisms should also enhance the accuracy of biological production models constructed for populations at any position in the food web.

MESOSCALE PLANKTON PATTERNING AND OFFSHORE ENRICHMENT BY EDDIES

Eddies arise from flow instability, uneven wind forcing and current deflection or separation at boundaries. They may be imbedded in the surrounding flow ("free"), or geographically stationary ("trapped"). Both free and trapped eddies can arise from frictional interaction with obstacles such as coastlines, islands and banks.

Planktonic communities, as well as some benthic and terrestrial populations, can be extended by eddy processes into otherwise marginal habitats, either continuously or sporadically. The fate and dilution rate of anthropogenic products (e.g. MacGregor, 1974) and their effect on island, coastal and oceanic populations are also in part determined by eddy-like perturbations. Eddies also affect such local environmental conditions as temperature and nutrient distribution in the water and cloud cover in the atmosphere. Genesis, maintenance and lysis of eddies are of particular interest because organisms and substances in transit become differently distributed in space and time within and between eddies; concentrations of organisms and substances are locally maintained at higher levels and for longer periods, their trajectories are markedly different, and plankton populations which would not otherwise interact are juxtaposed. Eddies greatly amplify rates of transfer of materials (and energy) between nearshore upwelling zones characteristic of eastern boundary margins and pelagic regions well seaward of the continental shelf. Fronts that frequently bound upwelling zones cause slow subduction of surface waters into deeper, vertically stable strata of the offshore pycnocline. Eddy motion, whether the small-scale result of flow instability along the front or of mesoscale impingement from offshore, produces both surface and subsurface transport from upwelling zones.

Satellite imagery of thermal patterns at the sea surface off California indicate extensive seaward transport of cold water from upwelling zones by eddy motion. Thermal plumes can be traced for several hundred km offshore across the mean flow of the California Current (Bernstein *et al.*, 1977).

Cyclonic eddies larger than 10 km in diameters and a week's duration may have a major role in sustaining the higher biological concentrations and productivity which are characteristic of the inshore 200 km of the California Current System (CCS). Baroclinic eddies deform the density field. A cyclonic eddy or meander of sufficient size and intensity exhibits a detectable dome in surfaces of constant density to the depth where the eddy motion vanishes. Doming signals that the thermocline layer, which marks a sharp increase in water density with depth, has risen and displaced surface mixed-layer water. The displaced water is usually stripped of nutrients and often poor in phytoplankton as well. In eastern boundary regions, the thermocline is nutrient-laden and comparatively close to the sea surface. Elevation of the thermocline due to cyclonic motion thus results in upward flux of nutrients into the photic zone, which supports growth of phytoplankton. The new availability of nutrients is sustained by upwelling (here meaning upward flow across density surfaces) in and near the eddy centre and can be augmented by mixing and entrainment due to shear flow across the thermocline layer of the eddy. Additional nutrients are supplied in episodic fashion during storm activity which is either long or severe enough to erode the dome, with its relatively exposed p $\acute{a}$ te (e.g. Blackburn, 1966).

The presence of a cyclonic eddy, however, does not assure photic layer enrichment. Such a case is provided by the transitory Hawaii Eddy phenomenon. Despite the large vertical displacement (50-150 m) of the thermocline attributable to doming (Patzert, 1969), nutrient-rich waters lie too deep for enrichment of the photic zone to occur. Water deeper than about 300 m would have to be raised more than 200 m to reach the bottom of the photic zone. McGary (1955) consequently found no evidence for photic zone enrichment that could be attributed to the Hawaii eddies. Other significant biological processes are, however, evidently affected; Sette (1955) describes evidence for the effect of the eddies on local fish populations.

If an eddy is stationary, e.g. topographically trapped, it can collect and locally conserve substances washed down from the boundary layer of the obstacle(s). Small eddies with short transit times thus extend the effective area of the boundary layer. Laboratory and field work with natural phytoplankton communities (recently, Thomas *et al.*, 1980; Estrada and Blasco, 1970) indicates that phytoplankton populations respond differentially to changes in nutrient flux and can create new sequences of community position on time scales greater than a few days. Transit times around mesoscale eddies are longer, so that new and distinguishable community compositions may arise at higher trophic levels as well as at the level of primary production. Thus seed populations in large trapped eddies can respond differentially and rapidly create new community sequences in transit. Close examination of biological effects of eddies seems warranted, for example, to determine whether eddy processes affect production of food organisms that support larvae and adults of the commercially and ecologically significant anchovy, *Engraulis mordax*. This may occur through effects of eddies on boundary layer extension, community structure, productivity and concentration of small plankton; all important factors in determining survival of the large numbers of anchovy spawned in such regions (Lasker, 1975; Smith, 1978).

Eddy genesis

In the vicinity of the island, bank and coastline systems, combinations of wind, current and topographic effects must be invoked to explain patterns of circulation (Pavlova, 1966; Arthur, 1965; Reid, 1965). The variability of flow impinging on obstacles couples with local topography to create or suppress eddy and front patterns. Wind patterns exercise significant control upstream by determining the impinging flow intensity and direction, and locally by augmenting or cancelling the topographic perturbations of water flow. Local-scale wind patterns are in turn affected by islands and coastlines. It is easy to understand why no theoretical treatment of flow consistently accounts for observed current patterns downstream of the islands, banks and coastlines of eastern ocean boundaries.

Large-scale eddy genesis by wind is indicated in Nelson's (1977) water transport calculations, derived from wind patterns off the west coast of North America. Flow directions are shown which are consistent with equatorward transport of the California Current, onshore transport south of the Southern California Bight, and nearshore poleward transport of the Southern California Countercurrent. These are elements of the Southern California Eddy, although Nelson's averaging scale is too large to resolve this eddy directly. On smaller scales, case studies (e.g. SIO 1962; Patzert, 1970) have shown that uneven wind distributions can create eddy circulations.

The distribution of wind speed and direction over the region of the Southern California Bight during northwest wind conditions (U.S. Dept. of Interior, 1978) may exhibit a two-jet system, consistent with wind retardation by the northern Channel Islands of a single jet impinging from the north. A high-wind zone is characteristic about 200 km off the California coast from April through August (Reid *et al.*, 1958; Alan Hancock Foundation, 1965). Its role in eddy genesis is unassessed as yet, although jet-like winds impart stress transport that would favour formation of small-scale mesoscale eddies.

Reports of atmospheric and oceanic eddy systems due to islands often taking the appearance of von Kármán vortex wakes, have become well documented in recent years. Barkley's (1972) oceanographic study of Johnston Atoll's wake is the definitive example of vortex shedding of water by an island. As Barkley states, increasing reports of atmospheric marine effects are due to "... a special combination of circumstances: the wind, an obstacle, the right kind and quantity of cloud cover at the proper level, and a satellite overhead taking pictures; all must be present." Vortex wakes and other types of eddy patterns due to boundaries are apt to be common in ocean and atmosphere. Berger and Willie (1972) and Chopra (1973) review these phenomena and their dynamics. Of obstacles in the CCS, only Isla Guadalupe receives direct mention, but Chopra also reports effects of both smaller and larger islands elsewhere which show that obstacles of virtually any size may produce systematic flow deviations. Boundaries and direct wind effects are not prerequisites for

eddy formation. Instability of flow can develop from current jets and convergences (e.g. Barkley, 1968) and eddies are commonplace in the open sea (Bernstein & White 1974). Uda and Ishino (1958) have identified patterns of enrichment resulting from free eddy systems off Japan. The eddies are comparable in scale to those off the Californias and Costa Rica. Areas of high concentrations of commercially and ecologically important fish, squid, whales, plankton and benthic fauna were found to coincide with areas of high eddy activity, both near to and far from land boundaries. Uda and Ishino distinguished between topographical and dynamic eddy systems and identified eddies affected both by topography and current collision (dynamic). Detection of eddies and their formation, persistence and decay by satellite sensing of sea temperature patterns shows particular promise (Bernstein *et al.*, 1977), although stratus clouds frequently obscure the sea surface in eastern boundary regions. Even in cloud-free periods, atmospheric path absorption effects need to be subtracted from sea-surface radiance patterns before satellite studies of eddies can proceed beyond qualitative detection.

Baroclinic eddy incidence and size

The geostrophic method has been shown to apply in particular to representing eddy flow at mid-latitudes. Baroclinic representation of an isolated eddy of about 80 km diameter in the CCS corresponded well with drogue trajectories (Reid *et al.*, 1963). This study demonstrated coherence of the velocity and mass fields and so confirmed the adequacy of the baroclinic mode for representing eddy flow on the mesoscale and for identifying smaller eddies as well. Reid *et al.* pointed out, perhaps as a cautionary note, that the particular eddy they described would have "slipped through the mesh of the CalCOFI station grid" used for geostrophic description if it were not for a hydrographic station added to the grid in response to the discovery of the eddy by drogue work. This illustrates the general limitations of eddy detection by the geostrophic method, as ship surveys cannot be conducted continuously, nor sample all appropriate scales.

Eddies in the California Current System, as defined by one or more closed streamlines of baroclinic flow, have been enumerated from the charts of Wyllie (1966) by season in four size classes and four sectors off the Californias. I chose the sectors to represent segments of roughly equal area off the coastline between San Francisco Bay (38° N), Pt. Conception (35° N), Cabo Colnett (31° N), Pta. Eugenia (28° N) and Bahia Magdalena (25° N). The sectors were covered, in part or totally, by 112 CalCOFI survey periods from 1949-1965. Separate counts were made of cyclonic and anticyclonic eddies because of their presumably different biological effects and modes of genesis. As a matter of convenience, eddy incidence is expressed as the mean number occurring in ten years although the record used was 16 years in duration. Mean ten-year eddy incidences, corrected for gaps in coverage, are shown in Table 1 (from Owen, 1980). The estimations of incidence of 20-100 km eddies are the least accurate because some eddies of this size range obviously were missed by the CalCOFI survey timing and grid and because interval waves can create images of small eddies. Larger eddies also were missed when survey frequency was reduced.

Table 1 summarizes eddy incidence in four regions of the CCS and shows that eddies of all sizes detectable from the CalCOFI grid usually are present throughout the region off the Californias. Eddy incidence demonstrated no obvious seasonal variation except perhaps in the southernmost sector. Large eddies are rarer than small eddies in the Baja California sectors, but off California eddies larger than 200 km occur more often than those of 100-200 km diameter. In all areas and seasons, eddies smaller than 100 km occur most frequently. In the sector containing the Southern California Bight, eddy incidence is dominated by the consistent (but not constant) presence of the Southern California Eddy. In this sector there is a corresponding paucity both of large anticyclonic eddies and of small cyclonic eddies. The high incidence of small anticyclonic eddies in this sector, as well as of the two adjacent sectors, indicates that the small eddies could have derived from larger and predominantly cyclonic eddies, perhaps as a result of flow instabilities. The dominance of cyclonic over anticyclonic eddies is seen in Table 1 to occur progressively with increasing eddy size in each of the four sectors and in all four seasons.

Table 1. Mean 10-year incidence of eddies by size, type, area and season in the California Current System, 1949-1965, coast to 300 n. mi. offshore

Eddy diam (km)		20-100		101-150		151-200		>200		All sizes		%c=
Eddy type*		a	c	a	c	a	c	a	c	Σa	Σc	100 $\frac{c}{a+c}$
Sector/Season**												
35-38°N	Winter	0.4	0.4	0.4	1.7	0	1.9	2.4	3.7	3.2	7.7	62.3
	Spring	2.8	0.9	1.3	1.3	0.9	0.3	0	1.8	5.0	4.3	
	Summer	3.6	2.3	0.9	1.9	0.9	0.9	0	2.0	5.4	7.0	
	Fall	0.6	1.0	2.7	3.3	0	2.9	0.6	2.7	3.9	10.0	
	Annual %c	7.4	4.6	5.3	8.2	1.8	6.0	3.0	10.2	17.5	29.0	
		38.3		60.7		76.9		77.3				
31-35°N	Winter	5.0	2.0	1.0	1.1	1.0	3.7	0	7.2	7.0	13.9	69.2
	Spring	3.7	2.3	0.2	1.3	0.9	2.6	0	6.4	4.9	12.7	
	Summer	6.2	1.9	0.3	1.6	0	1.0	0.3	9.2	6.7	13.6	
	Fall	3.0	2.1	1.6	2.4	0	0	0	7.3	4.6	11.9	
	Annual %c	17.9	8.3	3.1	6.4	1.9	7.3	0.3	30.1	23.2	52.1	
		31.7		67.4		79.3		99.0				
28-31°N	Winter	2.1	0.7	0.4	0.4	1.1	0	1.5	1.2	5.1	2.3	41.9
	Spring	4.1	1.5	2.8	2.4	1.0	1.1	0.4	1.6	8.3	6.6	
	Summer	3.1	0.6	1.4	1.7	2.0	2.2	1.4	0.6	7.9	5.1	
	Fall	1.6	0.5	1.6	1.3	0.3	1.0	0	1.1	3.5	3.9	
	Annual %c	10.9	3.3	6.2	5.8	4.4	4.3	3.3	4.5	24.8	17.9	
		23.2		48.3		49.4		57.7				
25-28°N	Winter	1.1	1.4	0.7	1.0	0	0.7	0.3	0.3	2.1	3.4	58.5
	Spring	3.2	0	1.8	0.5	0.7	0.9	0.3	0.3	6.0	1.7	
	Summer	4.0	2.2	1.8	2.1	0.3	2.7	0.3	1.0	6.4	8.0	
	Fall	3.3	6.1	2.3	3.3	0	2.0	0	3.8	5.6	15.2	
	Annual %c	11.6	9.7	6.6	6.9	1.0	6.3	0.9	5.4	20.1	28.3	
		45.5		51.1		86.3		85.7				
All areas 25-38°N %c		47.8	25.9	21.2	27.3	9.1	23.9	7.5	50.2	85.6	127.3	59.8
		35.1		56.3		72.4		87.0				

*a = anticyclonic
c = cyclonic

**Winter = January, February, March
Spring = April, May, June
Summer = July, August, September
Fall = October, November, December

Eddy characteristics

The Southern California (SC) Eddy is the most resolvable of the eddies in the California Current System by virtue of its large scale and degree of permanence, which usually exceeds the threshold for detection of both the sampling grid mesh and frequency of CalCOFI survey observations. Examples of free eddies at least as large and intense as the SC Eddy have been detected in the main flow of the California Current (e.g. Wyllie, 1966), but have not been measured in detail because of their transitory character.

The SC Eddy is a composite flow pattern. The offshore limb of the Eddy is formed by flow diverging off the coast near Pt. Conception at about 35° N (Hickey, 1979) and extending southward beyond the Cortez-Tanner bank system and is sometimes demonstrated by jet-like flow imbedded in the California Current (Wyllie, 1966). The lower limb occurs as onshore flow between 30°-32° N, likely a result of wind-driven transport (Nelson, 1977).

The nearshore limb is defined by the northward flow along the Bight coast of the SC Countercurrent (Tsuchiya, 1980) which can diverge offshore at Pt. Conception, continue northward along the coast, or episodically disappear. The SC Eddy is quite variable in its extent and circulation strength and may occasionally disappear entirely, for example, at the peak anchovy spawning period in March-April, perhaps even flushing the SC Bight unless replaced by smaller, transitory eddies (Owen, 1980).

It is of interest to compare SC Eddy characteristics with those of large cyclonic eddies elsewhere in the Pacific, particularly one which has been investigated more intensively. The best example of baroclinic doming and eddy upwelling effects is provided by studies of the Costa Rica Dome, produced by a major deflection to the north and east of the North Equatorial Countercurrent as it impinges from the west on the American Continent (Wyrski, 1964). The Dome is located in the bight of this deflection in a region where nutrients and thermocline both are close to the photic depth (Brandhorst, 1958; Thomas, 1970; Owen and Zeitzschel, 1970a). Its physical characteristics denote a trapped, cyclonic eddy large enough to demonstrate nutrient enrichment effects (Brandhorst, 1958; Broenkow, 1965; Thomas, 1970, 1977) and to detect elevated stocks of phytoplankton, zooplankton and small nekton (Blackburn *et al.*, 1970; Owen and Zeitzschel, 1970b).

Dimensions of several well-studied Pacific eddies and order of magnitude estimates of their mean vertical velocity and volume transport are compared in Table 2 (from Owen, 1980). Despite the varying eddy sizes, intensities and vertical velocities, vertical transport by upwelling is of the same order of magnitude in the SC Eddy, Hawaii Eddy, Costa Rica Dome and in a segment of the coastal upwelling domain 200 km in length (about the same distance along the California coast usually occupied by the SC Eddy). As may be seen from ambient nutricline and photic depths, nutrients are readily available for transfer up through the photic zone in all eddies considered except off Hawaii. Thus, the degree of enrichment and subsequent productivity of the SC Eddy is comparable to that of other major eddy systems. The SC Eddy appears only slightly less effective in total transport of nutrients into the photic zone than upwelling along a comparable segment of the California coastline. As noted above, the SC Eddy receives coastal upwelling products from the nearshore Bight as well as from Pt. Conception and north, although any biological consequences are only poorly understood from rather few and incomplete studies.

SC Eddy effects

During the time of the spring phytoplankton bloom and peak spawning of the northern anchovy (*Engraulis mordax*), the SC Eddy may periodically disappear for a month or more, flushing away the surface waters of the SC Bight. Flushing is episodic in character, most frequent in April (3 of 13 cases). The baroclinic representation of the eddy may also "dissolve" to such extent as to become an indeterminate field of flow. Such dissolution apparently often occurs in the same season as flushing (again, 3 of 13 April cases). The eddy can persist in the absence of the surface countercurrent. The countercurrent typically disappears in April-May, a period when the intensified California Current overrides the coastal countercurrent, to paraphrase Wyllie (1966). This pattern of events is corroborated by independent conclusions from drift bottle release-and-return statistics (Schwartzlose, 1962; Squire, 1977).

Table 2. Parameters of Pacific eddies and California coastal upwelling

	Southern California Eddy ¹	Johnson Atoll ²	Hawaii Eddy ³	Costa Rica Dome ⁴	Small CCS Eddy ⁵	California Coastal Upwelling ⁶
Effective obstacle diameter (km)	200	26	100 (wind) 300 (current)	-	-	200 (length**)
Eddy type	trapped	free vortex street	ephemeral wind-forced	trapped	free	(edge eddies occur)
Ambient* or incident flow (cm/sec)	20	60	30	55	20	20
Eddy flow (cm/sec) at 1/2 radius	30	80	50	40	20	-
Radius (km)	100	30	65	200	40	-
Decay time (dy to 1/e)	100	16	>65	-	>14	14
Vertical velocity (m/dy)	0.3	-	0.8(initial)	0.1	-	1.0
Upwelling volume (m ³ /dy)	10 ¹⁰	-	10 ¹⁰	-	-	10 ^{10**}
Pycnocline elevation ($\frac{\text{ambient-dome}}{\text{ambient}}$)	0.3-0.5	-	0.4	0.7	0.1	0.4-0.6
Ambient* photic depth (m)	60	100	100	70	70	60
Ambient* nutri-cline depth (m)	30-70	75	300	40	40	20-60

Sources: ¹ McEwen, 1948; Wyllie, 1966; Wyllie and Lynn, 1971; Owen, 1974

² Barkley, 1972; Frederick, 1970

³ Patzert, 1970; McGary, 1955; Frederick, 1970

⁴ Wyrski, 1964; Broenkow, 1965; Bennett, 1963; Owen and Zeitzschel, 1970a

⁵ Reid *et al.*, 1963; Owen & Sanchez, 1974

⁶ Bakun, 1973; Walsh *et al.*, 1974; McEwen, 1948; Wyllie and Lynn, 1971; Sverdrup and Fleming, 1941; Owen and Sanchez, 1974

* "ambient" refers to condition in absence of phenomenon.

** 200 km coastal strip 50 km wide for comparison with SC Eddy

Spatial variation of community structure and of population densities are evidently affected by the SC Eddy. Changes in community composition take place along flow streamlines: where such streamlines are closed, as in the SC Eddy, successive communities are inevitably juxtaposed. This is apparent from the observations of Allen (1945) and Sargeant and Walker (1948) showing that systematic changes occur in time and space from diatom species ensembles (characteristic of high nutrient injection by recent coastal upwelling) to dinoflagellate ensembles (characteristic of lower nutrient injection into older surface-layer waters). These ensembles were subsequently spatially juxtaposed into what may prove to be a characteristic state due to the Eddy. This effectively demonstrates (perhaps more crudely than actually occurs) the creation of community patchiness by stirring, as defined by Eckart (1948).

Patterns of high phytoplankton concentration which corresponds with that of the SC Eddy are shown by Owen (1974) and by Owen and Sanchez (1974) in terms of surface and depth-integrated chlorophyll a concentrations. These concentration patterns correspond spatially with patterns of higher surface layer and migrating nutrient concentrations of Thomas and Seibert (1974) and with higher zooplankton concentrations in Spring 1969 (Smith, 1974) when the Eddy was fully developed. Together with the evidence for persistence of the SC Eddy, these studies indicate that the observations of Allen and of Sargent and Walker are characteristic (rather than episodic) over the SC Bight. Primary production measurements within the Eddy are too sparse to demonstrate an enrichment effect. A single transect of such measurements (Owen, 1974, p. 98) showed primary production to be about six times greater within the Eddy than outside it. Obviously more observations are needed.

Effects of nutrient washdown into the SC Eddy are not likely confined to only the phytoplankton but certainly involve zooplankton and nekton as well. Arthur (1977) found maximum concentrations of copepod nauplii off the SC Bight at distances corresponding to the offshore limb of the SC Eddy. The maximum zone was associated with colder water, probably entrained from upwelling zones north of Pt. Conception. The pattern suggests that nutrient washdown enhanced reproduction by copepods, a response to their increased food supply.

From plankton surveys over the 1941 spawning season of one population of the California sardine (*Sardinops caerulea*), Sette and Ahlstrom (1948) determined that their eggs and larvae appeared to have been concentrated in an area corresponding closely to that of the SC Eddy and its characteristic elevated diatom densities (Allen, 1945; Sargent and Walker, 1948). This striking local correspondence suggests the susceptibility and possible sensitivity of the sardine stock to the Eddy. The surveys did not cover the entire range of spawning and it is probable that conditions beyond the SC Bight may also have supported spawning areas.

Since the change from dominance of the California sardine stocks to northern anchovy (*Engraulis mordax*), the CalCOFI plankton surveys have covered the spawning time and area of the anchovy. These have revealed (Smith, 1978) that the region inclusive of the SC Eddy, comprising about 12% of the spawning area of the anchovy's central subpopulation, contained 48% of their larvae on the average (1951-1975) and since 1966, 64%.

Berner (1959), in his study of food of anchovy larvae, noted that areas where larvae were found to be actively feeding corresponded to those of the copepod nauplii maximum as described by Arthur (1956). Comparison of areas of active larval feeding in the SC Bight, with corresponding charts of baroclinic flow (Wyllie, 1966, pp. 76, 79 and 82) show that the area of feeding larvae corresponded with the inshore limb of the SC Eddy, although Arthur (1977) subsequently showed that maximum concentration zones of copepod nauplii coincided with the SC Eddy axis or its offshore limb.

Brinton (1976) studied the population biology of *Euphausia pacifica*, a dominant species among the larger zooplankton of the SC Bight. He identified the SC Eddy and its associated upwelling regimes as a reproductive refuge for an identifiable population of the species.

Population persistence in benthic-dwelling organisms with planktonic life-history stages (usually larval) depends on their deposition at the end of the planktonic stage in waters shoal enough to permit survival on the sea bottom. Off the Californias, where flow frequently diverges from the coast, such populations depend on eddies and meanders in the mean flow to return a sufficient number of their meroplankton to appropriate habitat. Examples of this dependency include populations of the spiny lobster, *Panulirus interruptus* (Johnson, 1960) and the red crab, *Pleuroncodes planipes* (Longhurst, 1968). Both organisms spend extended periods as plankton in their early life history, yet maintain stationary and localized centers of the adult populations.

PATTERNING BY FRONTS

Within and between eddy systems, discontinuities known as "ocean fronts" occur which provide identifiable sites for smaller scale and more specific biological activity of likely significance to larval and adult fishes. Ocean fronts are line zones of laterally convergent flow that intensify vertical water motion. They occur singly or in series. Patterning of biological substances can occur mechanically, e.g., concentrating or dispersing organisms that move vertically through advection or convection. Patterning also occurs by indirect mechanisms: local nutrient enrichment and behavioural properties account at least qualitatively for localized responses to fronts by organisms including some types of phytoplankton, zooplankton, fishes, sea snakes, bird and whales.

Scales of variation of plankton tend to be much smaller in the presence of fronts as compared to patterns impressed by eddies. A basic and attractive tenet is that vertical displacements have greater ecological effects than similar horizontal displacements because environmental gradients of light, pressure, temperature, salinity, oxygen and nutrients are by far the steepest in the vertical dimension. Vertical motion in fronts is often vigorous and highly localized, whereas that in eddies is slower and spread over much larger areas. For this reason, coherent horizontal gradients of temperature, salinity and food supply are correspondingly sharper across convergent flows than across eddies. Their respective biological effects occur on accordingly disparate scales.

Scales on which ocean fronts have been observed to occur and to pattern organisms range laterally from 1 m - 10⁵ m, persisting (depending on size) from hours to virtual permanence. The smallest-scale fronts are by no means ecologically insignificant since they may extend (in diverse patterns) over large ocean areas.

Bénard and Langmuir Fronts

The smallest coherent frontal patterns that have been noted to collect organisms in the open sea were attributable to the Bénard mechanism. Bénard circulation occurs when cooling and salt gain through evaporation make surface water rapidly more dense: thermohaline circulation cells form a honeycomb pattern of surface convergences as the denser water exchanges with the less saline and warmer subsurface water. The resulting honeycomb pattern is easily deformed by wind or subsurface shear to form a series of small elongate, parallel fronts.

Surface convergences of this sort reported by Owen (1966) penetrated to less than a metre in depth, extended visibly for more than 30 m in unbroken length and were spaced at intervals of about 1.5 m. The patterns persisted in the absence of wind for at least two days. Taken singularly, such "micro-fronts" would have little ecological impact. However, this particular frontal system observed by Owen (1966) extended over several hundred km². Such fine-scale patterns can produce widespread alteration of concentration patterns and, presumably, concentration-dependent biological processes. In this instance, the surface convergences were marked by red bands less than 10 cm wide that consisted of upward swimming oikopleurans that had been highly concentrated in the upper 5 cm of the convergence planes. Their still-water swimming speed of about 0.2 cm/sec was used to set an upper limit on downwelling water speed in the convergence planes.

Under freshening and sustained winds, convergence systems of the better known and (usually) larger scale Langmuir circulation either develop into patterns like Bénard cells or create their own patterns, detectable as parallel windrows. These windrows lie along the wind axis and are often marked by assemblages of floating organisms or substances. These are swept by convergent surface flow to the frontal zones. Trapping efficiency of buoyant materials is virtually 100% under steady winds of constant direction. Surface convergences can become strong enough on occasion to submerge even highly buoyant

Sargassum weed, requiring a downwelling circulation of 5-7 cm/sec (Woodcock, 1950). Organic films on the sea surface are also rapidly collected along such convergences to give windrows their most common streaked appearance. Under lower winds, collected oils dampen capillary waves to give the windrows the appearance of parallel slicks. At higher wind speeds the organics can be partly frothed and convergences appear as foam lines.

The size and circulation strength of these convection cells increase with time and wind speed. Spacings between convergence lines from several metres to over 100 m are typical, and downwelling speeds may exceed 10 cm/sec. Depth of penetration is some fraction of the distance between convergences, usually half or somewhat less.

Extant theories that attempt to account for the Langmuir circulation include stability of vertical shear in the water, forcing by atmospheric vortices, wind-oriented thermal (Bénard) convection, wind profile modification by surface films, lateral radiation pressure on surface films, convergence of wave trains (reviewed by Scott et al., 1969), and vertical decay of surface wave oscillations (Faller, 1969). Failure of data to support or rule out any single mechanism led Scott et al. (op. cit.) to conclude that combinations of mechanisms could occur. A subsequent study (Harris and Lott, 1973) lends support to the possibility of development of Bénard cells into Langmuir cells: mean downwelling velocities ranging from 2.1 to 9.4 cm/sec in Langmuir convergences correlated well with wind speed during net surface cooling but not as well during net surface heating. Despite the lack of agreement on mechanisms, the Bénard-Langmuir circulation is now widely held to be an important mechanism for vertical transfer of heat and substances in surface waters of lakes and seas. Large temporal variations, with a strong diel component (Woods, in press) may be expected in both Langmuir and Bénard circulations.

The theoretical and mathematical description of particle trajectories in cellular convections was formulated by Stommel (1949) and subsequently elaborated to include swimming (e.g., Stavn, 1971). Direct observations to date confirm the applicability of the model to real particles and plankters in such circulations, despite the rather large difficulties of field measurement and the less-than-ideal behaviour of both the fluid and plankton.

A number of field studies confirm the effectiveness of the Langmuir circulation in collecting and patterning organisms and substances. The most visible examples involve buoyant animals and substances such as *Physalia* (Woodcock, 1944), Sargassum weed (Faller and Woodcock, 1964; Woodcock, 1950) and surface films (Szekiela et al., 1972). Sutcliffe et al. (1963) demonstrated that whitecapping and perhaps other wind action converts dissolved organics to particulate form available to zooplankton, and that a downwelling Langmuir convection, at 3-6 cm/sec, produced subsurface concentration zones of these particulates. The soluble inorganic phosphate concentration was also shown to be higher in such particulates. Sutcliffe et al. (1971) show, by detecting an increase in particle concentrations with increase in wind speed, that the process is highly effective. They found peak production to be particles of 6 μ m diameter. Higher concentrations of particles 2-13 μ m diameter were shown to occur below convergence zones.

Patterning of phytoplankton and microzooplankton by Langmuir circulations has been more widely reported than one would expect from the mismatch of their reported speeds. Bainbridge (1957) reviews several observations of dinoflagellate concentrations in Langmuir scale patterns. The mobile and prolific ciliate *Mesodinium rubrum*, which can "zig-zag" at speeds up to 2 mm/sec and also occur in bloom ("red-water") concentrations, has been reported to gather in Langmuir convergences. Powers (1932) found *Mesodinium* in windrows off Maine, and Bary (1953) observed windrows of these ciliates to orient along a changing wind axis in New Zealand. Packard et al. (1978) describe *Mesodinium* windrows spaced at 100 m intervals under 10-20 knot winds, and their dispersion through the water column at winds over 30 knots.

Patterning of larger zooplankton in Langmuir circulations is less apparent and notoriously difficult to sample. The best examples of Langmuir patterning of zooplankton

thus are from lakes, where populations of cladocerans and copepods migrate vertically into vortices in the epilimnion and concentrate in convergence planes (e.g., George and Edwards, 1973). Survival of Peru's larval anchoveta has been proposed by Ware et al. (in press) to be enhanced in the presence of small-scale patterning of their food supply in windrow circulations.

Internal wave effects

Internal waves, responsible for surface banding on continental shelves, do not actively produce organism patterns but may modify extant patterns. Interaction of waves with bottom topography, current shear, and diminished vertical stability can produce instabilities (and breaking waves) that disrupt pattern. Internal waves may interact with current boundaries and shelf-break fronts. Curtin and Mooers (1975) presented measurements that indicated generation of large amplitude, high frequency internal waves by breakdown of the semi-diurnal internal tide at the shelf-break front off Oregon. These induced major perturbation of a sonic scattering layer (organisms) inshore of the front. Earlier, Yasui (1961) presented a theoretical framework arguing for propagation of tidal-period internal waves along fronts of the sort encountered as Shiome, fronts due to current confluence, which are zones of high lateral shear as well as vertical circulation. Localized interaction between internal waves and eddies in mid-ocean also has been detected (Frankignoul, 1976), which may affect rates of vertical diffusion. As yet, these phenomena seem to be unexplored but may be expected to modify effects of fronts on populations of organism. Kamykowski (1975), for example, presented a mechanism by which phytoplankton can interact with the semi-diurnal internal tide to produce patterns of species concentrations. The biological result of internal wave interaction with fronts or eddies is obscure but may be significant. Internal waves are sensitive to current shear and to vertical density gradients, both of which vary at fronts and in eddies. It will not be surprising to find evidence of biological responses to these dynamic physical processes if adequate sampling techniques can be devised.

Tidal fronts

Simpson and Pingree (1978), Pingree et al. (1977) and Pingree et al. (1974) describe cases of genesis and decay of shallow sea fronts by variable tidal mixing on the European continental shelf. Surface convergent fronts of considerable physical and biological activity occur in zones where water types of different mixing histories impinge. Vertical mixing was induced in shallower waters by frictional dissipation on the bottom interface of (mainly) the principal lunar tidal component of flow and stratified cooler waters. In some areas of the shelf, such vertical mixing is sufficiently vigorous to prevent or override density stratification. Where tidally-mixed shoal water contacts stratified deeper water, a convergent front occurs. Thermal images of the Celtic Sea from the NOAA-5 satellite indicated the broad extent of tidal fronts like those examined in these studies have shown the genesis of a cold eddy from a frontal meander. Shipboard measurements of a similar front (Pingree et al., 1977) show its response to neap and spring tide cycles and its effect on phytoplankton chlorophyll concentrations in the stratified water well beyond the front. The study suggests that blooms of a dinoflagellate population offshore were caused by periodic release of nutrients from the destratified inshore side of the front by decay of the front during neap tides.

Admixture of water types at shelf fronts locally stimulates phytoplankton photosynthesis and thus sustains higher phytoplankton concentrations in the frontal zones. Savidge (1976) and Savidge and Foster (1978) describe such a process from surface measurements of chlorophyll, temperature and photosynthesis along transects on the European shelf between Ireland and Wales.

Zooplankton concentrated in shelf fronts is also commonly observed but descriptions from physical and biological measurements in such fronts are rare. Pingree et al. (1974)

describe activity in a vigorous tidal front of 15 km extent in the English Channel from temperature, salinity and current measurements and from direct underwater and surface observations of its effects on organisms and substances. Surface net hauls in the front showed greater concentrations of copepods, crustacean meroplankton, the euphausiid Nyctiphanes sp. and young fishes.

Plankton concentration at the front was confirmed by sub-surface visual observation. Underwater observation of motions of plankton and of dye injected at several depths also confirmed the turbulent, convergent character, which was apparent from temperature and salinity structure and from drogue measurements. The list provided of animals associated with floating macrophytes concentrated at the front consisted of a variety of post-larval fishes and crustacean species. Puffins, shearwaters and terns were seen feeding along the front, which also collected debris and oil lumps. The authors remark on the similarity of this front and its biota to the large, deep-ocean fronts described by Beebe (1926) and Amos et al. (1972).

Shelf-break fronts

Fronts of large extent commonly occur in the general vicinity of the shelf-break, i.e., where the slope of continental shelf steepens to become the continental slope (generally at about 100-300 m depth). Mooers et al. (1978) usefully distinguish between prograde fronts, those that separate more saline shelf water from offshore water; and retrograde fronts, those that separate less saline shelf water from offshore water. Shelf waters of both types are colder than offshore waters.

Prograde fronts arise by upwelling on the continental shelf. Seasonal and episodic wind-driven upwelling is characteristic of eastern boundary current systems, but occurs inshore of western boundary currents as well, where upwelling occurs by topographic deflection of currents. Retrograde fronts are due to shelf-water dilution from terrestrial runoff and thus predominate off large terrestrial water sheds. Their incidence and intensity usually vary with season.

Upwelling fronts

Prograde shelf-break fronts off upwelling zones bound the plankton-rich shelf waters. There is a dearth of studies that demonstrate higher plankton concentrations in these fronts than inshore, at least in part because field studies have been concerned more with the upwelling system as a whole and do not sufficiently sample frontal interfaces. Packard et al. (1978) describe the incidence and habitat of the pigmented ciliate, Mesodinium rubrum in an upwelling zone off Baja California. Surface-layer concentrations of this ciliate at prograde fronts appear to be facilitated by characteristics of its environment in combination with its phototactic behaviour, rapid reproduction rate and ability to use both inorganics and organics for food.

Laurs (unpublished thesis), working with measurements of concentration of phytoplankton zooplankton and micronekton in and beyond the Oregon upwelling system, detected higher stocks near the frontal zone and in an anticyclonic eddy (phytoplankton only) outside the front. Bang (1973) describes a strong upwelling front extending northwest off Cape Town in the eastern boundary current off South Africa. Mixing cells occurred and episodic overturn at the front produced subthermocline sheets of homogeneous water. Higher concentrations of large zooplankton or micronekton were detected at the front by fathometer records.

Albacore make annual trans-Pacific migrations to feed on relatively high concentrations of large plankton and small fishes in the California Current, seaward of the coastal upwelling zones. The offshore extent of these upwelling zones are frequently denoted by prograde (upwelling) fronts. Albacore caught, tagged with ultrasonic transmitters and subsequently

released, were tracked in the vicinity of such a front off Monterey Bay, California (Laurs *et al.*, 1977). Tracking results showed that such temperature fronts can influence local concentration of albacore; sonically tagged albacore moved about in the vicinity of the front, then moved away when the front weakened as upwelling ceased. These albacore also were seen to move more slowly when crossing fronts and to spend little time on the colder side ($T < 15^{\circ}\text{C}$), indicating a thermal barrier effect which would result in their collection at fronts. The enriching effects of large cyclonic eddies that predominate outside upwelling zones, and of eddies that transport substances away from upwelling zones (Owen, in press B) may also support higher forage levels beyond shelf-break.

As demonstrated for tidal fronts, an important aspect of upwelling fronts may be their periodic relaxation, their decay, and subsequent release into offshore water of nutrients and plankton previously accumulated in the shelf water. Frontal relaxation occurs upon cessation of upwelling. This can occur either seasonally or episodically depending on the wind system. Breaching, or destructuring dissipation occurs more locally than does relaxation. The causes of breaching have not been defined but likely involve meanders and eddies formed by local instabilities of frontal currents, impingement of eddies from outside the fronts, and perhaps wave interactions with the fronts. When clear weather permits, breaching is clearly evident in thermal images of sea surface temperature fields off California transmitted from satellites. Bernstein *et al.* (1977) demonstrate the possibility of using such infrared images to follow the genesis, lysis and incidence of fronts as well as eddies and upwelling zones in the California Current System.

Estuarine fronts

Retrograde estuarine fronts exhibit salinity gradients, because freshwater sources dilute surface waters on one side of such fronts. Iizuka and Arie (1969) showed concentrations of *Trichodesmium* (flagellate) for 80 km along an estuarine front off Japan. LeFevre and Grall (1970) showed similar convergent aggregations of *Noctiluca scintillans* off Brittany and also emphasized local competition that was apparent between *Noctiluca* and copepods for diatoms in the convergence area.

Owen (1968) studied effects of the Columbia River plume, which albacore encounter in their summer arrival off Oregon. Based on research vessel catch rates and oceanographic data, results showed that albacore moved through the outer plume boundary, defined by the 32.2‰ isohaline that defined the outer boundary of the salinity gradient of the plume-sea front (Owen, 1967). Albacore catches were somewhat lower in mid-plume than in the vicinity of its frontal limits, indicating an attraction to forage in fronts *per se* and possibly a combined attraction/aversion to the warmer temperatures/lower salinities of the plume core. Catch rates were higher near the seaward limit than inshore, where even stronger thermohaline fronts resulted between plume coastal upwelling zones.

Tsujita (1957) showed seasonal cross-shelf movements of stocks of the Japanese sardine off western Japan. Spawning and hatching occurs at depth in oceanic water off a retrograde (estuarine) coastal front. Larvae move shoreward through the shelf-break front, seek nearshore feeding grounds, grow to 7-10 cm length and diffuse seaward in summer in the upper layer of the shelf waters.

MICROSCALE PLANKTON PATCHINESS

Patterning of plankton occurs on the sub-metre scale. Cassie (1959a, b) demonstrated high variation of plankton concentrations at the sea surface, and Owen (in press b) showed similar variations at sub-surface depths. The role of circulation in the patterning process is obscure, particularly since this approaches the scale of turbulent dissipation. This section discusses some new measurements made to determine if small predators and grazers encounter food patches in excursions of less than 2 m extent. Variation in food supply available to fish populations is commonly examined to help determine causes of large interannual fluctuations frequently experienced in the availability of fish to fisheries. Yet concentrations of food ofrist-feeding northern anchovy (*Engraulis mordax* Girard) seem frequently to be too low in the California Current System for larval survival and growth (Lasker *et al.*, 1970). This may be because conventional sampling with plankton nets, which integrate over depth, distance and volume, has little relation to the comparatively tiny volumes searched by single larvae (Hunter, 1972). Survival of such larvae may, in fact, depend on the existence of food particle patchiness on scales considerably less than 10 m and 1 week (Vlymen, 1977).

Regions sampled

Southern California Bight waters tend to high vertical stability by virtue of characteristically slow flow (reduced shear) and year-round net heat gain, except in December, by the ocean's upper layer (Clark *et al.*, 1974). The mixed layer is relatively shallow (<30 m), due to the combined influences of wind shattering, heat gain, the California Current and the Southern California Eddy. Large temperature gradients predominate over salinity gradients in determining vertical stability. Maximum stability occurs in the upper pycnocline in the absence of steady winds. These characteristics are favourable to the development of small-scale patchiness but are episodically reversed by storm winds of a few days duration, which destroy shoaler layering (Lasker, 1978). Episodic upwelling, internal waves, and eddies may destratify the water column locally along the narrow shelf of the Southern California Bight margin and in even more restricted areas near islands and capes.

The region studied off Peru is functionally similar to the S.C. Bight in having a shoal pycnocline, destratification on the shelf, and high production rates of forage and fish. Differences between the sampled regions are mainly of magnitude: Peru's shelf is 1-2 orders of magnitude broader, the margin is more exposed to storm activity, and processes of destratification are more dynamic, somewhat more consistent, and more broadly effective than in the SC Bight. The role of eddy processes in the Peru region is unassessed. Well-defined prograde fronts are found on and near the Peru shelf. These frequently separate stratified from unstratified zones but cellular fronts also occur on smaller scales, e.g. Bénard-Langmuir on sized cells.

One would thus expect off Peru both a lesser degree of vertical microstructure of plankton and environment, and a lesser need of such microstructure by the larval fishes due to the increased general productivity compared to the Southern California region.

Microscale measurements

Samples to assess microscale patchiness at each site were obtained using an array of water samples on a varied frame. The micropatch sampler (MPS) sampled either in the mixed layer or in the upper pycnocline in the main chlorophyll maximum layer, as defined by pigment fluorescence in a water stream provided by continuously lowered pump and hose. Clamped either vertically or horizontally to the ship's hydro-wire and lowered to the depth desired, the MPS captured water at ten intervals on 20 cm centres in 5 cm (i.d.) tubes of 600 ml

capacity by simultaneous messenger-activated release of lanyards which restrain ball valves from their seats at either end of each sample tube. Replicates were obtained on some casts by strapping another sample tube alongside the original. When sampling vertically, vanes oriented the sample tube mouths to face a current of ~50 cm/sec induced by moving the ship slowly ahead. This minimized vertical mixing of the water by the MPS. When sampling horizontally (tubes vertical), the tubes were closed while raising the array. Water was aliquoted for various analyses from the well-stirred contents of the MPS tubes upon recovery aboard ship. Plant pigment determinations were made by the fluorometric method on acetone extracts, particle concentrations by Coulter TA, nutrients by autoanalyzer and salinity by inductive bridge. Samples for microscope analysis were preserved in <5% buffered formalin spiked with strontium chloride. These were counted ashore by the sedimentation method of Utermohl (1931).

Microstructure of organism populations

Results of microscope counts are summarized in Table 3 as coefficients of variation, $V = 100 \times \text{variance/mean}$, of concentrations determined over the 10 intervals sampled to represent the 2 m span. Where replicate samples were counted, average values between replicates were used in the computation. Coefficients are shown for population counts exceeding 10 in at least one of the samples in the set. Trends (i.e. mean gradients) over the 2 m span are represented by the coefficients, as are variations within the span (i.e. deviations from mean gradients). Both sources are taken to indicate microstructure degree because sampling was done in the absence of conventionally detectable biological gradients (i.e. in mixed layer and chlorophyll maximum). The V statistic was chosen because it scales variances for comparability and because it is widely used and understood. A measure of sampling and counting error is provided from counts on four MPS sets each consisting of five replicate sample pairs. The average coefficient of variation between replicates for 15 taxonomic groups counted was 10.9 (range was 4.0 - 18.5), not including the coefficient for ciliates associated with marine snow at two sites (7703J-MS1, MS2).

V-coefficients are considered to indicate significant microstructure if they exceed the average replicate V-coefficient by at least a factor of 3, Table 3 shows that:

- Microscale patchiness is apparent ($V > 33$) at all but one of the 13 Southern California Bight sampling sites and at both Peru sites for one or (usually) more kinds of organisms enumerated.
- Most types of organisms suitable as larval anchovy food display significant degrees of microaggregation. Non-food organism types are also aggregated, in many cases to an even greater degree, and not necessarily in the same zones as the presumed food organisms.
- Vertical profiles in the upper mixed layer of the SC Bight (the latter defined by absence of density gradients determined from standard STD casts) showed significant microscale patchiness for 5 of 8 food types and 3 of 8 non-food types at one site or the other, both occurred during the anchovy spawning season under calm wind conditions. At the shelf edge off Peru, in the lower part of the mixed layer under 20 kt winds, microscale patches of ciliates, copepod eggs and the diatom *Corethron* were detected.
- Microscale variation was usually greatest in the pycnocline and in the vertical axis for most food and non-food types alike (but see *Euxyiaella* sp. C - this flagellate species behaves rather differently on the microscale, being more randomly dispersed vertically than horizontally in the pycnocline and apparently capable of forming small patches in the mixed layer).
- Non-motile or weakly motile organisms (cf. *Nitzschia*, *Thalassiosira* and pennate diatom categories) may show as much or more patchiness as motile organisms (cf. *Euxyiaella*, *Prorocentrum* and ciliate categories).

- There is no evidence for a difference in degree of vertical microstructure in the pycnocline between periods of peak and minimal spawning activity (mean V = 49.3 and 50.0, respectively). This is perhaps partly due to too few comparable categories since species composition changed between periods sampled, complicating relevant interpretation regarding appropriate larval anchovy food.

Table 3. Coefficients of variation of organism concentrations sampled at ten 20-cm intervals (interval replicates averaged where obtained) in the mixed layer and upper pycnocline of the coastal shelf of the Southern California Bight and Peru (7711).

		Vertical casts in pycnocline at chlorophyll maximum layer										V	Horizontal casts in pycnocline			V	Vertical casts in mixed layer			V
TCP DEPTH (m)		22	23	25	29	20	20	14	20	15			17	18	21		10	10	15	
DATE (Year/Month)		7509	7509	7509	7509	7603	7603	7703	7708	7711			7603	7603	7603		7603	7703	7711	
MPS No.		1	2	4	5	1	5	2	1	3			3	10	11		2	1	2	
FOOD TYPES	<i>Euxyptella</i> sp.C					22.7	17.3						27.4	29.1	21.8		12.8	76.6		
	<i>Oxytaum septum</i>					27.7														
	<i>Prorocentrum gracile</i>	69.8	52.6	130.4		45.4											37.6			
	<i>Peridinium</i> (2 spp.)					50.9											25.4			
	<i>Peridinium minutum</i>					174.1		25.0						19.2			35.5	21.2		
	<i>Cochlodinium calanatum</i>	28.4		51.2	44.9				22.0					35.2						
	<i>Cyclodinium</i> sp. 5					22.2														
	<i>Torodinium robustum</i>								29.8											
	naked flagellate 30x50 µm					67.4			14.5				27.3	21.4	17.3			41.6		
	diatoms 100 µm						98.6			51.9							22.2	34.2		
	free ciliates			54.6	44.2	64.1	11.5	63.2					26.2	14.3	24.4		9.9	23.4	43.2	
	copepod nauplii					32.0	25.4							29.6			10.7	31.8		
	<i>Prorocentrum micans</i>									59.5										
	Copepod eggs, 35-80 µm									30.7										
												49.6				24.5	123.0			36.6
P&A-FOOD TYPES	<i>Hitzschia seriata</i>					51.8	44.9							35.7			29.2			
	<i>Eucampia zoodiacus</i>							115.7									31.0			
	<i>Thalassiothrix frauenfeldi</i>							27.3									25.1			
	<i>Thalassiosira</i> sp.A																			
	pennate diatom 30 µm			158.2	92.2															
	silicoflagellate			55.3	60.4															
	<i>Ceratium kofoidii</i>	39.1				58.4							39.2							
	<i>Dinoflagellate</i> spp. 5x10 µm					27.9								31.1						
	<i>Pseudo-nitzschia dolifolus</i>	95.7	104.6	56.8													27.0			
	<i>Thalassiosira</i> sp.B								28.9											
	<i>Skeletonema costatum</i>														37.3		40.1	65.6		
	pollen grain 70x40 µm																52.4			
	oikopleurans																21.5			
	<i>Noctiluca</i> sp.					29.0	21.2												33.9	
	<i>Corythron</i> sp.																			
	<i>Pleurosigma elongatum</i>									59.5										
	<i>Pleurosigma nicobaricum</i>									86.9										
												63.9				33.5				36.2

In the 15 micro sampler sets enumerated by microscope, 20 species of phytoplankton, 6 categories of microzooplankton, and 4 size categories of detritus were sufficiently populous to examine their microscale variation. Microstructure occurred in 94% of profiles of phytoplankton species, 92% of microzooplankton profiles, and 85% of detritus profiles in 3 size categories ranging from 16 to 200 µm.

The maximum concentrations of food and non-food organisms do not usually coincide on the microscale. A characteristic experience is shown in Figure 1, taken from a vertical MPS cast in the pycnocline, in the vicinity of the main chlorophyll maximum. This effect may augment the increase in availability of food organisms due to microstructure by reducing local abundance of undesirable strike targets in zones where food organism concentrations are highest. The argument assumes varying degrees of distinguishability and desirability among the food types by the fish larvae, as there are no consistent patterns apparent between food and non-food organism distributions on this scale.

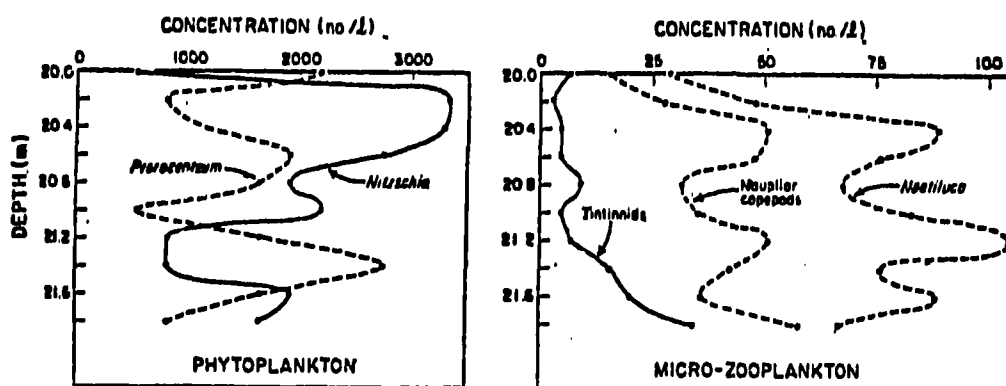


Figure 1. Microscale variation of larval anchovy food and non-food organisms in the pycnocline of the Southern California Bight

Concentrations of suitable food in one MPS cast of 13 analyzed from the SC Bight exceeded the "critical concentration" criteria of Lasker and Zweifel (1978) for survival and growth of anchovy larvae. This incidence would likely be higher if (1) all food type organisms had been enumerated rather than those selected only for clear identification and abundance, or if (2) high plankton standing stock had been among criteria for choosing sampling sites.

Patch shape

Results of four casts made horizontally at depths comparable to those of vertical profiles permit a rough estimate of the *in situ* shapes of particle patches. Variation in concentration of the more numerous components of the microplankton community present averaged three to five times greater in the vertical sets than in the horizontal sets, as measured by the coefficient of variation, s/X , of counts made on these components. This leads me to speculate that populations were concentrated in partly overlapping lenticular patches with horizontal dimensions three to five times greater than vertical dimensions. This geometry provides an interesting contrast with shapes of plankton patches discerned on larger scales, whose characteristic vertical dimensions are reported in metres and horizontal dimensions are reported in km (e.g. Bainbridge, 1957). This indicates a marked tendency towards isotropy with diminishing scales and bears further investigation for confirmation.

The observations suggest no simple relationship between organism types, but show a large degree of variation on short intervals. Results confirm Vlymen's (1977) postulate that some degree of small-scale patchiness (on the scale order reported here) must necessarily occur to support even the minimum fraction of anchovy larvae surviving to recruitment size. The results also suggest sampling precautions to be taken wherever minimum or maximum plankton concentrations need to be known or where "critical concentrations" need to be detected.

Microstructure of bulk properties and organisms

Vertical sampling of the water "column" by water-capturing devices at intervals usually spaced more than 5 m apart or by continuously-lowered pump and hose, both underestimate the *in situ* variations of concentration and thus lead to underestimates of the maximum concentrations actually present. The degree to which this can occur is shown in Figure 2, where a small inversion in plant pigment concentration, detected *in vivo* by fluorescence of a sample stream from a pump profiling system, was resampled within 5 minutes by the micro-sampler array and acetone extracts of filtered samples analyzed by fluorometer for chlorophyll and phaeo-pigment concentrations. Unlike determinations from filtered, extracted samples from the micro-sampler, the *in vivo* measurement does not differentiate between chlorophyll a and phaeo-pigment (photosynthetically inactive degradation products of chlorophyll). Hence both are shown in the insert. Noting that the pigment concentration scales are the same for pump and micro-sampler array, the degree of averaging by the pump system is apparent: the variation of pigment concentration over the 0.6 m depth interval was an order of magnitude greater as sampled by micro-sampler than by the pump. This case displays the greatest disparity yet encountered between pump and MPS profiles of plant pigment.

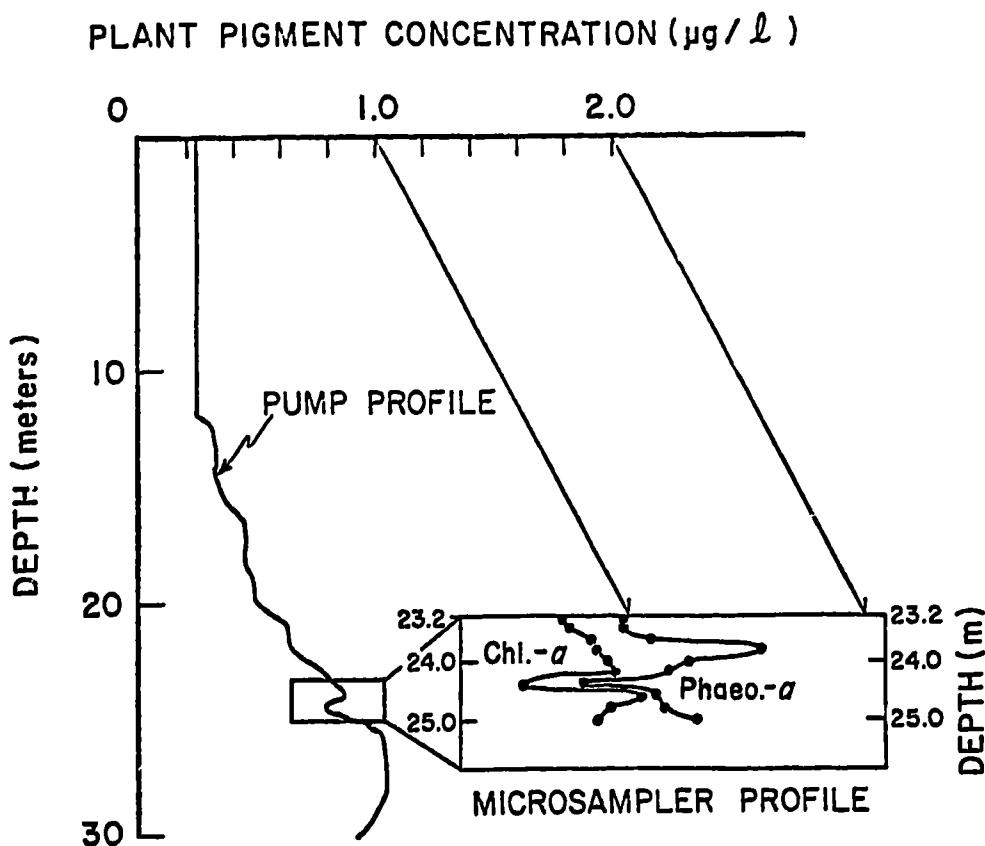


Figure 2, Comparison of small-scale change of phytoplankton pigment concentration by pump profiling and by 20-cm discrete sampling in California coastal waters. Pigment concentration scales are the same for both displays.

To date, 33 vertical and 4 horizontal microprofile sets have been obtained from mixed and stratified coastal waters in the Southern California Bight and on the Peru shelf under all but full-storm conditions. Of these, all except a horizontal set made in the mixed layer exhibited variations beyond sampling and measurement error of one or more of the parameters measured over the 2 m interval. As examples, two microprofile sets are shown in Figure 3. Also shown (lower panel) are concentration profiles of chlorophyll, an integrative measure of phytoplankton density; phaeopigments, photosynthetically inactive derivatives of chlorophyll; particulates 16 to 160 μm diameter, indicative of detrital particle load in this region; and inorganic nitrate, important for phytoplankton growth. Both were obtained from the SC Bight in the density-stratified portion of the water column where the bottom depth was about 200 m. They were selected because most parameters in these two sets displayed small-scale variations that exceeded sampling and measurement error. Greater variation existed within any single parameter in other sets. Concentration profiles of a motile phytoplankter, *Euxyiaella* sp. C; oligotrich ciliates; and copepod nauplii were selected to depict microscale variations of species and of functionally similar groups (upper panel). Each is a food item of larval anchovy.

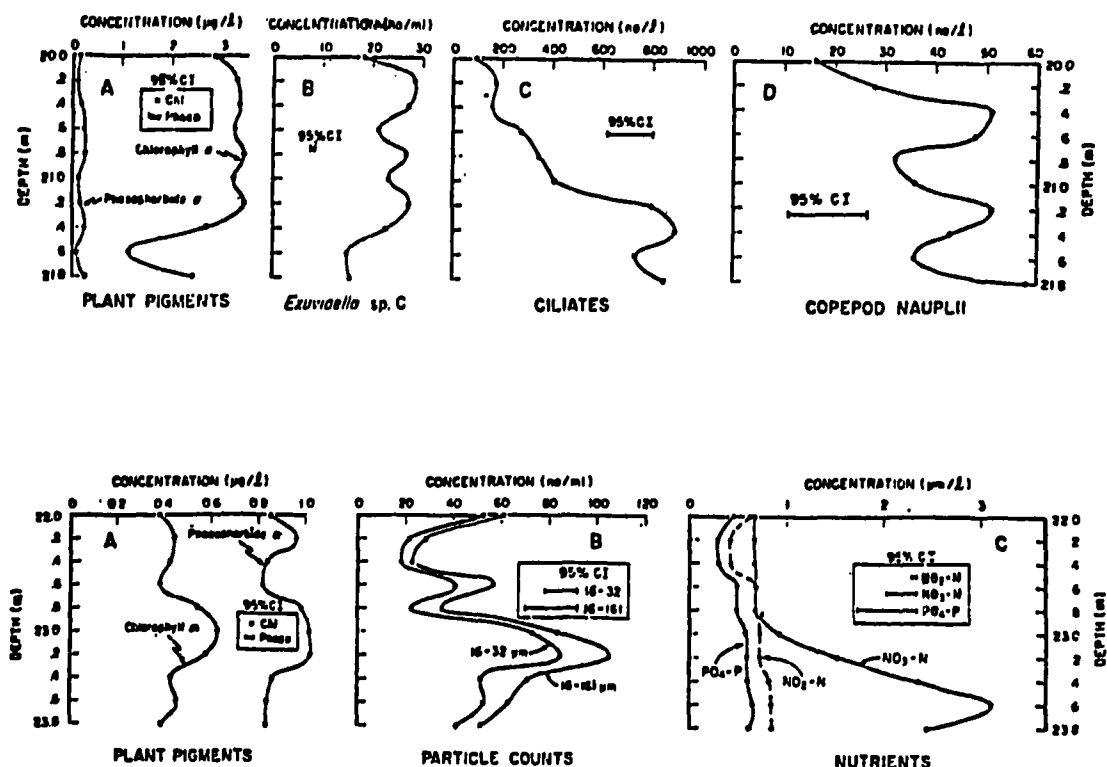


Figure 3. (Upper panel). Microscale variation of plant pigments and three organism types from the pycnocline in the Southern California Bight in March (7603/MPS-1). (Lower panel). Microscale variation of plant pigments, particles and nutrient salts from the pycnocline in the Southern California Bight in September (7509/MPS-1).

Results of a September cast in the SC Bight demonstrates the small-scale variation commonly present in plant pigments, particle concentration and nutrients. The incidence of microstructure was high; significant fine-structure existed in 16% of 22 particle profiles and 11 of 21 nitrate profiles and in both of two ammonium profiles. The particle coincidence of particle and plant pigment maximums centered at 23.2 m is fortuitous; virtually all particle profiles were independent of the corresponding plant pigment profiles (15 sets). Incidence of plant pigment microstructure was quite high. All 23 sets analyzed showed variation of chlorophyll concentration indicating microstructure of the phytoplankton community as a whole. Fewer (19%) showed cm-scale variation of phaeopigments. In the set shown in Figure 3 (lower panel), the phaeopigment profiles resembles that of chlorophyll *a*. However, of 23 such profiles, 14 exhibited unrelated profiles of chlorophyll and phaeopigments and 4 exhibited inverse relationships. This inconsistency demonstrates a degree of independence on the microscale which is not apparent in pigment concentration profiles from the usual sampling intervals of 5 to 10 m. This independence may be due to local effects of grazing or to differential rates of local production and sinking of the two particle types. These measurements thus may reflect the spatial scales on which these processes are first apparent.

Microstructure was not, of course, always detected. Sample series from the wind-mixed upper layer of the SC Bight showed less variation of organisms, particulates and nutrients than did sample series from density-stratified waters. However, significant microstructure of motile and non-motile organism populations, as well as of detrital particles, was detected in 2 of 4 casts made within the mixed layer in the absence of measurable density gradients, when mixing by wind was not in progress. The nutrient salts phosphate and nitrite-nitrate exhibited low incidence of microscale variation over distances less than 2 m in both regions sampled. Widely varying values of silicate concentration suggest microstructure for that nutrient but occasional wide disagreement between replicate samples vitiate the case for silicate microstructure. Salinity (5 sets) varied monotonically in the presence of nutrient and organism microscale variation. Temperature microvariation was not measured.

Peru microscale

Microstructure of biological materials apparently occurs under a variety of environmental conditions. Off Peru during Project ICANE (Doe, 1978), MPS-3/7711 sampled 5 km from shore near Chimbote below a surface layer stabilized by surface layer heating after recent weakening or cessation of upwelling. Large quantities of the "weed" diatom *Chaetoceros* were present at the surface and at the sampled depths. Microstructure of two types was evident among populations enumerated from 15-17 m depth. Concentrations of the diatoms *Pleurosigma elongatum* and *P. niobarium* exhibited nearly monotonic, stepwise decreases with depth (Fig. 4, upper panel), whereas spheres, tintinnid ciliates and *Prorocentrum micans* exhibited yet smaller-scale variations by pronounced maxima and minima between 15 and 17 m (Fig. 4, lower panels). Nutrient salt concentrations, nitrate-nitrite, ammonia, phosphate and silicate at this site exhibited no microstructure (Fig. 5). Particle concentrations, by Coulter Counter, indicated significant microstructure of particulates likely dominated by detrital substances (Fig. 6). By contrast with stabilized conditions at the coastal site, MPS-2/7711 sampled 10 km seaward of the shelf-break at about the same latitude (9°S) as MPS-3. More labile conditions prevailed at this site; MPS-2 sampled from 15-17 m in the virtually isopycnal layer that extended from the sea surface to 21 m depth under 20 kt winds. Standing stocks of phytoplankton were less than at the coastal station, tintinnids were supplanted by oligotrich ciliates, and copepod nauplii were more abundant.

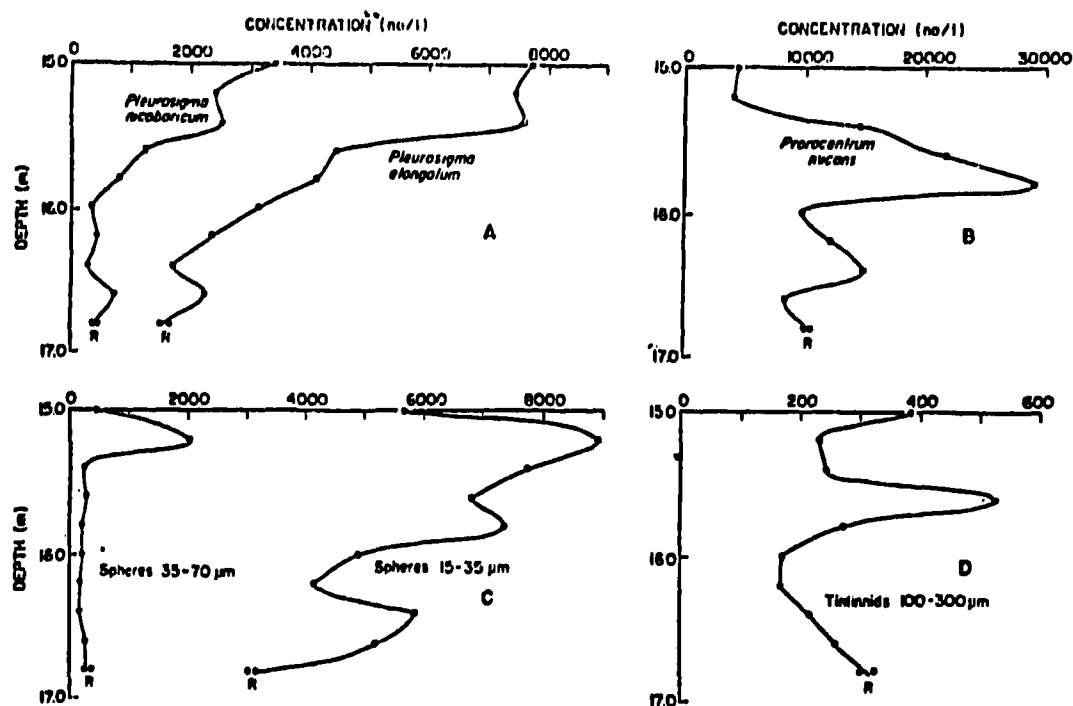


Figure 4. Microscale variation of larval anchovy food and non-food organisms in the pycnocline near Peru's coast in November 1977 (7711/HPS-3).

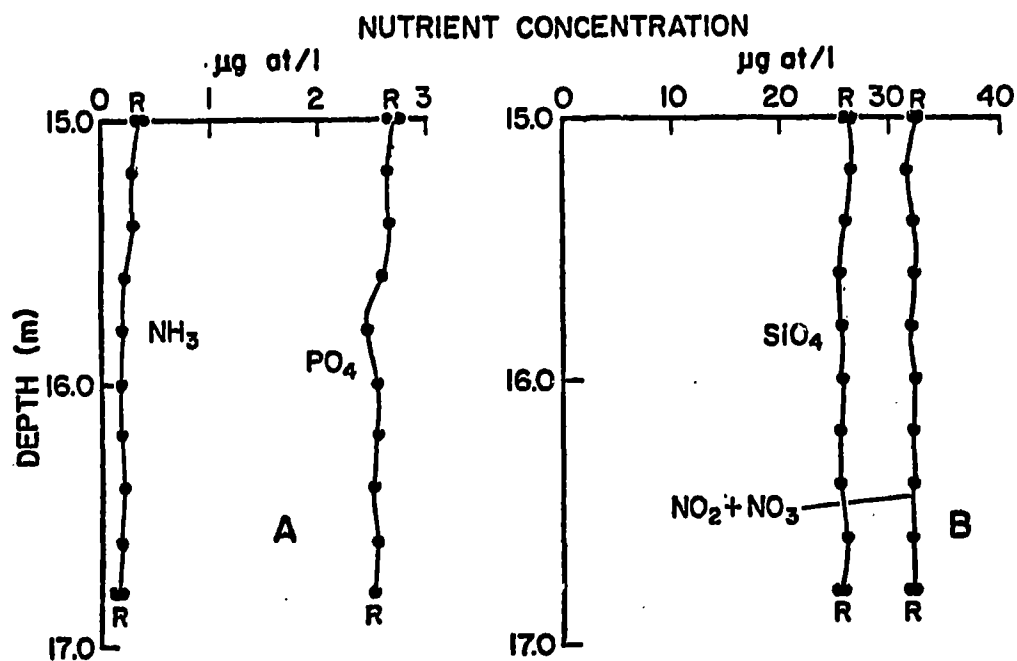


Figure 5. Microscale variation of nutrient salts in the pycnocline near Peru's coast in November 1977 (7711/HPS-3).

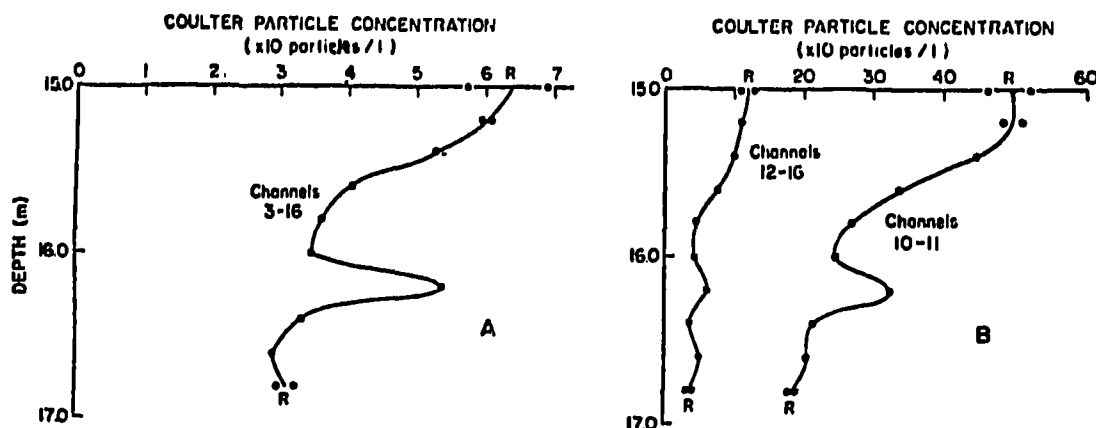


Figure 6. Microscale variation of particle counts (Coulter TA) in the pycnocline near Peru's coast in November 1977 (7711/MPS-3).

Despite the dynamic conditions encountered, microstructure of the several organisms was at least as pronounced in the "mixed layer" near Peru's shelf-break as in the more stable layer at the same depth near the coast. None of the variations were in the form of stepped trends but were all of sub-metre extent (Fig. 7). Small ciliates (20-50 μ m) were less numerous and covaried with the small ciliates.

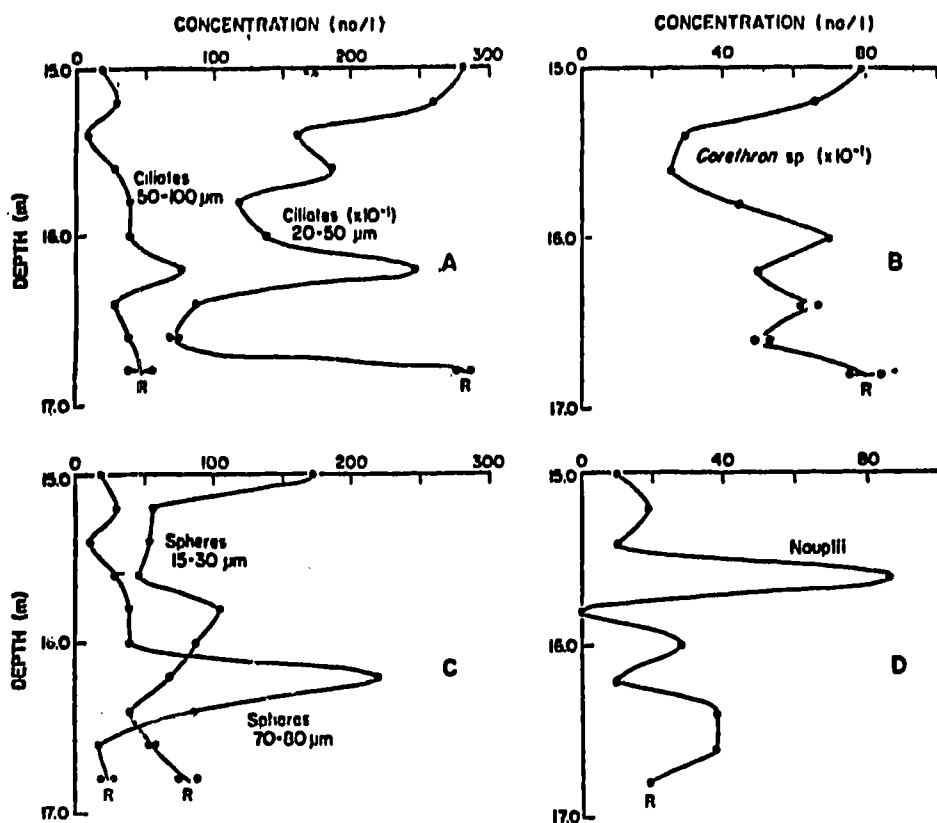


Figure 7. Microscale variation of larval anchovy food and non-food organisms off Peru's shelf-break in November 1977 (7711/HPS-2).

Covariation with ciliates of 70-80 µm sphere concentrations indicates that ciliates had actively associated with copepod eggs in the stratum between 16.0 and 16.6 m or alternatively that these spheres were actually ciliates (an artifact of sample preservation). The former seems more likely, as the spheres were quite smooth and regular in shape, and of nearly uniform size.

Copepod nauplii, also food items, exhibited large vertical variation and close replication. A pronounced maximum of their concentration was detected 60 cm above the presumed "egg" maximum, and 20 cm above a sample containing no nauplii.

Microscale variation of nutrients was greater at the slope station than at the coastal station, despite the difference in layer stability (Fig. 8). Nutrients were lower than at the coastal station but not limiting to phytoplankton growth. Microscale variation was not as pronounced as in the SC Bight, but was detectable for silicate (which covaried with the diatom *Corethron*) and perhaps for ammonia and phosphate. Nitrite-nitrate was constant over the 2 m interval.

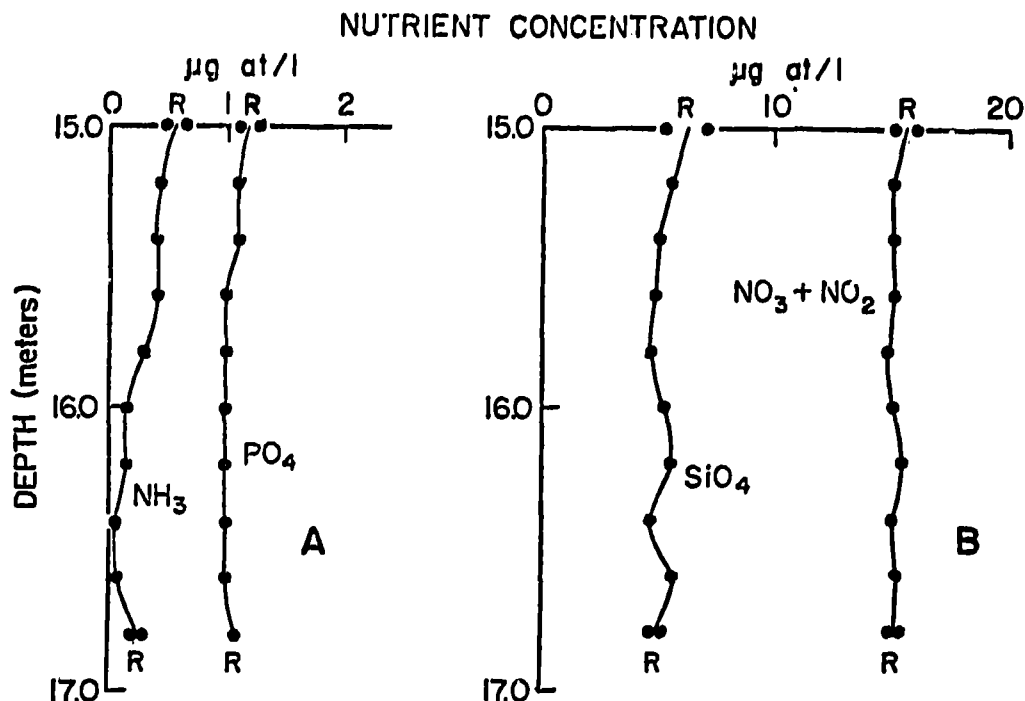


Figure 8. Microscale variation of nutrient salts off Peru's shelf-break in November 1977 (NPS-2).

Particle concentration counts from Coulter Counter was lower and less variable with depth than at the coastal station, except for the 16-50 μm category, which also showed variation on the 5 cm scale (Fig. 9). Chlorophyll a and phaeopigments, by contrast with Fig. 5, varied reciprocally with depth (Fig. 10) indicating either physical control by fine-scale lateral interleaving or biological control by localized grazing. No particular correspondence is evident between plant pigment concentration and variation of the population enumerated.

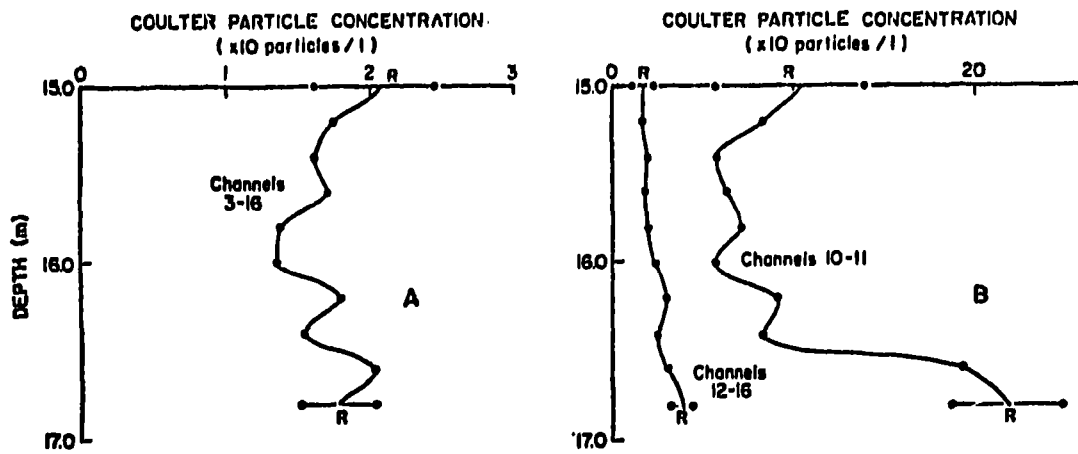


Figure 9. Microscale variation of particle counts (Coulter TA) off Peru's shelf-break in November 1977 (7711/HPS-2).

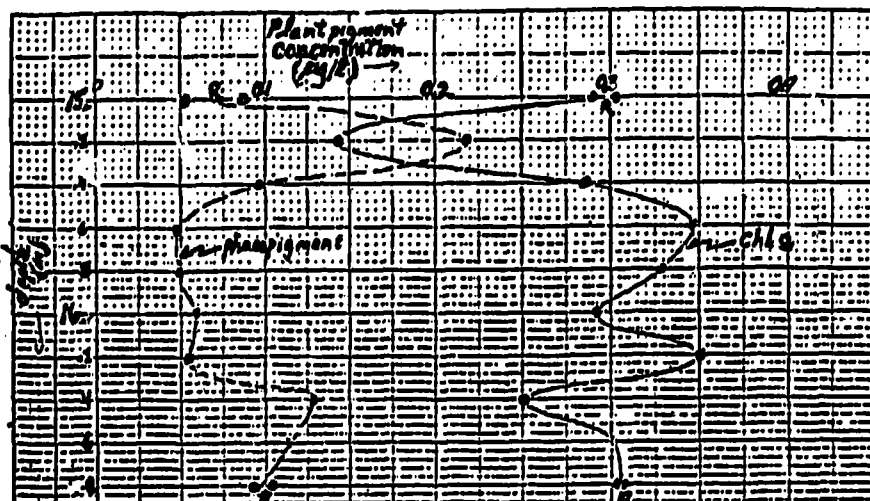


Figure 10. Microscale variation of phytoplankton pigment concentration off Peru's shelf-break in November 1977 (7711/HPS-2).

DISCUSSION

Association of plankton and biologically active substances with macroscopic flocs ("marine snow") has been reported and represents micro-distribution on the sub-cm scale. This work is of interest because it suggests yet another dimension to the complex ecological structure of the mixed layer and thermocline, e.g. organisms residing on marine snow are not available to the same predators or grazers as free-living individuals. The seaward extent of influence of marine snow is not known. My work indicates the presence of flocs affected concentrations of ciliates and detritus within 1 to 2 km of the coast but not beyond. This is confirmed by the lower incidence of aggregates in water of recent offshore origin than in neritic water, as reported by Trent *et al.* (1978).

Yet to be determined is the extent to which physical mixing mediates the microstructuring process. Dye studies by Kullenberg (1974) and Woods (1968) conducted elsewhere in density-stratified waters, show that layers of sub-metre thickness scale can persist for at least a day in the absence of storm-force winds and that disruptive processes can operate on the same scale. Only broad agreement was found during this study between degree of microstructure and estimates of vertical diffusivity from current shear and density stratification spanning layers in which microstructure was measured off California. The current meters, however, were separated vertically by 20 m. It is likely that any important mixing processes occurred on smaller scales.

The micro structure sample data suggest that small planktonic organisms overcome dispersive processes such as diffusive mixing to a degree sufficient to form laminae on the cm scale. Their vertical variation is pronounced in density-stratified water but detectable in the mixed layer as well. By water movement, reproductive rate and behaviour, plankton become differentially layered in what may prove to be microniches. The existence of the microniche is indicated in my work by the accompanying cm-scale variation of non-living particulates and of nutrient salts, particularly that of nitrogenous nutrients, which are commonly limiting to phytoplankton growth in these waters. Spatial partitioning of micro-plankton populations likely increases the capacity of the habitat to support greater community diversity and higher standing stocks because interspecific competition for resources is reduced, in much the same fashion as in terrestrial communities. Unlike terrestrial communities, however, such partitioning in the sea is inherently less stable on the short term. As examples, increased mixing during wind storms would modify if not destroy fine-scale variation, and the nearly synchronous diel reproduction (at times depending on species) of diatom and dinoflagellate populations likely produces daily changes in plankton microstructure. How such processes of mixing and restructuring of layers affect development and evolution of plankton communities is a topic of considerable interest.

It now appears that niches for plankton organisms may identifiably occur in midwater on a variety of spatial scales. For example, Reid *et al.* (1978) were able to distinguish between coastal phytoplankton communities of the upper mixed layer and the density-stratified layer from larger scale, vertically integrative pump samples, and below the sub-metre niche proposed here is the sub-centimetre niche created by marine snow for both phytoplankton and small zooplankton, as identified by Alldredge (1972) and by Silver *et al.* (1978).

REFERENCES

- ALAN HANCOCK FOUNDATION, UNIVERSITY OF SOUTHERN CALIFORNIA. 1965. An oceanographic and biological survey of the southern California mainland shelf. Calif.State Water Quality Control Board, Publ., 27, 232 p.
- ALLDREDGE, A.L. 1972. Abandoned larvacean houses: a unique food source in the pelagic environment. Science 177:885-887
- ALLEN, W.E. 1945. Vernal distribution of marine plankton diatoms offshore in southern California in 1940. Bull.Scripps Inst.Oceanogr., 5:335-369
- AMOS, A.F., M.G. LANGSETH, Jr. and R.G. Markl. 1972. Visible oceanic saline fronts, p. 49-62. In A.L. Gordon (ed.), Studies in Physical Oceanography, Vol. 1, Gordon and Breach, New York, pp. 194
- ARTHUR, D.K. 1956. The particulate food and the food resources of the larvae of three pelagic fishes, especially the Pacific sardine, *Sardinops caerulea* (Girard). Ph.D. Thesis, Univ.Calif.Scripps Inst.Oceanogr. La Jolla, 231 p.
- _____. 1976. Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax* and *Trachurus symmetricus*. Fish. Bull.U.S., 74:517-530
- _____. 1977. Distribution, size and abundance of microcopepods in the California Current System and their possible influence on survival of marine teleost larvae. Fish.Bull.U.S., 75:601-611
- ARTHUR, R.S. 1965. On the calculation of vertical motion from determinations of horizontal motion. J.Geophys.Res., 70:2799-2803
- BAINBRIDGE, R. 1957. The size, shape and density of marine phytoplankton concentrations. Biol.Rev., 32:91-115
- BANG, N.D. 1973. Characteristics of an intense ocean frontal system in the upwelling region west of Cape Town. Tellus 25:256-265
- BARKLEY, R.A. 1968. The Kuroshio-Oyashio front as a compound vortex street. J.Mar.Res., 26:83-104
- _____. 1972. Johnston Atoll's wake. J.Mar.Res., 30:201-216
- BARY, B.M. 1953. Sea-water discoloration by living organisms. N.Z.J.Sci.Technol., 34:393-407
- BEEBE, W. 1926. The Arcturus adventure. Putnam and Sons, New York, pp. 439
- BENNETT, E.B. 1963. An oceanographic atlas of the eastern tropical Pacific Ocean, based on data from EASTROPIC expedition, Oct.-Dec. 1955. Bull.Inter-Am.Trop.Tuna Comm., 8:33-165
- BERGER, E. and R. WILLE. 1972. Periodic flow phenomena. Ann.Rev.Fluid Mech., 4:313-340
- BERNER, L. Jr. 1959. Food of the larvae of the northern anchovy *Engraulis mordax*. Bull. Inter-Am.Trop.Tuna Comm., 4:3-22
- BERNSTEIN, R.L., L. BREAKER and R. WHIRTNER. 1977. California Current eddy formation: ship, air and satellite results. Science 195:353-359

- BERNSTEIN, R.L. and W.B. White. 1974. Time and length scales of baroclinic eddies in the Central North Pacific Ocean. *J.Phys.Oceanogr.* 4:613-624
- BLACKBURN, M. 1966. Biological oceanography of the eastern tropical Pacific: summary of existing information. *U.S.Fish Wildl.Serv.SSRF* 540:1-18
- BLACKBURN, M. *et al.* 1970. Seasonal and areal changes in standing stocks of phytoplankton, zooplankton and micronekton in the eastern tropical Pacific. *Mar.Biol.* 7:14-31
- BRANDHORST, W. 1958. Thermocline topography, zooplankton standing crop, and mechanisms of fertilization in the eastern tropical Pacific. *J.Cons.perm.int.explor.mer.* 24:16-31
- BRINTON, E. 1976. Population biology of *Euphausia pacifica* off southern California. *Fish. Bull.U.S.*, 74:733-762
- BROENKOW, W.W. 1965. Nutrient distribution in the Costa Rica Dome in the eastern tropical Pacific ocean. *Limnol.Oceanogr.*, 10:40-52
- BROWN, D.M. 1965. Results of current measurements with drogues 1963-1964. *Scripps Inst. Oceanogr. Data Report* 65-3, pp. 42
- CASSIE, R.M. 1959a. An experimental study of factors inducing aggregation in marine plankton. *N.Z.J.Sci.*, 2:339-365
- _____. 1959b. Micro-distribution of plankton. *N.Z.J.Sci.*, 2:398-409
- CLARK, N.E. *et al.* 1974. Heat exchange between ocean and atmosphere in the eastern North Pacific for 1961-71. *NOAA Tech.Rept.NMFS SSRF Fish No.* 682:108 p.
- CHOPRA, K.P. 1973. Atmospheric and oceanic flow problems introduced by islands. *Adv. Geophysics*, 16:297-421
- CURTIN, T.B. and C.N.K. MOOERS. 1975. Observations and interpretation of a high-frequency internal wave packet and surface slick pattern. *J.Geophys.Res.*, 80:882-894
- DE MENDIOLA, B. 1974. Food of the larval anchoveta *Engraulis ringens* J. In J.H.S. Blaxter (ed.), *The Early Life History of Fish.* Springer-Verlag, Berlin, pp. 765
- DOE, L.A.E. 1978. Project ICANE. *Bedford Inst.Oceanogr.Rept.Ser.*, BI-R-78-6, pp. 211
- ECKART, C. 1948. An analysis of the stirring and mixing processes in incompressible fluids. *J.Mar.Res.*, 7:265-275
- FALLER, A.J. and A.H. WOODCOCK. 1964. The spacing of windrows of *Sargassum* in the ocean. *J.Mar.Res.*, 22:22-29
- FRANKIGNOUL, C. 1976. Observed interaction between oceanic internal waves and mesoscale eddies. *Deep-Sea Res.*, 23:805-820
- GEORGE, D.G. and R.W. EDWARDS. 1973. *Daphnia* distribution within Langmuir circulations. *Limnol.Oceanogr.*, 18:798-800
- HARRIS, G.P. and J.N.A. LOTT. 1973. Observations of Langmuir circulations in Lake Ontario. *Limnol.Oceanogr.*, 18:584-589
- HICKEY, B.M. 1979. The California Current System - hypotheses and facts. *Progress in Oceanogr.* 8:191-279

- HUNTER, J.R. 1972. Swimming and feeding behavior of larval anchovy *Engraulis mordax*. Fish. Bull.U.S., 70:821-838
- _____. In press. The feeding ecology of marine fish larvae. In The Physiological and Behavioral Manipulation of Food Fish as Production and Management Tools. J.E. Bardach (ed.), Intl.Center for Living Aquatic Resources Mgmt.
- JOHNSON, M.W. 1960. Production and distribution of the larvae of the spiny lobster *Panulirus interruptus* (Randall) with records on *P. gracilis* streets. Bull.Scripps Inst. Oceanogr., 7:413-462
- KAMYKOWSKI, D. 1974. Possible interactions between phytoplankton and semi-diurnal internal tides. J.Mar.Res., 32:67-89
- KULLENBERG, G. 1974. Investigation of small-scale vertical mixing in relation to the temperature structure in stably stratified waters. Adv.Geophys. 18A:339-351
- LASKER, R. 1975. Field criteria for survival of larval anchovy: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish.Bull.U.S., 73:453-462
- _____. 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp.P.-V.Réun.Cons.int.explor.mer. 173:212-230
- LASKER, R. et al. 1970. Feeding, growth and survival of *Engraulis mordax* larvae reared in the laboratory. Mar.Biol., 5:345-353
- LAURS, R.M. and R.J. LYNN. 1977. Seasonal migration of north Pacific albacore, *Thunnus alalunga*, in relation to ocean features as indicated by ultrasonic tracking and oceanographic sampling. Fish.Bull.U.S., 75:347-355
- LEFEVRE, J. and J.R. GRALL. 1970. On the relationships of *Noctiluca* swarming off the western coast of Brittany with hydrological features and plankton characteristics of the environment. J.exp.mar.biol.ecol., 4:287-306
- LONGHURST, A.R. 1968. Distribution of the larvae of *Pleuroncodes planipes* in the California Current. Limnol.Oceanogr., 13:143-155
- MACGREGOR, J.S. 1974. Changes in the amount and proportions of DDT and its metabolites, DDE and DDD, in the marine environment off southern California, 1949-1972. Fish. Bull.U.S., 72:275-293
- MCALICE, B.J. 1970. Observations on the small-scale distribution of estuarine phytoplankton. Mar.Biol., 7:100-111
- MCGARY, J.W. 1955. Mid-Pacific oceanography, Part VI, Hawaiian offshore waters, Dec. 1949 - Nov. 1951. U.S.Fish Wildl.Serv. SSRF-152, 138 p.
- MOOERS, C.N.K., C.N. Flagg and W.C. Boicourt. 1978. Prograde and retrograde fronts. In M.J. Bowman and W.E. Esaias (eds.), Oceanic Fronts in Coastal Processes. Springer-Verlag, Berlin, pp. 114
- NELSON, C.S. 1977. Wind stress and wind stress curl over the California Current. NOAA Tech. Rept.NMFS SSRF 714, 26 p. + 19 figs.
- OWEN, R.W. 1966. Horizontal vortices in the surface layer of the sea. J.Mar.Res., 24:56-66
- _____. 1967. Atlas of July oceanographic conditions in the northwest Pacific ocean, 1961-64. U.S.Fish Wildl.Serv.SSR 549, pp. 85

- OWEN, R.W. 1968. Oceanographic conditions in the northeast Pacific and their relation to the albacore fishery. *Fish.Bull.U.S.*, 66:503-526
- _____. 1974. Distribution of primary production, plant pigments and Secchi depth in the California Current region, 1969. *CalCOFI Atlas 20*, A. Fleminger and J.G. Wyllie (eds.), 4 pp. + 19 figs.
- _____. 1980. Eddies of the California Current System: physical and ecological characteristics. In D.M. Power (ed.), *The California Islands*. Santa Barbara Mus.Nat.History (Calif.) pp.787
- _____. In press, A. Fronts and eddies in the sea: mechanisms, interactions and biological effects. In A.R. Longhurst (ed.), *Analysis of Marine Ecosystems*. Academic Press, London
- _____. In press, B. Microscale plankton patchiness in the larval anchovy environment. *Rapp.P.V.Réun.Cons.int.explor.mer*, 178
- OWEN, R.W. and C.K. Sanchez. 1974. Phytoplankton pigment and production measurements in the California Current region, 1969-1972. *NOAA/NMFS Data Rept. 91*, 5 pp. + 2 tables
- OWEN, R.W. and B. ZEITZSCHEL. 1970a. Phytoplankton standing stocks and production. In C.M. Love (ed.), *EASTROPAC Atlas*. *NOAA-NMFS Circ.*, 330(4):9-10 + figs.
- _____. 1970b. Phytoplankton production: seasonal change in the oceanic eastern tropical Pacific. *Mar.Biol.*, 7:32-36
- PACKARD, T.T., D. BLASCO and R.T. BARBER. 1978. *Mesodinium rubrum* in the Baja California upwelling system. In R. Boje and M. Tomczak (eds.), *Upwelling Ecosystems*. Springer-Verlag, Berlin, pp. 303
- PATZERT, W.C. 1970. Eddies in Hawaiian waters. *Hawaii Inst.Geophys.Rep.*, 69-8, 51 pp. + figs.
- PAVLOVA, Yu.V. 1966. Seasonal variations of the California Current. *Oceanology* 6: 806-814
- PINGREE, R.D., G.R. Forster and G.K. Morrison. 1974. Turbulent convergent tidal fronts. *J.Mar.Biol.Assoc.U.K.*, 54:469-479
- PINGREE, R.D., P.M. HOLLIGAN and R.N. HEAD. 1977. Survival of dinoflagellate blooms in the western English Channel. *Nature* 265:266-269
- POWERS, P.B.A. 1932. *Cycolotrichium meunieri* sp. nov. (protozoa, ciliata); cause of red water in the Gulf of Maine. *Biol.Bull.*, 63:74-80
- REID, F.M.H., et al. 1978. Spatial distribution of phytoplankton species in chlorophyll maximum layers off southern California. *Limnol.Oceanogr.*, 23:219-226
- REID, J.L. Jr., R.A. Schwartzlose and D.M. Brown. 1963. Direct measurements of a small surface eddy off northern Baja California. *J.Mar.Res.*, 21:205-218
- REID, J.L. Jr., G.I. RODEN and J.G. WYLLIE. 1958. Studies of the California Current system. *Calif.Coop.Oceanic Fish.Invest.Rept.*, 1 July 1956 to 1 January 1958, pp. 27-56
- ROUSE, H. 1963. On the role of eddies in fluid motion. *Am.Sci.*, 51:284-314
- SARGENT, M.C. and T.J. WALKER. 1948. Diatom populations associated with eddies off southern California in 1941. *J.Mar.Res.*, 7:490-505
- SAVIDGE, G. 1976. A preliminary study of the distribution of chlorophyll a in the Celtic and Western Irish Seas. *Estuarine and Coastal Mar.Sci.*, 4:617-625

- SAVIDGE, G. and P. FOSTER. 1978. Phytoplankton biology of a thermal front in the Celtic Sea. *Nature* 271:155-157
- SCHWARTZLOSE, R.A. 1962. Nearshore currents of the western United States and Baja California as measured by drift bottles. Part 2, Scientific Contributions, Calif.Coop. Oceanic Fish.Invest.Rept., 1 July 1960 to 30 June 1962, pp. 15-22
- SCOTT, J.T. *et al.* 1969. On the mechanism of Langmuir circulations and their role in epilimnion mixing. *Limnol.Oceanogr.*, 14:493-503
- SETTE, O.E. 1955. Consideration of midocean fish production as related to oceanic circulatory systems. *J.Mar.Res.*, 14:398-414
- SETTE, O.E. and E.H. AHLSTROM. 1948. Estimations of abundance of the eggs of the Pacific pilchard (*Sardinops caerulea*) off southern California during 1940 and 1941. *J.Mar.Res.*, 7:511-542
- SILVER, M.W., A.L. SHANKS and J.D. TRENT. 1978. Marine snow: microplankton habitat and source of small-scale patchiness in pelagic populations. *Science* 201:371-373
- SIMPSON, J.H., C.M. ALLEN and N.C.G. MORRIS. 1978. Fronts on the continental shelf. *J.Geophys.Res.*, 83:4607-4631
- SIMPSON, J.H. and R.D. PINGREE. 1978. Shallow sea fronts produced by tidal stirring. In M.J. Bowman and W.E. Esaias (eds.), *Oceanic Fronts in Coastal Processes*. Springer-Verlag, Berlin, pp. 114
- SMITH, P.E. 1974. Distribution of zooplankton volumes in the California Current region, 1969. *CalCOFI Atlas* 20. A. Fleminger and J.G. Wyllie (eds.), 3 pp. + 8 figs.
- _____. 1978. Biological effects of ocean variability: time and space scales of biological response. *Rapp.P.-V.Réun.Cons.int.explor.mer*, 173:117-127
- SQUIRE, J.L. Jr. 1977. Surface currents as determined by drift card releases over the continental shelf off central and southern California. *NOAA Tech.Rept.NMFS SSRF-718*, 12 pp.
- STOMMEL, H. 1949. Trajectories of small bodies sinking slowly through convection cells. *J.Mar.Res.*, 8:24-29
- SUTCLIFFE, J.H. Jr., E.R. BAYLOR and D.W. MENZEL. 1963. Sea surface chemistry and Langmuir circulation. *Deep-Sea Res.*, 10:233-243
- SUTCLIFFE, W.H. Jr. *et al.* 1971. Relations between wind speeds, Langmuir circulation and particle concentration in the ocean. *Deep-Sea Res.*, 18:639-643
- SZEKIELDA, K.H. *et al.* 1972. Element enrichment in organic films and foam associated with aquatic frontal systems. *J.Geophys.Res.*, 77:5278-5282
- THOMAS, W.H. 1970. Nutrient chemistry. In C.M. Love (ed.), *EASTROPAC Atlas*, NOAA/NMFS Circ., 330:8 pp. + figs.
- _____. 1977. Nutrient-phytoplankton interrelationships in the eastern tropical Pacific ocean. *Bull.Inter-Am.Trop.Tuna Comm.*, 17:173-212
- THOMAS, W.H. and D.L.R. SEIBERT. 1974. Distribution of nitrate, nitrite, phosphate and silicate in the California Current region, 1969. *Calif.Coop.Oceanic Fish. Invest.Atlas* 20, A. Fleminger and J.G. Wyllie (eds.), 4 pp. + figs.

- THOMAS, W.H., M. POLLOCK and D.L.R. SEIBERT. 1980. Effects of simulated upwelling and oligotrophy on chemostat-grown natural marine phytoplankton assemblages. *J.Exp.Mar.Biol.Ecol.*, 45:25-36
- TRENT, J., A. SHANKS and M. SILVER. 1978. *In situ* and laboratory measurements on macroscopic aggregates in Monterey Bay, California. *Limnol.Oceanogr.*, 23:626-635
- TSUCHIYA, M. 1980. Inshore circulation in the Southern California Bight, 1974-1977. *Deep-Sea Res.*, 27:99-118
- TSUJITA, T. 1957. The fisheries oceanography of the East China Sea and Tsuchima Strait. 1. The structure and ecological character of the fishing grounds. *Bull.Seikai Reg.Fish.Res.Lab.*, 13:1-47
- UDA, M. and M. ISHINO. 1958. Enrichment pattern resulting from eddy systems in relation to fishing grounds. *J. Tokyo Univ.Fish.*, 44:105-129
- U.S. DEPT. INTERIOR. 1978. Draft environmental statement, OCS Sale No. 48. Proposed 1979 outer continental shelf oil and gas lease sale, offshore southern California, Vol. 1, 620 pp.
- UTERMOHL, H. 1931. Neue Wege in der quantitativen Erfassung des Planktons. *Verh.Int.Ver. theor.angew.Limnol.*, 5:567-596
- VLIMEN, W.J. 1977. A mathematical model of the relationship between larval anchovy *Engraulis mordax* growth, prey microdistribution and larval behavior. *Env.Biol. Fish.*, 2:211-233
- WARE, D.M., B. ROJAS DE MENDIOLA and D.S. NEWHOUSE. In press. Behavior of first-feeding Peruvian anchoveta larvae, *Engraulis ringens* J. Rapp.P.-V.Réun.Cons.int.explor. mer, 178
- WOODCOCK, A.H. 1944. A theory of surface water motion deduced from the wind-induced motion of the *Physalia*. *J.Mar.Res.*, 5:196-205
- _____. 1950. Subsurface pelagic *Sargassum*. *J.Mar.Res.*, 9:77-92
- WOODS, J.D. 1968. CAT under water. *Weather* 23:224-235
- _____. (In press). Diurnal and seasonal variation of convection in the wind mixed layer of the ocean. *Q.J.Roy.Met.Soc.*, (MS, pp. 32)
- WYLLIE, J. 1966. Geostrophic flow of the California Current at the surface and at 200 meters. *Calif.Coop.Oceanic Fish.Invest. Atlas* 4, 13 pp. + figs.
- WYRTKI, K. 1964. Upwelling in the Costa Rica Dome. *Fish.Bull.U.S.*, 63:355-372
- YASUI, M. 1961. Internal waves in the open sea. *The Oceanogr.Mag.*, 12:157-183

THE CONSEQUENCES OF CANNIBALISM IN THE STOCK-RECRUITMENT
RELATIONSHIP OF PLANKTIVOROUS PELAGIC FISHES SUCH AS *ENGRAULIS*

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INTRODUCTION

Recruitment in clupeoid fishes is usually highly variable (see Sharp, this volume, also Cushing, 1971; Cushing and Harris, 1973). This variability obscures the nature of the underlying relationship between the expected value (in the statistical sense) of recruitment and the abundance of the parental stock. A wide variety of mathematical models of the relationship have been proposed, but in very few cases have empirical observations been sufficient to justify a choice between models. While greater awareness of "The Stock Recruitment Problem" has been gained in the last two decades, remarkably little progress has been made in solving it. As a case in point, the classic debate between Frances N. Clark and John C. Marr (Clark and Marr, 1955) regarding density dependence versus independence in the stock-recruitment relationship of the Pacific sardine (*Sardinops sagax caerulea*) is being renewed in discussions regarding management of the northern anchovy (*Engraulis mordax*) fishery which succeeded it in California.

No doubt, given a long time series of data, empirical stock-recruitment models can be developed. However, in management's quest for maximizing consumptive benefit from most of these fisheries, we are faced with two problems: 1) an incorrect interim choice of management strategy is likely to terminate collection of the necessary data due to collapse of the fishery; and 2) overly conservative management is usually unacceptable due to pressing social and economic needs which can be met by fishery expansion. In this context, we cannot simply choose to wait until sufficient data have been accumulated to justify a particular empirical model; given the natural variability of recruitment, this approach could require more than a century. The alternative is to attempt to elucidate the mechanisms determining recruitment, and to construct rational "cause-and-effect" models.

This paper examines one cause-and-effect mechanism which leads to a characteristic family of stock-recruitment curves. While it is often difficult to demonstrate specific density dependent mechanisms by which clupeoid populations are regulated (albeit weakly), cannibalism is indisputably such a mechanism. The following discussion of cannibalism includes a variety of species, but the clearest and most complete information is available for the genus *Engraulis*.

THE RICKER CURVE

Ricker (1954) developed what has come to be known as the "Ricker curve" to describe a stock-recruitment relationship wherein initial production of offspring is proportional to stock size, but their subsequent mortality rate is also proportional to adult stock size. One common form of the Ricker curve is:

$$R = aSe^{-bS} \quad (1)$$

where R is recruitment, and S is spawner abundance. Fitted coefficients a and b reflect density independent and dependent factors respectively. In particular, coefficient b describes the proportionality between spawner abundance and the instantaneous coefficient of mortality of offspring up to the age of recruitment. Two mechanisms by which mortality is likely to be proportional to parental abundance are 1) cannibalism by the parents themselves (ibid), and 2) food limitation, whereby the length of time spent in some vulnerable stage is proportional to the initial number in this stage, and the mortality rate is constant over this time (Chapman, 1973). *Engraulis* eggs and yolk sac larvae would only be subject to cannibalism, but feeding larvae are conceivably subject to both density dependent mechanisms.

The food limitation mechanism is difficult to study. Probably the first step would be to demonstrate the existence of sufficiently small coherent patches of larval fish food such that predation by the larvae is a significant determinant of the density of food in the patch. Current thinking (Lasker, 1978) is that favourable food patches are very large with respect to distances travelled by larvae, i.e. larval ambits. An alternative possibility which is presently being investigated (J. Trent, Scripps Institution of Oceanography, personal communication) is that larvae are able to successfully feed on the cloud of plankton that surrounds particles of "marine snow". The size of these food patches is sufficiently small that feeding by larval fish could affect local food density. This mechanism will not be discussed further here.

Cannibalism has been the rationale for using the Ricker curve in models of several engraulid and clupeid populations, but its appropriateness has not been justified quantitatively; cannibalism has not been shown to be of sufficient magnitude to account for an appropriate portion of the mortality of spawning products. More often the Ricker curve is used because it appears to fit the data. Schaaf and Huntsman (1972) fit a Ricker curve to Atlantic menhaden (*Brevoortia tyrannus*) data with no discussion of an underlying mechanism. Murphy (1966, 1967) fitted Ricker curves to Pacific sardine data, citing cases of cannibalism by that and other species of *Sardinops*.

Gulland (1973) suggested that the Ricker model may be appropriate for the Peruvian anchoveta (*Engraulis ringens*), again based on non-quantitative considerations of cannibalism. Gulland suggested that mortality from cannibalism could, in principle, be determined from detailed examination of stomach contents. At the Third Session of the Panel of Experts (Instituto del Mar del Peru, 1973), J. Csirke presented a Ricker curve fit to catch per unit effort (CPUE) indices of adult and recruit abundances, but the mechanisms were discussed in only general terms. Interestingly, nearly all of the data points fell on the descending limb of the stock-recruitment curve. This tendency for recruitment to decline at increasing stock sizes clearly dictated rejection of a monotonically increasing stock recruitment curve such as that developed by Beverton and Holt (for a comparison of Ricker and Beverton-Holt curves, see Ricker 1973, 1975).

Csirke (1980) modified the usual Ricker curve in order to better distinguish between density dependent and independent mechanisms assumed to underly the model. Density independent processes were assumed to be a function of anchoveta stock abundance as calculated by cohort analysis (VPA). He realized that density dependent processes indeed were a function of density (biomass per unit volume or area) rather than overall abundance. Csirke's method

of quantifying this difference was ingenious; he utilized CPUE as an index of density, effectively taking advantage of the very problem which has made CPUE a poor index of abundance of pelagic fishes. Csirke's model will be discussed further in a later section. As before, Csirke assumed that cannibalism is the most likely mechanism determining the shape of the stock-recruitment relationship. He cited several reports of stomach contents, some of which indicated extensive consumption of spawning products.

QUANTIFICATION OF CANNIBALISM

Until recently quantification of the impact of cannibalism has been difficult because little was known about egg production. Hunter and Goldberg (1980) have resolved this problem by histological analysis of anchovy gonads. The frequency of occurrence of one-day-old post-ovulatory follicles led them to conclude that *E. mordax* spawned every 6 to 8 days during the peak of the season. This allows daily production to be compared with estimated consumption of spawning products over a similar period. Hunter and Kimbrell (In press) have attempted such calculations. Based on a mean of 5.1 eggs per stomach and an instantaneous coefficient of gastric evacuation of 0.701/hr., they estimated daily consumption to be 85.8 eggs, or 5.1 eggs/g of fish weight. This compares with an average batch fecundity of 29.7 eggs/g for all fish (including males).

If we think of cannibalism as analogous to fishing, the catch equation describes the relationship between consumption ("catch"), initial abundance and rates of mortality. Thus we have

$$C_c = E_o F_c (1 - e^{-(F_c + M)t_e}) / (F_c + M) \quad (2)$$

where C_c is daily egg consumption per gram of adults (5.1 eggs/g)

E_o is daily egg production per gram of adults (29.7 eggs/g)

F_c is coefficient of mortality due to cannibalism

M is coefficient of mortality due to other causes, and

t_e is length of time eggs are subject to mortality, i.e. time to hatching

Two estimates of instantaneous coefficient of total mortality (Z) for anchovy eggs are available. Hunter and Kimbrell used an estimate given by Smith and Lasker (1978) of about 53%/day ($Z = 0.775$). This is an average over the years 1951 through 1969 and includes a wide range of anchovy abundances. The second estimate of Z is based on extensive sampling of egg abundance-at-age (Stauffer and Picquelle, 1980). This estimate of $Z = 0.39$ is somewhat lower and is associated with a level of anchovy abundance similar to that presumed to exist in 1976 and 1977 when Hunter and Kimbrell obtained their samples. Under typical conditions (ca. 15°C), anchovy eggs hatch in about 2.5 days (Theilacker, this volume). For purposes of the present calculations, I assume that a single day's consumption of eggs from the past three days' cohorts is equivalent to the consumption over three days of a single cohort. For the larger estimate of Z (Smith and Lasker, 1978), F_c is 0.153, and accounts for 20% of total mortality. The smaller estimate of Z gives an F_c of 0.108, accounting for 28% of total mortality.

These estimates of F_c allow evaluation of the significance of cannibalism to the stock-recruitment relationship of anchovy. The Ricker curve (Equation 1) has a maximum when $S = 1/b$ (Ricker, 1973). At this stock size the density dependent term is e^{-1} , and the survival rate from density dependent sources of mortality is 36.8%. If cannibalism is the only source of density dependent mortality, recruitment is maximal when

$$\int_0^{t_R} F_c(t) dt = 1 \quad (3)$$

That is, when the age specific coefficients of density dependent mortality ($F_c(t)$) integrated over the time from spawning to recruitment (t_R) is equal to unity. If the integral exceeds unity, recruitment will decrease because of density dependent effects. This provides a convenient reference level for assessment of density dependent effects. If we evaluate the above integral over the egg stage alone (2.5 days), we obtain values of 0.383 and 0.270 for our two estimates respectively. Thus, in the egg stage alone, this accounts for one-third of the "reference" level of density dependent mortality.

Similar calculations are difficult to make for larvae. Hunter and Kimbrell (in press) report that anchovies digest small larvae beyond recognition in 30 min., so the apparent residence time is very short. Also, with digestion proceeding this rapidly, many larvae could be decomposed between the time the adult is captured and when the preservative effectively stops digestion. For example, midwater trawls for adult *E. mordax* are often 20 mins., in duration, and retrieval of the net takes another 20 mins. By the time the samples are preserved, at least 30 mins. have elapsed since the average time of capture. This indicates that only the larger larvae could resist digestion long enough to be observed, which is consistent with reported stomach contents. If cannibalism on larvae is to be quantified, rapid sampling methods will have to be developed. One possibility is a preservation system acting in the cod end of the sampling net.

In the absence of quantitative data on larval mortality caused by cannibalism, I offer the following speculation. The instantaneous coefficient of total mortality of *E. mordax* larvae has been estimated by Smith and Lasker (1978) as 0.14, and by Hewitt (In press) as 0.16. This is considerably lower than estimated egg mortality rates (also see Jones and Hall, 1974); it seems reasonable that rates of cannibalism will decrease similarly. Anchovy eggs and larvae are patchily distributed at all ages; however, patchiness is minimal at an age of about 18 days (Hewitt, In press). Dispersion may help decrease the rate of cannibalism, as the schools of adult anchovies orient preferentially to concentrations of food. However, anchovy larvae are susceptible to cannibalism for many weeks. The one measurable anchovy larva encountered by Hunter and Kimbrell (In press) was 17 mm, which corresponds to a likely age of over 30 days based on the growth curve given by Hunter (1976). If the average daily coefficient of mortality due to cannibalism were as low as 0.02, its action over 30 days would account for enough additional density dependent mortality to reach or exceed the "reference" level of 1.

The only comparable observations (i.e. quantified and taken during the spawning season) for the Peruvian anchoveta are reported by Rojas and Ochoa (1973). Rojas and Ochoa did not encounter anchovy larvae in the anchoveta stomachs, but did encounter 235 anchoveta eggs in 95 stomachs taken at four stations (I have omitted their station 52 in which the stomachs were nearly empty). The average stomach therefore contained 2.5 anchoveta eggs, or about one-half that observed by Hunter and Kimbrell. Rojas and Ochoa hypothesized a minimum feeding rate of three times per day, which is considerably less than Hunter and Kimbrell's gut evacuation rate would suggest. However, Rojas and Ochoa also indicated that phytoplankton may be digested more rapidly than zooplankton, and feeding rates could be generally higher for phytoplankton. Because *Engraulis* eggs are of a size that is usually consumed by filter-feeding (O'Connell, 1972; Hunter and Kimbrell, in press), we may expect higher rates of cannibalism when adults are filter-feeding upon phytoplankton. Because no egg production rate estimates are available for the Peruvian anchoveta, no firm conclusions can be drawn from Rojas and Ochoa (1973).

MODELS OF CANNIBALISM

Effective rates of cannibalism are undoubtedly influenced by a wide variety of factors, such as adult size, distribution and behaviour, adult and larval food quality and concentration, and abiotic factors such as mixing and temperature. It would be premature to attempt to treat all of the possible factors in a cannibalism model, given our present limited knowledge. Rather we may gain an indication of the nature, direction, and perhaps magnitude of these influences based on very simple models. These simple models may also provide some insight as to appropriate management of cannibalistic planktivores.

Hunter and Kimbrell (In press) argued that a random filtering model could not describe the apparent consumption rate of eggs. Under simple assumptions of habitat volume and egg density, they found that an anchovy would have to randomly filter from 17 to 25 h/day, which they interpreted as indicating non-random, selective feeding behaviour. This does not mean that we should not begin a modelling effort with a random filtering model. Contrary to Hunter and Kimbrell, a random filtering model may be sufficient to approximate the effects of cannibalism as a regulatory mechanism. It would certainly form a reasonable point of departure for construction of cannibalism models based on non-random filtering behaviour.

The following models assume the time of year to be the spawning season. Many stochastic considerations will be omitted so as to limit the scope of the discussion to the fundamental framework. Initially, the models will consider only local dynamics. A more integrative view is presented in the discussion following development of the models.

Random filtering model for eggs

A cohort of eggs will be subject to mortality from cannibalism, with rate coefficient F_c , and to the rest of natural mortality, including predation and starvation, with rate coefficient M , as in Equation (2). The rate of cannibalism is given by

$$F_c = Nvp/V \quad (4)$$

where N is number of adult fish (cannibals)

v is average volume of water filtered per fish per unit time

p is fraction of time spent filtering, including fraction of habitat occupied by eggs,

and V is habitat volume

The egg mortality rate is therefore given by

$$dE/dt = -E(M + F_c)$$

or

$$dE/dt = -E(M + Nvp/V) \quad (5)$$

Upon integration we obtain the number of eggs (E_h) surviving the period in the egg stage (t_e), i.e. the number of eggs that hatch.

$$E_h = E_0 e^{-(M + Nvp/V)t_e} \quad (6)$$

The initial abundance of eggs (E_0) is the product of the number of fish and the average individual fecundity (f), including males and prespawners. This gives

$$E_h = fNe^{-(M + Nvp/V)t_e} \quad (7)$$

This equation has the form of a Ricker curve (Equation 1)

where

$$a = fe^{-Mt_e}$$

$$b = vpt_e/V$$

and number of eggs hatching is analogous to recruitment.

In modelling the events influencing the abundance and survival of pelagic fish larvae, initial conditions must include the number of eggs effectively hatched into the larval environment, which will be called "effective fecundity". Effective fecundity (E_h) can be divided into pre-spawning and post-spawning components. "Virtual fecundity" is the number of eggs released into the environment, and as Tsukayama and Alvarez (this volume) have shown, this component can be a compensatory function of population size, i.e. $E_0 = f(N)N$. The second component involves the subsequent survival of spawning products. Natural mortality and cannibalism will reduce the number of eggs which actually hatch to produce larvae. Again, cannibalism clearly leads to compensatory changes in effective fecundity as a function of population size or density.

As stated previously, the Ricker curve has a maximum when the density dependent exponent is equal to unity. Thus effective fecundity will be maximal when

$$Nvpt_e/V = 1$$

or

$$Nvpt_e = V \quad (8)$$

That is, effective fecundity is maximal when the local population filters a volume of water equivalent to the habitat volume exactly once during the length of time it takes the eggs to hatch. Note that the location of the maximum is independent of natural mortality, although the value of the maximum is not.

Note that intensity of cannibalism is associated with fish density (N/V) rather than abundance alone. The density of fish which maximizes effective fecundity according to this model can be compared with actual fish densities. This provides an independent test of whether cannibalism is likely to be an important factor in population regulation. Johannesson and Vilchez (this volume) give most of the information necessary to perform the calculations. They base their biomass estimates on anchoveta averaging 6.7 g. Leong and O'Connell (1969) estimate that an *E. mordax* of this size would filter 1.64 l/min, and I will assume that this is valid for *E. ringens* as well. If time to hatching is 2.5 days, each fish would be capable of filtering 5900 l in this period. One metric ton would contain 150 000 fish, so one ton could filter 0.88×10^9 l in 2.5 days. Johannesson and Vilchez report that most of the biomass was detected in the upper 40 m of the water column. One square nautical mile at this depth would contain 1.37×10^{11} l. If filtering were random and continuous over the entire 2.5-day period ($p = 1.0$), maximum effective fecundity would correspond to a density of 156 tons/mile². Johannesson and Vilchez found average anchoveta densities of 600 or more tons/mile² in the years 1973, 1976 and 1978. Local densities reached much higher levels, occasionally exceeding 2000 tons/mile². Even if p is small, cannibalism is likely to have a significant effect on the proportion of anchoveta eggs being hatched.

Recruitment model

As was discussed previously, cannibalism continues for at least one month following hatching, although the rate may be lower. Whereas the anchovy feeds on eggs by filter feeding, larvae are of a size which is captured by biting (Leong and O'Connell, 1969; O'Connell, 1972; Hunter and Kimbrell, in press). The ratio of biting to filtering activity varied with the relative abundance of large and small food particles. O'Connell (1972) estimated that the ratio of particle sizes in southern California waters suggested that biting activity could exceed 50% of the total feeding activity. While individual fish did not tend to alternate feeding modes when faced with a mixture of particle sizes, fish at the front of the school showed more biting activity, while fish at the rear of the school showed more filtering activity. Although it may be attractive to model biting and filter feeding as mutually exclusive events (the time spent consuming larvae cannot be spent consuming eggs, and vice-versa), a more practical approach is to assume that a school consumes all eggs and larvae in its path. Either approach requires more knowledge of school sizes and behaviour than is presently available.

If a model incorporating cannibalism on larvae were to be constructed, it would be analogous to the egg model (Equation 7). Larval life may be divided up into three periods: t_e is the length of the egg period, t_1 is the length during which larvae are subject to cannibalism, and t_r is remaining time to recruitment. Each period has a natural mortality coefficient, M_e , M_1 and M_r respectively. The model would now give expected recruitment (R) as a function of population size and density:

$$R = fN e^{-(M_e t_e + M_1 t_1 + M_r t_r)} e^{-Np(vt_e + ct_1)/V} \quad (9)$$

where c is rate of cannibalism on larvae. Recruitment will be maximized when

$$Np(vt_e + ct_1) = V \quad (10)$$

This is analogous to Equation (8), and may be interpreted similarly. If the appropriate unit of cannibalistic activity is the school rather than the individual fish, then recruitment will be maximal when a volume of water equivalent to the habitat volume is swept once by the schools over the period from spawning to end of vulnerability ($t_e + t_1$), assuming $p=1$. If the speed and average cross-sectional area of schools were known, it would be possible to attempt calculations similar to those for eggs.

Evaluation of terms

The recruitment model (Equation 9) contains three terms bearing on recruitment strength: fecundity, density independent mortality, and density dependent mortality. These terms are clearer if we transform the equation by taking logarithms:

$$\log_e(R/N) = \log_e f - \sum M_i t_i - (vt_e + ct_1)pN/V \quad (11)$$

Here the coefficient of density independent mortality has been generalized to $\sum M_i t_i$, where an arbitrary large number of stages replace the three simplified stages in Equation 9.

Relative roles of the three terms in determining recruitment can be evaluated by considering probable values in Equation (11). Hunter and Goldberg (1979) estimate the batch fecundity of female *E. mordax* to be 389 eggs/g. If half the fish are female and they average 17 g, the average batch fecundity is 3 300 egg/fish per spawning batch. If females spawn once every 6-8 days during the spawning season (ibid), perhaps 15 batches are spawned, giving a total fecundity of 50 000 egg/fish for the year. Thus $\log_e f$ is approximately 11. The pre-

vious discussion of density dependent mortality indicates that we should expect this coefficient to be approximately 1. For a short-lived fish such as *Engraulis*, the adult natural mortality rate commonly exceeds 50% annually. At 50%, the replacement level of recruitment is equal to the spawning stock, so $\log_e (R/N) \approx 0$. The only remaining value is ΣM_{it_i} for which there is no direct measure; however, it must be approximately 10 for Equation (11) to balance.

These values indicate that the ratio of density independent to density dependent factors (neglecting density dependent effects on fecundity) is 10 to 1. The preponderance of density independent influences tends to mask the relatively weak regulation of stock abundance. This is consistent with the large variability characteristic of clupeid and engraulid stocks. The large contribution of density independent variability does not allow the population to equilibrate at a stable level. Rather, equilibrium takes the form of a probability distribution of abundances centred about a mean value (see MacCall 1980, Sharp this volume). A production or equilibrium yield curve may be derived, but it should be used with caution: it must be interpreted in a probabilistic rather than deterministic sense.

Equation (11) also provides a framework for consideration of variability in recruitment. For a given population size, fecundity and density dependent mortality have fixed average values, with variability being dependent on environmental conditions. The probability distribution associated with the density independent term will tend to characterize recruitment at all population sizes. A variation in any M_{it_i} will have an equivalent effect on recruitment independently of the stage (i) in which it occurs. The final convolution of the probability distributions of M_{it_i} for all i may be complicated. For example covariance is possible, as in the case where the high density of esculent particles required for successful first feeding will tend to increase the probability of subsequent successful feeding and survival.

Alternatively, it may be possible to define a number of stages for which the probability distributions of M_{it_i} are independent. The sum of several such random variates (ΣM_{it_i}) may approach a normal probability distribution according to the Central Limit Theorem. If variability in density independent mortality dominates overall variability, we would expect $\log_e (R/N)$ to approach a normal distribution. Recruitment itself would tend to be distributed log-normally about its expected value for a given stock size. There is little direct evidence to demonstrate the true probability distribution of recruitment; indeed, the proper regression function is seldom clear. Use of log-log transformation often yields a constant variance of recruitment over a wide range of stock sizes, giving some support to the hypothesis of log-normality.

DISCUSSION

These models employ parameterizations which simplify complicated conditions and processes. The following discussions are centred on various types of considerations and their associated parameters.

Effects of fish size

Whereas fish size has not explicitly appeared in these models, several parameters can conveniently be expressed as power functions of fish weight or length. Leong and O'Connell (1969) estimated that the volume of water filtered by *E. mordax* per unit time increases approximately as the square root of fish weight. Hunter and Macewicz (1980) have estimated that batch fecundity increases as the 1.6 power of ovary-free female weight of *E. mordax*. Collins (1969) fitted allometric weight-length curves for *E. mordax*, obtaining exponents very near 3.0 for anchovies from southern California, but exponents were smaller (2.7 to 2.8) for fish from central California. If we standardize these variables to length of southern California anchovies, weight increases as the 3.0 power, filtration volume increases as the 1.5 power, and fecundity increases as the 4.8 power.

These relationships allow the model to be expressed in terms of biomass rather than numbers of fish. Biomass (B) is given by number of fish multiplied by their average weight (w), so $N=Bw^{-1}$. For example, the above filtration volume relationship can be substituted in Equation (8) to give maximum effective fecundity as a function of fish weight and biomass:

$$B/V = \sqrt{w}/a p t_e \quad (12)$$

where a is a constant of proportionality in the filtration volume relationship. This indicates that optimum density of biomass is proportional to the square root of the average fish weight, or the 1.5 power of average fish length. In other words, if anchovies are physically large, a larger equilibrium biomass would be expected than if they are physically small. As corollary, insofar as a fishery reduces the average age, and therefore the average size, the optimum density of the resource itself may be diminished. This argument holds only for the filter feeding mode of cannibalism (eggs). Leong and O'Connell (1969) estimated that particulate feeding rate increased as the 1.1 power of anchovy weight. This relationship is more appropriate to cannibalism of larvae, and the analog of equation (12) would indicate that the relationship is nearly independent of fish size.

Habitat volume and fish density

The preceding models have been restricted to local effects. The overall stock-recruitment relationship is an integrative average over extensive geographic and temporal variability. Neither the population (density dependent effects) nor environmental conditions (density independent effects) are uniformly distributed. While effective fecundity and production of larvae is likely to conform to a Ricker curve for a local area, the overall stock-recruitment relationship will be different. Ricker (1975, p. 294) states that nonuniformity of spawner distribution is likely to result in a flatter dome and more gently inclined descending limb than the simple Ricker curve would indicate. Johannesson and Vilchez (this volume) clearly show the extent of this nonuniformity: "estimates derived from the 7302 cruise data showed that 55% of stock biomass was concentrated in only 13% of the total area of distribution. Likewise, during the cruise 7603, 36% of the biomass fell within only 3.4% of the total area." It may be worthwhile to undertake a simulation study to examine possible shapes of stock-recruitment curves arising from observed patterns of stock distribution.

Habitat volume is essentially composed of three dimensions: alongshore, inshore-offshore, and vertical depth. The first two can be combined as a geographic area inhabited by the stock. Engraulid and clupeid fishes often show a characteristic pattern of changes in distribution with changes in population size. Murphy (1977) states "all or nearly all of the (clupeoid) stocks contract their feeding and spawning range as the population is reduced". Specific examples of this pattern are given by Smith (1972) for *E. mordax*, and Santander (this volume) for *E. ringens*.

The relationship of this pattern to reproduction may be elucidated by the following model. Consider a set of n discrete parcels of water V_i , $i = 1 \dots n$. The first parcel corresponds to the centre of population distribution, and subsequent parcels are at progressive distances from the centre. I assume that density independent mortality is least (i.e. conditions are most favourable for larvae) at the centre, and that conditions are progressively less favourable at greater distances from the centre. Within each parcel the stock-recruitment relationship is a Ricker curve (Equation 1), and each parcel has a density independent survival rate a_i which decreases in value as i increases ($a_i > a_{i+1}$). The total population ($N_{tot} = \sum N_i$) is distributed among the parcels, and each parcel has a coefficient of fish concentration $c_i = N_i/N_{tot}$. Coefficients of concentration are estimated from the distribution of population among the parcels.

Given the above model, I wish to estimate the vector of coefficients of concentration which will maximize recruitment for the entire stock, and to examine how this vector changes with population size. Without actually solving the equations, I will offer a heuristic argument that this model generates distribution patterns similar to those observed for clupeoids. At very low population sizes, most of the population will be in the first parcel, where reproduction will be the most successful. As the population size increases, density dependent mortality will reduce the per capita recruitment rate in the first parcel until combined mortality rates in the first parcel are equal to the density independent mortality rate in the second parcel. At this point the population will begin expanding into the second parcel. Each successive parcel will be similarly occupied. At each level of N_{tot} the vector of c_i will be such that the sum of density dependent and density independent mortality rates (i.e. the total mortality rate) will be the same for all parcels. Under this condition there is no reproductive advantage in migrating to another parcel. There should be some level of N_{tot} which maximizes total recruitment. Above this population size maximum recruitment would be obtained by shunting the excess spawners to the least favourable area (increasing c_n) but this will not happen as long as fish individually attempt to maximize their own reproduction.

As a result of this pattern of distribution, average fish density increases relatively more slowly than total population size. This suggests that clupeoid stock-recruitment relationships may be better described by a generalized Ricker curve such as

$$R = aNe^{-bN^c} \quad (13)$$

where $0 < c \leq 1$. When $c = 1$, a Ricker curve results. As c becomes smaller, the ascending limb becomes steeper, and the peak becomes broader with a progressively shallower descending limb. Csirke's (1980) stock-recruitment model is nearly equivalent to equation (13). Catch per unit effort (C/f) for pelagic fishes may commonly behave as a power function of stock abundance,

$$C/f = aN^\beta \quad (14)$$

where $\beta < 1$ (MacCall, 1976; Ulltang, 1976; Gulland, 1977). Thus Csirke assumes that β is a useful approximation of c in equation (13). It should also be noted that MSY will be overestimated if stock-recruitment data are fit by a Ricker curve ($c = 1$) when the actual relationship is characterized by $c < 1$. This is because the latter curve has a less pronounced peak.

I have hypothesized that habitat volume changes with population size in order to maximize individual reproduction. The mechanisms by which habitat volume changes are not known. One likely possibility is a tendency for adults to follow gradients of increasing food concentration. Without specifying any actual processes, it is safe to say that population expansion and contraction may occur by partially different mechanisms. For example, random diffusion will increase the range of fish as age increases. There is considerable evidence that older anchovies are distributed more widely than young anchovies in southern California (Mais, 1974). Larval drift patterns may result in some areas receiving more recruits than others, resulting in a tendency to contract toward these areas. If there are different mechanisms for expansion and contraction, and if the balance of effects determines the stock distribution, then habitat volume for the same total population size is likely to be characteristically different for increasing and decreasing trends in abundance. Thus, we may expect to see a "hysteresis" in the trajectory of population sizes over a cycle of decrease and increase. The concept of a single underlying stock-recruitment curve may be inappropriate.

Another consequence of the above geographic model is that the apparent overall stock-recruitment curve varies with the pattern of fishery removals. Segments of the population residing in the central "most favourable" areas will be reproducing closer to the peak or on the descending limb of their local stock-recruitment curves, while peripheral segments will be reproducing on the ascending limb of their stock-recruitment relationships. This indicates that fishery removals from the periphery may reduce recruitment proportionally to the fishery harvest, while removals from the centre may have little effect or may even increase recruitment. The most productive pattern of fishing should be to fish central areas of high density, and to discourage fishing at the edges of the population. Dispersion and migration of the fish will tend to reduce the relative benefit of this geographic fishing strategy.

The preceding discussion has not addressed the aspect of depth as a determinant of habitat volume. Over much of the range of the Peruvian anchoveta, maximum habitable depth is determined by low oxygen concentration. Limiting concentrations of oxygen may be as shallow as 10 to 20 m in inshore areas off northern Peru (see Richman and Smith, in press). The depth and intensity of oxygen depletion is a function of the rate at which organic material falls out of the overlying water. By consuming large amounts of primary and secondary production in the surface waters, the anchoveta may reduce the rate of detrital fallout, thereby depressing the depth of limiting oxygen concentration. Thus, within a given geographic area, increasing density of anchoveta may result in increased habitat volume, and increased reproductive rate due to decreased intensity of cannibalism.

Effects of food and feeding behaviour

Intensity of cannibalism is closely linked to the feeding behaviour of adults. The following discussion examines this relationship from three standpoints: responses to food abundance and to food composition, and non-random feeding behaviour. These considerations affect the value of parameter p , the effective time spent feeding.

Clearly, the amount of time spent feeding will decrease as food abundance increases (O'Connell 1972). The relationship between these two variables is poorly known because of our lack of knowledge of digestion patterns. Hunter and Kimbrell (In press) assumed a constant rate of gut evacuation, but their data appear to support the existence of an initial period of reduced gut evacuation, perhaps lasting 1 hour. Such a delay would increase the average residence time from 1.4 hours to 2.4 hours, decreasing estimates of total consumption by 40%. Rather than a continuous feeding model, Rojas and Ochoa (1973) appear to support a batch-feeding model. Until gut evacuation patterns are better known, it is difficult to compare gut contents with concentration of food in the environment in order to estimate volume of water swept or length of time spent feeding.

Bakun and Parrish (this volume) have compared oceanographic characteristics of the Peru and California currents with respect to larval habitat. Their discussion indicates that Peruvian conditions are favourable to formation of microlayers of larval food (see Lasker, 1978) because the ratio of wind mixing to upwelling decreases toward the equator. To this I would add that the high densities of food may result in less water being swept during feeding, and a lower *per capita* rate of cannibalism (b in Equation 1), so the peak of the Ricker curve occurs at a higher density of anchoveta than for the northern anchovy off California. Also, because food density may vary on a local scale, it may be appropriate to modify the geographic model presented earlier so that coefficients of density dependence (b_i) also vary among water parcels.

El Niño conditions may pose a compounded problem for the anchoveta. Not only may the density of spawners be high due to crowding into areas of upwelling (i.e. N/V is high), but if food abundance is low, the fish will spend more than a usual proportion of their time feeding (p is high). This combination may result in greatly reduced recruitment due to intense cannibalism. It may be appropriate to harvest these El Niño-induced inshore concentrations of anchoveta in order to increase recruitment. However, if density independent mortality of larvae is high, it may be more appropriate to maximize adult survival to the following year.

Adult *E. mordax* will feed either by biting or filtering depending on the size of food particles and their relative abundance (O'Connell, 1972). Thus eggs will tend to be cannibalized in the presence of phytoplankton, which is filtered, and larvae will tend to be cannibalized when in the presence of adult zooplankton, which is bitten. Rojas and Ochoa (1973) suggest that digestive rates may be higher for phytoplankton than for zooplankton, in which case the fraction of time spent feeding (p) would be higher in the presence of phytoplankton.

For the purposes of the following discussion, random feeding implies that feeding activity is independent of the abundance of eggs or larvae in the water. Hunter and Kimbrell may have prematurely dismissed the utility of simple random filtering models. They argue that the assumption of random filtering necessitated an unrealistically large proportion of time be spent to give the rate of egg cannibalism that they observed. However, if the mean residence time of eggs in the anchovy gut is 2.4 hours rather than 1.4 hours (see above), estimated daily consumption, and accordingly estimated fraction of time spent filtering (17h) would decrease by 40% (10h). Hunter and Kimbrell's second argument was based on their estimate that 17% of daily egg production was consumed by cannibalism. If we substitute the values of F_c derived earlier in this paper (0.108 to 0.153), which are more appropriate to the calculation, the length of time spent filtering will drop by 10% to 36% from the 25 hours they estimated. These lengths of time spent filtering (10 to 22 h/day) are consistent with O'Connell's (1972) calculations of the length of time necessary to obtain a daily food ration by filtering in areas of food abundance off southern California.

Non-random feeding behaviour is more strongly indicated by Hunter and Kimbrell's comparison of mean number of eggs per stomach and egg density in the same area as determined by towed plankton nets. Consumption of eggs increases as the 1.6 power of egg abundance, although the true functional shape of the relationship is unclear. It seems reasonable to hypothesize that at low egg concentrations consumption by filter feeding is incidental, whereas at higher concentrations eggs may contribute to the stimuli which elicit filter feeding.

Non-random feeding is more likely as food patchiness increases. Lloyd's (1967) "mean crowding" is a measure of the density of individuals within a patch and is therefore closely related to the stimuli eliciting feeding by adult anchovies (Leong and O'Connell, 1969; O'Connell, 1972). Mean crowding decreases as overall population density decreases, while patchiness (Lloyd, 1967) is a measure of mean crowding relative to mean density. Hewitt (in press) has examined these aspects of the spatial pattern of *E. mordax* larvae, and has shown that Lloyd's patchiness decreases from 10 to 8 during the first three days following hatching. From spawning to a corresponding total age of six days, numerical abundance decreases by about 75% ($M_e = 0.4$, $M_i = 0.1$, $t_e = 2.5$). Assuming that the patchiness of eggs is the same as newly hatched larvae, the combined result is an approximately 80% decrease in mean crowding over the first six days of life. Thus, any potential tendency for concentrations of eggs or larvae to elicit a feeding response by adults should diminish rapidly with time. Correspondingly, random feeding models of cannibalism may provide sufficiently good approximations that non-randomness can be ignored or can be parameterized by an increase in the proportion of time spent feeding (p).

SUMMARY AND CONCLUSIONS

Major points discussed in this paper were:

- 1) The Ricker curve often has been used to describe clupeoid stock-recruitment relationships, but quantitative justification has been lacking.
- 2) Cannibalism is an important regulatory mechanism if $F_c t \geq 1$, where F_c is the coefficient of cannibalistic mortality and t is the length of time eggs and larvae are subject to cannibalism.
- 3) Quantitative information on stomach contents and spawning rates of *E. mordax* indicate that $F_c t$ is in the range of 0.27 to 0.38 for anchovy eggs. Further cannibalism on larvae may be of reduced intensity, but the total effect indicates that cannibalism is sufficiently intense to be a regulatory mechanism.
- 4) Cannibalism on eggs is represented by a random filtering model. The rate of cannibalism is proportional to adult abundance and is inversely proportional to habitat volume: stock density rather than stock size is the important consideration.
- 5) Acoustic surveys of Peruvian anchoveta have shown densities sufficiently high that cannibalism is likely to have had a significant effect on net egg production.
- 6) Rates of cannibalism on larvae are not known. A complete stock-recruitment model cannot yet be calibrated with respect to cannibalism.
- 7) Evaluation of terms in a complete stock-recruitment model for *E. mordax* indicates that total coefficients of density independent and density dependent mortality are approximately 10 and 1 respectively. The preponderance of density independent influences tends to mask the relatively weak regulation of stock abundance. Clupeoid stock-recruitment and production curves must be interpreted in a probabilistic rather than a deterministic sense.
- 8) If the intensity of density independent mortality is a random variable, and is independent for several different life stages, recruitment may tend to be distributed log-normally about its expected value.
- 9) Biomass density giving maximum net egg production is proportional to the square root of average adult fish weight.
- 10) The rate of cannibalism on larvae, for a given level of biomass, is nearly independent of average adult fish size.
- 11) Because clupeoids expand and contract their ranges with changes in abundance, adult fish density is not proportional to stock size. The standard Ricker model is not appropriate; a generalized Ricker model such as $R = aN \text{EXP}(-bNC)$ is more realistic, where $0 < c < 1$. The standard Ricker model ($c=1$) will overestimate the maximum sustainable yield from clupeoid stocks.
- 12) Contraction and expansion of range with changes in total abundance is predicted by a geographic model wherein spawners cannibalize their young, density independent survival of young decreases toward the periphery of the range, and spawners distribute themselves so as to maximize individual reproduction. As adult density in the most favourable area increases, cannibalism causes the total larval mortality rate to increase until peripheral, poorer areas become equally attractive spawning locations.

- 13) The optimal distribution of spawners results is a constant total mortality rate of off-spring throughout the inhabited range. This mortality rate is equal to the density independent mortality rate at the edge of the range.
- 14) This geographic model suggests that harvests taken from the center of the range will have a smaller impact on abundance than harvests taken from the periphery of the range.
- 15) If Peruvian anchoveta consume sufficient production to decrease the rate of detrital fallout, it may cause a deepening of the level of limiting oxygen concentration. A larger anchoveta stock may thereby increase its own habitat volume, and in turn increase its own reproductive potential.
- 16) Rates of cannibalism are likely to depend on the size and abundance of adult food organisms. The *per capita* rate of cannibalism may be lower for *E. ringens* than for *E. mordax* because the high density of food off Peru may result in less time being spent feeding.

Cannibalism is one of the important mechanisms tending to regulate the highly variable abundance of clupeoids such as *Engraulis*. An initial framework was constructed which allows integration of life history information, physiology, behaviour, and quantitative ecology into a theory of clupeoid population dynamics. Further work can proceed in many directions; perhaps the most important is to incorporate environmental variability in order to fully describe the volatility of clupeoid populations. Finally, a number of speculations and hypotheses have been presented. Some of these may be tested in the field or laboratory.

ACKNOWLEDGMENTS

I wish to thank John Hunter (Southwest Fisheries Center, La Jolla, California) for his extensive comments on the manuscript. I also wish to thank the many people with whom I have discussed various topics, especially Reuben Lasker, John Radovich and Gary Stauffer. Finally, I wish to thank Pesca Peru and IMARPE for their warm hospitality and for the opportunity to develop my thoughts on the topic of this paper.

REFERENCES

- BAKUN, A. and R.H. PARRISH. Environmental inputs to fishery population models for eastern boundary current regions. (This volume)
- CHAPMAN, D.G. 1973. Spawner-recruit models and estimation of the level of maximum sustainable catch. Rapp.P.-V.Réun.Cons.Int.Explor.Mer, 164:325-332
- CLARK, F.N. and J.C. MARR. 1955. Population dynamics of the Pacific sardine. Calif.Coop. Ocean.Fish.Invest., Prog.Rep., 1 July 1953 to 31 March 1955:11-48
- CSIRKE, J. 1980. Recruitment in the Peruvian anchovy and its dependence on the adult population. Rapp.P.-V.Réun.Cons.Int.Explor.Mer, 177
- CUSHING, D.H. 1971. The dependence of recruitment on parent stock in different groups of fishes. J.Cons.Int.Explor.Mer, 33:340-362
- CUSHING, D.H. and J.G.K. HARRIS. 1973. Stock and recruitment and the problem of density dependence. Rapp.P.-V.Réun., Cons.Int.Explor.Mer, 164:142-155
- GULLAND, J.A. 1973. Can a study of stock and recruitment aid management decisions? Rapp. P.-V.Réun.Cons.Int.Explor.Mer, 164:368-372
- _____. 1977. The stability of fish stocks. J.Cons.Int.Explor.Mer, 37:199-204
- HARRIS, J.G.K. 1975. The effect of density dependent mortality on the shape of the stock and recruitment curve. J.Cons.Int.Explor.Mer, 36:144-149
- HEWITT, R. In press. The value of pattern in the distribution of young fish. Second Early Life History of Fish Symposium.
- HUNTER, J.R. 1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull.(U.S.), 74:81-88
- HUNTER, J.R. and S.R. GOLDBERG. 1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish.Bull.(U.S.), 77:64 -652
- HUNTER, J.R. and C.A. KIMBRELL. In press. Egg cannibalism in the northern anchovy, *Engraulis mordax*. Fish.Bull.(U.S.), 78(3)
- HUNTER, J.R. and B.J. MACEWICZ. 1980. Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning northern anchovy, *Engraulis mordax* during the 1979 spawning season. Calif.Coop.Ocean.Fish.Invest.Rep., 21:139-149
- INSTITUTO DEL MAR DEL PERU. 1973. Third session of the panel of experts on the population dynamics of Peruvian anchovy. Bol.Inst.Mar Peru-Callao, 2(9):525-599
- JOHANNESSON, K. and R. VILCHEZ. A preliminary note on hydroacoustic observations of changes in distribution and abundance of some common pelagic fish species in the coastal waters of Peru, with special emphasis on anchoveta. (This volume)
- JONES, R. and W.B. HALL. 1974. Some observations on the population dynamics of the larval stage in the common gadoids. pp 87-102 In J.H.S. Blaxter (ed) The Early Life History of Fish. Springer-Verlag, New York. 765 p.
- LASKER, R. 1978. The relation between oceanographic conditions and larval anchovy food in the California current: identification of factors contributing to recruitment failure. Rapp.P.-V.Réun., Cons.Int.Explor.Mer, 173:212-230

- LEONG, R.J.H. and C.P. O'CONNELL. 1969. A laboratory study of particulate and filter feeding of the northern anchovy (*Engraulis mordax*). J.Fish.Res.Bd, Canada, 26:557-582
- LLOYD, M. 1967. Mean crowding. J.Anim.Ecol., 36:1-30
- MacCALL, A.D. 1976. Density dependence of catchability coefficient in the California Pacific sardine (*Sardinops caerulea*) purse seine fishery. Calif.Coop.Oceanic Fish.Invest.Rep., 18:136-148
- _____. 1980. Population models for the northern anchovy (*Engraulis mordax*). Rapp. P.-V.Réun., Cons.Int.Explor.Mer, 177
- MAIS, K. 1974. Pelagic fish surveys in the California current. Calif.Dept.Fish and Game, Fish Bull., 162:1-79
- MURPHY, G.I. 1966. Population biology of the Pacific sardine (*Sardinops caerulea*). Proc. Cal.Acad.Sci.4th Ser., 34(1):1-84
- _____. 1967. Vital statistics of the Pacific sardine (*S. caerulea*) and the population consequences. Ecology, 48:731-735
- _____. 1977. Clupeoids. pp 283-308 In J.A. Gulland (ed), Fish Population Dynamics. John Wiley and Sons, New York. 372 p.
- O'CONNELL, C.P. 1972. The interrelation of biting and filtering in the feeding activity of the northern anchovy (*Engraulis mordax*). J.Fish.Res.Bd.Can., 29:285-293
- RICHMAN, J.G. and S.L. SMITH. On the possible enhancement of oxygen depletion on the coastal waters of Peru between 6°S and 11°S. In ICANE Experimental Results. Bol.Inst. Mar Peru-Callao. (In press)
- RICKER, W.E. 1954. Stock and recruitment. J.Fish.Res.Bd.Can., 11:559-623
- _____. 1973. Critical statistics from two reproduction curves. Rapp.P.-V.Réun.Cons. Int.Explor.Mer, 164:368-372
- _____. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada, Bulletin (191), 382 p.
- ROJAS DE MENDIOLA, B. and N. OCHOA. 1973. Observations on the food and feeding habits of the anchovy *Engraulis ringens* Jenyns made during cruise 6908-09. pp 457-461 In R. Fraser (comp.) Oceanography of the south Pacific. New Zealand Nat.Comm. For UNESCO, Wellington, New Zealand
- SANTANDER, H. Fluctuaciones del desove de anchoveta y algunos factores relacionados. (This volume)
- SCHAAF, W.E. and G.R. HUNTSMAN. 1972. Effects of fishing on the Atlantic menhaden stock: 1955-1969. Trans.Amer.Fish.Soc., 101:290-297
- SHARP, G.D. Colonization: modes of opportunism in the ocean. (This volume)
- SMITH, P.E. 1972. The increase in spawning biomass of northern anchovy, *Engraulis mordax*. Fish.Bull. (U.S.), 70:849-874
- SMITH, P.E. and R. LASKER. 1978. The position of larval fish in an ecosystem. Rapp.P.-V. Réun.Cons.Int.Explor.Mer, 173:77-84

- STAUFFER, G.D. and S.J. PICQUELLE. 1980. Estimates of the 1980 spawning biomass of the central subpopulation of northern anchovy. Southwest Fisheries Center, Admin. Rept. LJ-80-09
- TSUKAYAMA, I.K. and M.A. ALVAREZ. Fluctuaciones en el stock de anchoveta desovantes durante 1964-1978. (This volume)
- ULLTANG, O. 1976. Catch per unit effort in the Norwegian purse seine fishery for Atlanto-Scandian (Norwegian spring spawning) herring. FAO Fish.Tech.Pap., 155:91-101

SUMMARY OF THE STUDIES ABOUT FOOD AND FEEDING HABITS OF
THE ANCHOVY (*Engraulis ringens* J.)

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INTRODUCTION

The Peruvian anchovy (*Engraulis ringens* J.) is one of the most important species of fish for the Peruvian coastal fisheries, the catch amounting 12 million t in 1970. This high production may be due, as suggested by Schaeffer (1965), to the fact that the anchovy's principal food is phytoplankton.

However, the catch has declined since then and reached a minimum of 4 million t in 1972 as a consequence of hydroclimatic changes caused by "El Niño", the phenomenon which modified the natural environment, principally north of 14° S.L., where the anchovy fishery is more important.

Because of its economic importance the anchovy is the object of much work carried out by the Instituto del Mar del Perú. The principal problems centred around the proper exploitation of the anchovy stock is full knowledge of the different phases in the life history of this species as a prerequisite for prediction of availability and understanding of migratory patterns and behaviour.

Stock-recruitment relationship is one of the most important points that gives an adequate basis for good administration of the fisheries stock. Food supply, and its critical effect on school concentration, growth, migration and behaviour, is a major factor in regulating the fisheries. Anchovy survival is dependent on both the quality and quantity of available food.

SUMMARY

The anchovy (*Engraulis ringens* J.) is a pelagic fish with very fine and thin gill-rakers. Based on the number and sizes of these and the presence of small particles of food in the stomach content, we consider the anchovy a plankton filter feeder.

Few studies have been done on the food and feeding habits of anchovy (*Engraulis ringens* J.). Using material obtained on the Peruvian coast, Vogt (1940), Sears (1941) and Rojas de Mendiola (1953), found a preference for phytoplankton in anchovy feeding; using material from the Chilean coast Schneider (1943) and Mann (1954) reached different conclusions.

Coincident with these findings, Rojas de Mendiola (1971), on the basis of characteristics considered (stomach content, standard-intestine length relation, and gill raker counts) suggested possible existence of two groups of the same species of anchovy with different alimentary habits: one group from southern Peru and northern Chile as a second distinct group from northern Peru.

Previous studies and those carried out at the Instituto del Mar del Perú indicate that changes take place in feeding habits of the anchovy in accordance with age. Such changes are necessary for the proper development in growth and physiological functions.

Several papers on food and feeding habits of adult and juvenile anchovies have been published but information on larval stages is lacking; in all the literature only one published account by Rojas de Mendiola (1974) exists.

The adult anchovy, i.e., after it is one year old and has attained a length of more than 100 mm standard length, is phytophagous and has a preference for the diatoms. Any dominance of dinoflagellates and zooplankton in their stomach contents must be related to anomalous environmental conditions, and mixing of species with phytoplankton.

In normal conditions our anchovy feeds primarily on phytoplankton, but as I have mentioned before, we have two different groups. The northern group feeds primarily on phytoplankton while the southern group feeds principally on zooplankton. During 1973 it was still possible to observe in southern Peru the presence of adult anchovies larger than 100 mm with a predominance of phytoplankton in the stomach content.

In the Report of the Fourth Session of the Panel of Experts on Stock Assessment of Peruvian Anchovy (1974) it was suggested that part of the total fish population at southern Peru might as well be original from the northern area, driven south by the "El Niño" effects. Yet within a short time, because of the warm water and low primary production, all of the anchovies that remained along our coast were feeding on zooplankton as well as predating their own eggs and small larvae. So definite a difference in distinct feeding habits of the two groups observed in the past is no longer found because of continued environmental conditions.

In the northern part of Peru, the most important components of the food of the anchovy are the following diatoms: *Skeletonema costatum*, *Schroederella delicatula*, small species of *Chaetoceros* which change through the year, *Nitzschia pungens*, *Lithodesmium undulatum*, *Rhizosolenia delicatula*, *Thalassiosira subtilis*, *Thalassionema nitzschioides*, and after 1972 *Thalassiosira partheneia*. The contributions of dinoflagellates are not very important.

The finding of phytoplankton in the stomach content of the adult anchovy can be correlated with the length of the intestine: Harder (1958) mentions a ratio of 1.71:1 between intestine and standard lengths for *Engraulis ringens* J. and 0.85 for *Anchoa starksii* G. and P., the latter feeding on zooplankton. Barrington (1957) dealt with other species and states that those with large intestines (ratio greater than 1) are vegetarians while those with small intestines are carnivorous. We found for the anchovies in the Chimbote area of northern Peru a ratio of between 1.65 and 1.89:1 for intestine and standard lengths.

This finding of phytoplankton can also be correlated with the average number of gill-rakers in the first arch: Tsukayama (1965) found a north to south gradient of 87 for Chimbote to 83 for Mollendo. This smaller number of gill rakers in the south suggests feeding on larger organisms, presumably zooplankton.

In the southern part of Peru the adult anchovy feeds principally on zooplankton. The most frequent species are *Nyctiphanes simplex*; *Euphausia simplex*; *Euphausia mucronata*; *Calanus chilensis*; *Centropages brachiatus*, and different species of *Oncaea*.

With respect to the feeding regime our data are too scanty to show how often or at what time the anchovy feeds. However considering the condition of the food in the stomachs in relation to the time of catch, the data suggest that anchovies feed once at night around midnight, once in the morning around 09.00 hours, and again between 18.00 and 20.00 hours. These observations suggest that the anchovies feed three times in 24 hours.

Little is known of the relative food value or rates of digestion of plant and animals in the anchovy. But if phytoplankton is digested more rapidly than is zooplankton, as it is in sardine (Andreu and Roda, 1951), then anchovies might be expected to feed more frequently. This means that the anchovy should be found in those areas where the available food is richer in phytoplankton.

This assumption corroborates some of our earlier findings. Of one sample of 37 specimens, caught at midnight at 20 m. depth near Salaverry (8° 44' S. 79° 18' W.) on 17-9-69, 12 had the gastric stomach replete and 24 had it full; none was empty or less than half full. The anchovies had very high weights of stomach content, no doubt due to recent feeding. Phytoplankton in the initial stage of degradation and *Lithodesmium* and *Chaetoceros* chains were observed and whole small copepods were also present. In 54% of the fish the pyloric stomach was half full with half digested phytoplankton. No copepods were seen, even as remains. Apparently, the degradation of copepods had not started in the gastric stomach; whereas the phytoplankton was already undergoing decomposition. This suggests that the phytoplankton is degraded faster than the zooplankton.

Before 1972, the normal weight of stomach content ranged between 0.03-1.19 g. The differences in weight are due mainly to the amount of food ingested and its state of degradation.

After 1972, a large drop in stomach content weight and a definite lowering of fat content of the larger fish was observed. These might well be due to poor feeding conditions associated with "El Niño" 1972 and low production (phytoplankton).

These anchovies caught along our coast showed a predominance of zooplankton in the stomach content and a very low weight, ranging from 0.03-0.10 g. Exceptionally higher weight was observed, for example, in San Juan area during the late winter 1974. In one anchovy, 160 mm length and 38 g the total weight of stomach content was 1.10 g consisting of 59 *Euphausia mucronata*.

If the heaviest weight of stomach content that is found is assumed to correspond to the weight of newly ingested food, then we can correlate these data with the total weight of the corresponding anchovy and determine a ratio between body and food weights. Together we obtained an average relation of 20:1, suggesting the anchovy digests approximately one twentieth of its total weight. Whether these relations refer to accumulated food weight or the weight of one ingestion is a matter of ongoing studies.

Although this suggestion is limited to a small number of observations, we can surmise the amount of phytoplankton necessary to maintain the great population of anchovies, over and above the other competitors that feed on phytoplankton. The greatest weights of stomach content are found during late winter (August and September), corresponding with high primary productivity.

The anchovy has the capacity to consume its own eggs and larvae. The maximum number of eggs found in the stomach content of a single anchovy caught off Huacho during September 1954 was up to 304. Off Salaverry during 1969 the number was 95 and off Supe during September 1974 it was 116. These changes in number could be related with the availability of food supply.

We consider anchovies to be juveniles when they are up to 50 mm total length. Studies being carried out show that these eat almost entirely zooplankton and that phytoplankton is not as significant. However, the quantity of phytoplankton becomes important when the anchovies are over 80 mm in length.

The items most important are the copepods: *Calanus australis*; *Centropages brachiatus*; *Paracalanus parvus* and different species of Oncaea. Occasionally Euphausiids, especially juvenile stages, appendicularians and eggs of invertebrates are also eaten.

Changes in feeding in accordance to age have been published for other related species of Engraulids. Fuster de Plaza and Boschi (1958); and Fuster de Plaza and Angelescu (1962) mention that the diet of juveniles (50-100 mm) of *Engraulis anchoita* is mainly diatoms, while adults feed primarily on zooplankton.

Kubo (1961) found that the juveniles of *Engraulis japonicus* feed principally on zooplankton and Jamasita (1957) mentions that this same species as an adult feeds mainly on phytoplankton. The feeding habits of this species would be the same as we have found for *Engraulis ringens* J.

The success of any fishery depends on the survival of the new stock. The availability of suitable food is therefore, one of the important factors influencing the survival of larval fish. A knowledge of their food habits is important if we are to understand their role in the economy of the sea.

In order to understand the lack of correlation between the magnitude of the spawned anchovy eggs and the magnitude of new recruits we must suppose that the greatest mortality is present during the larval phase. Survival depends on the quantity and quality of available food for the larval stage.

Hjort (1926, 1914) suggests that survival through these stages might be affected in two ways: (1) by a lack of food at the time the larvae begin to feed, and (2) by currents that could transport larvae to areas unfavourable to their further development, resulting in high mortality.

Several studies have been made relating feeding incidence with food availability. Berner (1959) found *Engraulis mordax* larvae with food in their guts only in areas where food was concentrated. Nakai et al. (1966) reported significant correlation between the density of copepod nauplii and the feeding incidence of Japanese anchovy larvae (*Engraulis japonicus*). Shelbourne (1957) assessed the physical condition of plaice (*Pleuronectes platessa*) larvae from good and bad plankton patches and concluded that a truly critical stage depending on food conditions may occur at the end of the yolk sac stage. During this period the appropriate quantity of food available to the larvae is the most important factor for survival.

Behavioural studies emphasize the importance (at least for clupeoid larvae) of finding food as soon as possible after the yolk is absorbed. As Hunter (1972) has suggested, small-scale patchiness of food and the ability of larvae to locate and remain in a patch may be crucial to early larval survival.

With respect to the effect of delayed initial feeding, Lasker et al., 1970 found that anchovy (*Engraulis mordax*) larvae could be delayed up to 1.5 days after yolk absorption without increasing mortality, but a delay of 2.5 days resulted in catastrophic mortality and a survival curve almost identical to that of larvae which received no food at all.

Engraulids like *Engraulis ringens* hatch in a poorly developed state after a short incubation period of 50 h and their length at hatching ranges from 1.72-2.25 mm. The size at which the yolk sac disappears is between 2.50 and 4.00 mm (Einarsson and Rojas de Mendiola, 1963).

Following Pavloskaia (1961) for *Engraulis encrasicolus* and Cienchowski (1967) for *Engraulis anchoita*, I have defined the larval stage as extending from the end of yolk sac reabsorption until the appearance of the stomach diverticula and pyloric caecae, generally at length of 30 mm, occasionally at 23-25 mm. The size 30-50 mm has been considered post-larvae.

After the yolk is reabsorbed, the anchovy larvae feed to a small degree small centric diatoms like *Actinocyclus tenuissimus*; *Coscinodiscus decrescens*; *Thalassiosira* sp.; small dinoflagellates like *Diplopsalis lenticula* and *Peridinium minttum*; and ciliates like *Codonelopsis pusilla*. The principal bulk, however, corresponds to small copepod eggs and copepod nauplii as well as other invertebrate eggs. When the larvae are over 10 mm only zooplankton is observed in the gut content, the staple food throughout the year being copepods in different stages of development.

Although phytoplankton is not observed significantly in the food of larvae, they are present in the gut contents of larvae smaller than 9 mm. From this finding, assuming that phytoplankton is digested more quickly than zooplankton (Andreu and Roda, 1951) we can expect that the larvae ingest more phytoplankton than is observed. This corroborates the findings of Lasker (1974), who mentions that the best food for the anchovy (*Engraulis mordax*) larvae is *Gymnodinium splendens*, and also the work of Menzel (1960) who mentions that the amount of nitrogen is high in the phytoplankton and identifies it as a good source of food. At the same time, however, Menzel indicates that it is improbable that an exclusive phytoplankton consumer can survive without feeding on animal material to assure proper growth.

If it is true that the phytoplankton is most important as a food to ensure survival right after the yolk sac is reabsorbed, then the ingestion of zooplankton would become more useful with time. Wyatt (1974) mentions that the smallest sand eel (*Ammodytes marinus*) larvae feed to a considerable extent on phytoplankton, and those larger than 12 mm begin to introduce copepods and other items into their diet.

Of particular interest is the range of size of food organisms when feeding commences. Larval anchovy appear to select food of a certain size range varying with the size of the larvae. Small diatoms of less than 50 microns in diameter, copepod eggs and copepod nauplii are principal food of larvae less than 5 mm. These items become less important as larval sizes increase. Older copepodites and adult *Paraoalanus parvus* at least twice the size of the aforementioned food were the major prey of the larger larvae (20-30 mm).

Rojas de Mendiola (1974) mentions that 92% of the anchovy larvae containing food were collected during daylight hours. This strongly supports the hypothesis that feeding in anchovy larvae, as in the larvae of many other fish species, is a response to visual stimuli (Blaxter, 1963).

The incidence of feeding in larval anchovy changes with the length of the larvae, the greatest being found in larvae of 3.1 to 5.0 mm. The feeding incidence is much lower in larvae from 5 to 12 mm, but above 21 mm the percentage feeding appears to increase again. Berner (1959), working with *Engraulis mordax* larvae, found the same decrease in incidence of feeding above a size of 5 mm. Cienchowski (1967) however found the greatest incidence of feeding in larvae of *Engraulis anchoita* between 3.0-4.0 mm body length with a lesser incidence between 5.1-9.0 mm and an increase again at greater length.

A low incidence of feeding has been a feature of many investigations of larval food and two possible explanations for this have been put forth. Arthur (1966) suggested that the apparent low level of feeding could be due to the sampling gear catching only larvae in poor condition. The alternative explanation that feeding is intensive over short intervals of time, and digestion rate is very fast (Krogh, 1931; Lebour, 1919) seems more feasible in this instance.

Seasonal and area variations in the plankton play an important role in the diet of fish larvae. We have observed seasonal variations in the gut content: the most abundant food items are eggs and nauplii of copepods during the winter; copepodites during the spring and *Paraoalanus parvus* (adults) in the summer; all the larvae examined had an empty gut.

During the last two years (1977, 1978) three experiments have been carried out using larvae reared at the laboratory. The first experiment on first feeding larvae was done on board the BAFFIN (Canadian Research Vessel). For this experiment we used food like wild plankton and culture of *Gyrodinium aureolum* and the results showed that the anchovy larvae start feeding 40 h after the disappearance of the yolk sac when the eyes are completely pigmented and the mouth is open. The minimum concentration for feeding in this experiment was about 80 particles per millilitre and the size of the particle was 14-20 microns. Larvae did not feed on phytoplankton species forming chains but they did on dinoflagellates.

Experiments at Samanco Bay (Ware, Mendiola and Newhouse, 1979) showed that the *Engraulis ringens* larvae did not feed on species forming chains and it appeared that the preferred width of a food particle for 3.5 mm larvae is about 1% of the body length, increasing to about 2% by 5.5 mm. At this rate, it follows that the natural transition from small phytoplankton particles to copepod nauplii ought to occur at a length of about 4.3 mm; this result would be close to the findings with wild larvae to form a larger proportion of their diet between 5 and 6 days after complete yolk reabsorption. Following the previous criteria related with growth rate of anchovy larvae the zooplankton can be expected to be an approximated length of 4.5 mm of the larvae.

Experiments on first feeding were done at Callao Bay; the purpose was to determine the minimum particle number, size and quality of food that the larvae need to start first feeding.

For this experiment 100 *Engraulis ringens* larvae were reared from the eggs, using small containers with 10 l of filtered sea water and aeration. The temperature was maintained at 16°C. The experiment started just after complete yolk sac absorption adding wild plankton at concentration of 200 particles per millilitre. A sufficient number of particles were added every morning in order to maintain the same concentration.

The particle size ranged between 40 and 80 microns: the particle size is the diameter of the single cell (*Actinocyclus*, *Coccolithodiscus*, dinoflagellates) or the length of the chain (*Chaetoceros*, *Thalassionema*). Each chain was considered as one particle for the particle counts.

The daily observations of the gut of the larvae for evidence of feeding showed the gut to be empty and no sign of food intake previous to the observations. The qualitative and quantitative analysis of the wild plankton offered like food showed that from the total number of particles (200 particles per millilitre) we offered in average daily: 4 particles per millilitre of *Actinocyclus*; 5 particles per millilitre of dinoflagellates, copepod nauplii 0.7 particles per millilitre and eggs of invertebrates 2 particles per millilitre.

~ 85% of the total particle number corresponded to species that form spirals like *Chaetoceros debilis*; long chains like *Leptocylindrus danicus* or stars like *Thalassionema nitzschioides*. It means that the principal species that we consider as a good source of food for first feeding *Engraulis ringens* larvae like dinoflagellates, single diatoms or small copepod nauplii were not in the minimum concentrations although the total particle number was 200 particle per millilitre with 40-80 particle size.

With this result we can assume that an important requirement for first feeding larvae is not only the quantity or the size but also the quality; and that the anchovy larvae do not feed on species that form chains. These findings are similar to those that we found during our experiments on board the BAFFIN and the results of Lasker (1975) for *E. mordax*.

Observations of gut content of the larvae during the experiments at Samanco Bay showed that small larvae fed on small rounded diatoms like *Actinocyclus* and as the larvae increase in size small zooplankton mixed with the phytoplankton start to be present. Only once did we observe a larva 3.1 mm with the gut full of *Gymnodinium splendens* when the concentration of the wild plankton was 870 particles per millilitre and *Actinocyclus* was in concentration of 180 particles per millilitre, *Gymnodinium splendens* 36 particles per millilitre and 12 copepod nauplii per millilitre.

If we accept that the anchovy larvae feed on *G. splendens* when they are in high enough concentration as *E. mordax* (Lasker, 1975) and the larvae can survive with this kind of food until they are 6 mm length (Hunter, in press) when the larvae can eat larger particles such as nauplii of copepods or *Paracalanus parvus*, we can assume that the presence of *G. splendens* during the last months of 1975 and the beginning of 1976, upon acquiring bloom proportions, could be one of the reasons for the survival of the *Engraulis ringens* larvae resulting in an abundant year class that increased the level of the anchovy population as was observed the first months of 1976.

On the other hand, as the larvae are visual predators it is possible that they require motile prey, like dinoflagellates, in order to initiate first feeding behaviour. The role of phytoplankton like *Actinocyclus* or other small rounded cells during the earliest stage of the life history can perhaps be seen as an adaptation by the larvae to meet maintenance metabolic requirements while they learn to feed on zooplankton (Ware et al., 1979).

Simultaneously observations on survival and time of rest were carried out.

For survival experiments we followed the same procedure described by Lasker, Teilacker, Feder and May (1970) with only differences in the time of adding food to the container: we add food in the first container at the 3rd day of hatching it means when the yolk sac has been complete reabsorbed, the second container the next day and we continued until the 6th day. We used as a control a container of larvae which is not fed during the experiment.

The food added was wild plankton at 200 particles per millilitre; most of the plankton were diatoms that form chains like *Chaetoceros debilis* or form stars like *Thalassionema nitzschioides*. Very few particles were observed which we would consider to be good food sources for anchoveta larvae. Previous studies include a preference for small rounded diatoms or

dinoflagellates. The analysis at the microscope of the gut of the larvae in all containers always showed an empty gut with no signs of debris or particles at any time; this means that the larvae in all containers were in starvation.

The survival in the experiment showed a similar curve for all the containers including the control. The mortality was about 50% at the fifth day and 80% at the eighth day after hatching.

In our previous experiment we demonstrated that the *Engraulis ringens* larvae first feeding is 4.5 days after hatching or 1.5 days after yolk reabsorption; if we consider this time 4.5 days as the time that the larvae need to get food and if more than 80% died at the 8th day, we suppose that the larvae can survive 3.5 days with no food.

Although our results need more experiments to confirm this first finding we can suppose that the *Engraulis ringens* larvae has an advantage over the *Engraulis mordax* larvae because these larvae will die after 1.5 days (Lasker et al., 1970) if they do not have appropriate food while the *Engraulis ringens* larvae have 3.5 days to survive without food. Food should, of course, be got between 2 or 3 days to maximize the survival.

Some observations about activity pattern of *E. ringens* larvae reared at the laboratory are very similar to those described by Hunter (1972) for *E. mordax* larvae. During our experiments at Callao we found that the activity was maximum at the 6th day after hatching but then diminished as the larvae weakened and became moribund, compared with the Hunter (1972) results. We have one day of difference that could mean that this activity is developed more slowly in *E. ringens* than in *E. mordax*, although this result may not be directly comparable if activity depends on larval size or food concentration. Similar findings about the maximum activity of *E. ringens* was observed from Samanco experiments by Ware, Mendiola and Newhouse (1978) who suggested that this regressive change in the swimming pattern denoted the point of no return (Blaxter and Hempel, 1963). If it is true, death is an inevitable consequence if feeding does not start within 48 to 72 h after the beginning of the postlarval stage, at temperatures between 15°-19°C.

All the observations about first feeding of the larvae of *E. ringens* show that their survival depends primarily on the availability of the food in terms of size, quality and quantity of the particle and a correspondance between the kind of food available in time and space with the length of the fish larvae.

I have attempted to summarize our present knowledge about the food and feeding habits of the anchovy *Engraulis ringens* J. throughout their life history.

We recognize that it is necessary to continue these studies because we are totally lacking in information about several important points related to adult anchovies, including behaviour during the feeding; alimentary rhythm, and nutritive value of phytoplankton and zooplankton. Almost all important aspects related to the feeding of fish larvae are unknown; aspects as important as daily food requirements compared with the quantities of food available; rate of growth of larvae related to the quality and quantity of food; size range of the food organisms consumed, assuming the anchovy *Engraulis ringens* J. larvae to be size-selective feeders; metabolism; quantitative estimates of the magnitude of larval mortality due to starvation and predation and abiotic factors.

Biological characteristics of *Engraulis ringens* J. larvae

General: (1) Einarsson and Mendiola, 1963; (2) Santander and O. de Castillo, 1973; (3) Rojas de Mendiola, 1974

	<u>BAFFIN (Nov. 1977)</u> (Mendiola, Gómez)	<u>Samanco Bay</u> (Ware, Mendiola and Newhouse)	<u>Callao Bay</u> (Mendiola, Gómez)	<u>General</u>
Egg size				
Length (mm)	-	1.26 (1.09-1.47)	1.28 (1.15-1.36)	1.42 (1.19-1.60) ⁽¹⁾
Width (mm)	-	0.71 (0.57-0.74)	0.06 (0.57-0.64)	0.71 (0.57-0.86) ⁽¹⁾
L/W	-	2.07	-	2.00
Incubation period	-	-	-	48-52 hours ⁽²⁾ (14-16° C)
Time of hatching	-	6 hours (18°C)	-	-
Length at hatching	-	2.60 (2.49-3.02)	1.72-2.25	2.45 (2.19-2.72) ^(1a)
Length at hatching/egg length	-	2.06	-	1.73 ⁽¹⁾
Duration of yolk sac stage	3.0 days	2.75 days	3.0	-
Length at the end of yolk sac reabsorption	3.0 mm	4.09 (3.9-4.2)	3.6	3.72 (2.97-4.46) ^(1a)
Age at first feeding	4.5 days	4.4 (3.5-6.8)	-	-
Length at first feeding	3.1 mm	4.0 (3.7-4.4)	-	-
Age at maximum activity	-	4.5	6	-
Percentage of mortality (Larvae with no food)				
50%	-	-	4.5 days	-
80%	-	-	8 days	-
Optimum food with: (% Larval length)		1.2-2.3	-	2.05 ⁽³⁾
First food	<i>Gyrodinium</i> <i>fillum</i>	<i>Actinocyclus</i> dinoflagellates nauplius (3.68 mm)	-	<i>Actinocyclus</i> dinoflagellates copepod eggs (>3.00 mm)

REFERENCES

- ANDREU, B. y J. RODRIGUEZ-RODA. 1951. Estudio comparativo del ciclo sexual, engrasamiento y repleción estomacal de la sardina, alacha y anchoa del mar de Catalán, acompañado de relación de pescas de huevos planctónicos de estas especies. P. Ints.Biol.Aplic. 9:193-232
- ARTHUR, DAVID K. 1956. The particulate food resources of the larval of three pelagic fishes, especially the Pacific sardine, *Sardinops caerulea* (Girard). Unpublished Doctoral Dissertation, on file in the Library of Scripps Institution of Oceanography, University of California, La Jolla, 231 pp.
- BARRINGTON, E.J.W. 1957. In Hoar, W.S. and D.J. Randall (eds.). The Physiology of fishes. III Alimentary canal and digestion. New York, Academic Press Inc.
- BERNER, L. Jr. 1959. The food of the larvae of the Northern anchovy *Engraulis mordax* Inter.Amer.Trop.Tuna.Comm.Bull. 4(1):1-22
- BLAXTER J.H.S. 1965. The feeding of herring larvae and their ecology in relation to feeding. Calif.Coop.Ocean.Fish.Invest.Rept. X:79-88
- CIECHOMSKI, JANINA Dz DE. 1967. Investigations of food and feeding habitats of larvae and juveniles of the Argentine anchovy *Engraulis anchoita*. Calif.Coop.Ocean.Fish.Invest.Rept. XL: 72-81
- EINARSSON, H. y ROJAS DE MENDIOLA. 1963. Descripción de huevos y larvas de anchoveta peruana (*Engraulis ringens* J.), Bol.Invest.Recurs.Mar, Perú, Nº(1):1-23
- FUSTER DE PLAZA, M.L. y E.E. BOSCHI. 1958. Estudios biológicos pesqueros de la anchoita (*Engraulis anchoita*) de Mardel Plata. Secr.Agric.Ganad., Depto.Invest. Pesquer.Public. (7):1-19
- FUSTER DE PLAZA, M.L. y V. ANGELESCU. 1962. El papel de la anchoita en la bioeconomía general del mar argentino (sector bonaerense, resultados preliminares) 1a. Reunión Com.Consult.Reg.Pesca Atlant.Sud-Occidental, Río de Janeiro, Tema 6/6: 1-13
- HARDER, WILHELM. 1958. El intestino como carácter diagnóstico para la identificación de ciertos clupeoides (Engraulidae, Clupeidae, Dussumeriidae) y como carácter morfométrico para la comparación de las poblaciones de anchoveta (*Cetengraulis mysticetus*) Inter.Amer.Trop.Tuna Comm.Bull. 11, 8
- HJORT, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Réun.Cons.Perm.Int.Explor.Mer 20:1-228
- _____ 1926. Fluctuations in the year classes of important food fishes, J.Cons. 1:5-38
- HUNTER, J.R. 1972. Swimming and feeding behaviour of larval anchovy *Engraulis mordax* Fish.Bull., U.S. 70:821-838
- KROGH, AUG. 1931. Dissolved substances as food of aquatic organisms. Biol.Rev. 6:412-442
- LASKER, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish.Bull.U.S.73(3): 453-462
- LEBOUR, M.V. 1920. The food of young fish N^o3 Mar.Biol.Assoc.U.K.J. 12:261-324

- MANN, GUILLERMO F. 1954. La vida de los peces en aguas chilenas (Minist.Agric. y Univ. de Chile) pp. 342
- MENZEL, D.W. Utilization of food by a Bermuda reef fish, J.Cons. 25:216-222
- PAVLOVSKAIA, R.M. 1961. La survie des larves de l'anchois de la mer Noire en fonction de leur alimentation. Rapp.Comm.Int.Mer.Médit. 16:345-350
- ROJAS DE MENDIOLA, B. 1953. Estudios preliminares del contenido estomacal de las anchovetas. Bol.Cient. de la Cía. del Guano. 1(1):32-42
- _____, 1971. Some observations of the feeding of the Peruvian anchoveta *Engraulis ringens* J. in two regions of the Peruvian coast. Fertility of the Sea. Vol.2: 417-440
- _____, in press. Food of the larval anchoveta *Engraulis ringens* J. in the early life history of fish. Ed. by J.H.S. Blaxter, Springer-Verlag
- SCHAEFER, M.B. 1965. The potential harvest of the sea. Trans.Am.Fish.Soc., 94:123-8
- SCHNEIDER, OLIVER C. 1953. Catálogo de los peces marinos del litoral de Concepción y Arauco, Museo de Concepción. Chile.
- TSUKAYAMA, ISABEL. 1966. El número de branquispinas como carácter diferencial de sub-poblaciones de anchoveta (*Engraulis ringens* J.) en las costas del Perú. I. Seminario Latino-Americano sobre el Océano Pacífico Oriental Univ.Nac. Mayor de San Marcos
- YAMASHITA, HIDEO. 1957. Relations of the foods of sardine, Jack Mackerel, Mackerel, and so on, in the waters adjacent to west Kyushu. Bull.Sekai Reg.Fish.Res.Lab. II:45-53
- ROJAS DE MENDIOLA, B. y O. GOMEZ Daily rings in otoliths of larval anchovy *Engraulis ringens* J., ICES/ELH Symp. Woods Hole, Mass, April 2-5, 1979, in press
- WARE D.M., ROJAS DE MENDIOLA y D.S. NEWHOUSE, Behaviour of first feeding anchoveta larvae *Engraulis ringens* J. Symp. on Early Life History of Fish, Woods Hole, Mass April 1979. Rapp.P-V Réun.Cons.Int.Explor.Mer 178, in press

FLUCTUACIONES EN EL STOCK DE ANCHOVETAS DESOVANTES DURANTE
LOS CICLOS REPRODUCTIVOS DE PRIMAVERA 1964-1978

por

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y

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Este documento es parte del Proyecto INCANE (Investigación Cooperativa de la Anchoveta y su Ecosistema) basado en la cooperación entre IMARPE y CIDA (Canadian International Development Agency)

Fluctuations in the Spawning Stock of Anchoveta
during the Spring Reproduction Cycles
from 1964 to 1978

by
Isabel Tsukayama
and
María A. Alvarez

Abstract

The decline in the anchoveta population from levels of 20 to 30 million tons to levels of 2 to 4 million tons motivated increased research into the mechanisms controlling the behaviour of the anchoveta biomass which result from interactions between the ambient and biological elements of the ecosystems. Subsequent evaluation of size distribution and gonadal state from samples collected from landings and research cruises, accompanied by estimates of total biomass from several sources has given insights into the 1964-1978 phenomena in changing anchoveta biomass.

Mature females were identified from the samples and they were used to estimate the proportions of spawners to total adults comprising the biomass. In the spring spawning cycle the adult biomass represents a nearly constant 90 percent of the biomass. The decrease in total biomass after 1968-1969, particularly after 1972 is a well recognized fact. The proportion of spawners to adults has varied between the values of 0.04 and 0.30 during the study period.

Upon analysis, the data show that in "near normal" years when temperatures during the spawning seasons were "typical", the stock comprised anchoveta of primarily 14 cm in length. In years when temperatures were elevated the stock was dominated by anchoveta of less than 14 cm. This implies that changes in ambient temperature alters the growth and physiological state of the anchoveta. This can be realized by changes in both availability and abundance of food, and changes in metabolism and activity of anchoveta in response to thermal correlates in the ecosystem and anchoveta metabolism.

There appear to be distinct differences in the proportions of spawners as well as size which result from comparisons of warm and "typical" years. In typical years the average proportion of spawners (above 14 cm in length) is about 0.15, ranging from 0.08 to 0.24. In contrast the warm years range in proportion from 0.04 at high biomass levels to 0.30 at low biomass; also the dominant size in the population is smaller than the "typical" years. This increased variance in proportion of spawners along with the dominance of smaller fish certainly has significant effects on subsequent egg abundance and quality, resulting in even greater potential variance in recruitment from these periods. Far more study of these properties are required.

INTRODUCCION

La fuerte declinación de la población de anchoveta de 20-30 millones de toneladas que tuvo al inicio de la pesquería industrial, hasta niveles tan bajos de 2 a 4 millones de toneladas en los años recientes, han motivado que se intensifiquen una serie de investigaciones orientadas al entendimiento de los mecanismos que inciden en el comportamiento de su biomasa, como consecuencia de las interrelaciones con el medio ambiente y elementos bióticos del ecosistema.

Dentro de esta problemática, uno de los aspectos relevantes en la dinámica poblacional de la anchoveta es el que se refiere al proceso stock-reclutamiento y como parte de esta problemática, el presente documento examina las variaciones en la biomasa del stock desovante, partiendo del hecho que la renovación del stock o reclutamiento se sustenta en primer término en un adecuado stock de reproductores.

MATERIAL Y METODO

El material consiste de información sobre distribución por tamaños y por madurez de gonadas procedentes de los muestreos de los desembarques, cruceros y eureka's así como de los estimados de biomasa total. Este material abarca los ciclos reproductivos de primavera, de junio a octubre, desde 1964 a 1978.

Se ha considerado como stock desovante a las hembras en estadios de madurez avanzada o pre-desove (Estadio IV) y como stock adulto a los ejemplares mayores de 11 cm, excepto en los años 1976 y 1977 en que se consideró como adultos a aquellos ejemplares mayores de 9,5 cm.

Para obtener la biomasa de desovantes y de adultos se han relacionado las informaciones de distribución por tamaños y madurez de gonadas con los estimados de biomasa total.

La biomasa del stock desovante se ha calculado tomando el mes que presentó la mayor proporción entre los pesos de hembras maduras a adultos, representando por lo tanto la biomasa instantánea de desovantes.

La ecuación que se ha aplicado para describir las variaciones en la proporción desovantes a adultos, en relación con el tamaño del stock adulto es:

$$S = a \cdot e^{-bP}$$

donde: S = Biomasa de desovantes/biomasa de adultos o tasa de desovantes

P = Biomasa de adultos

a, b = Constantes

RESULTADOS Y DISCUSION

Se observa que durante los ciclos reproductivos de primavera, la biomasa de adultos, esto es, la población apta para reproducirse, representa la mayor parte de la biomasa total. La disminución de la biomasa total, así como la de adultos es notoria a partir del año 1969, siendo la declinación más severa desde 1972.

La biomasa de desovantes en cambio, no ha seguido la misma tendencia de disminución como la ocurrida con la biomasa de adultos (Figura 1). La proporción entre las biomazas de desovantes a adultos, o tasa S, ha fluctuado en años no calientes entre 0,08 y 0,24 y en años calientes entre 0,04 y 0,30 (véase Figura 1 y Cuadro en la siguiente página).

De otro lado, analizando la estructura por tamaños del stock desovante, se observa que durante periodos reproductivos no calientes, el stock está constituido en su mayor parte por anchovetas mayores de 14 cm, los que corresponderían, según la curva de crecimiento preparada

por Tsukayama y Zuzunaga (1974) a ejemplares con más de 15 meses de edad, pero durante períodos con temperaturas elevadas, este patrón en la estructura por tamaños varía, con un incremento en la proporción de anchovetas menores de 14 cm como se muestra en las Figuras 2a y 2b, y que se suman en el siguiente cuadro:

Composición por tamaños del stock de hembras desovantes, durante períodos no calientes y períodos calientes

AÑO	STOCK DESOVANTE	
	Por ciento Anchovetas <14 cm	Por ciento Anchovetas >14 cm
Años Normales		
1964	10,1	89,9
1966	0	100,0
1967	3,3	96,7
1968	5,7	94,3
1970	5,0	95,0
1973	9,3	90,7
1974	0,9	99,1
1975	0	100,0
Años Calientes		
1965	32,4	67,6
1969	34,9	65,1
1971	55,1	44,9
1972	60,2	39,8
1976	62,9	37,1
1977	35,0	65,0
1978	72,2	27,8

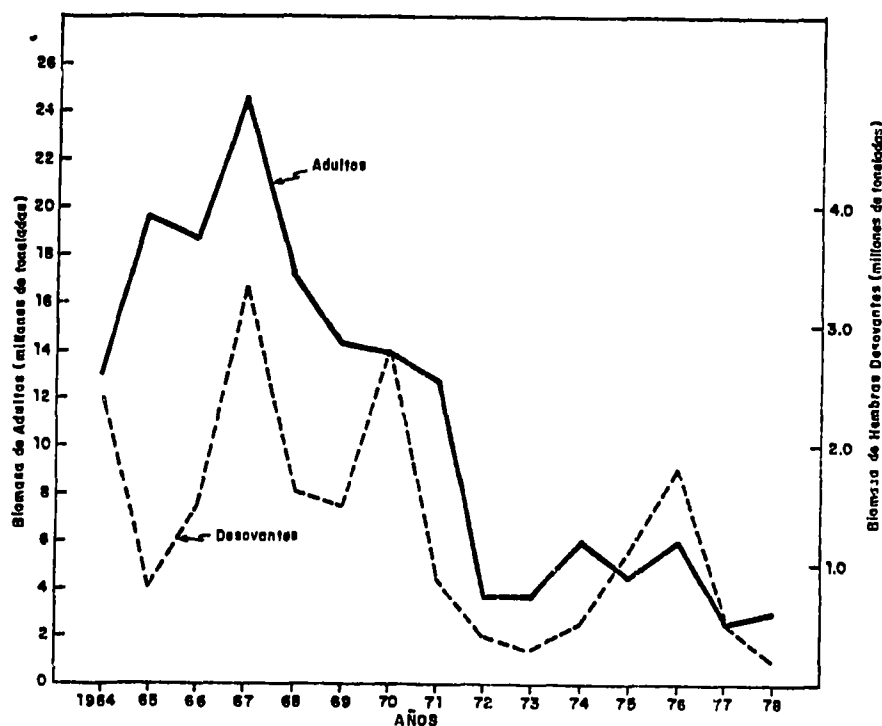


Figura 1. Biomasa de adultos y de hembras desovantes, durante las temporadas reproductivas de primavera, 1964 a 1978.

Año	Adultos (P x 10 ⁻⁶ T.M)	Desovantes (D x 10 ⁻⁶ T.M)	Desovantes
			Adultos = S
1964	13,0	2,4	0,184
1965	19,6	0,8	0,041
1966	18,7	1,5	0,080
1967	24,6	3,3	0,134
1968	16,6	1,6	0,097
1969	14,3	1,5	0,105
1970	13,9	2,8	0,201
1971	12,7	0,9	0,071
1972	3,7	0,4	0,108
1973	3,7	0,3	0,081
1974	6,0	0,5	0,083
1975	4,5	1,1	0,244
1976	6,0	1,8	0,300
1977	2,5	0,5	0,200
1978	3,0	0,2	0,067

Estas observaciones indican que en años calientes, la condición fisiológica de las anchovetas reproductoras se encuentran alteradas, con la participación en el desove de ejemplares con tamaños más pequeños.

Evidencias acerca de la disminución en la tasa de crecimiento se registraron en 1976, período que mostró un cuadro ambiental semejante al de 1965. En efecto, a comienzos del ciclo reproductivo de primavera 1976, los ejemplares con 15 meses de edad, sólo habían alcanzado tamaños promedios de 12,5 cm con pesos inferiores hasta de 28 por ciento con respecto a años normales, atribuyéndose este hecho a que la cantidad de alimento sufrió una baja en relación con otros años, y además, la composición especiológica del plancton estuvo alterada con la presencia de organismos de aguas cálidas (Instituto del Mar del Perú, 1976).

Ware(1980) en un documento basado en relaciones bioenergéticas establece que el crecimiento y la reproducción son procesos que se cumplen a expensas de la energía excedente, a la que define como la energía neta que se almacena en el cuerpo del pez luego que se han deducido las demandas de manutención del pez (metabolismo, standard y actividad).

Las observaciones con respecto a la disminución en la tasa de crecimiento se explicarían por lo tanto, como una consecuencia de la escasez de alimento y/o cambios en la calidad del alimento y ante tal situación la población responde, realizando el proceso reproductivo aun a expensas de su crecimiento corporal.

Los cambios habidos en el ecosistema del mar peruano a partir de 1972 con el incremento de otras poblaciones pelágicas, principalmente sardina, deben estar creando, desde luego, una competencia interespecífica entre la población de anchoveta y la población juvenil de sardina, al estar compartiendo el mismo hábitat.

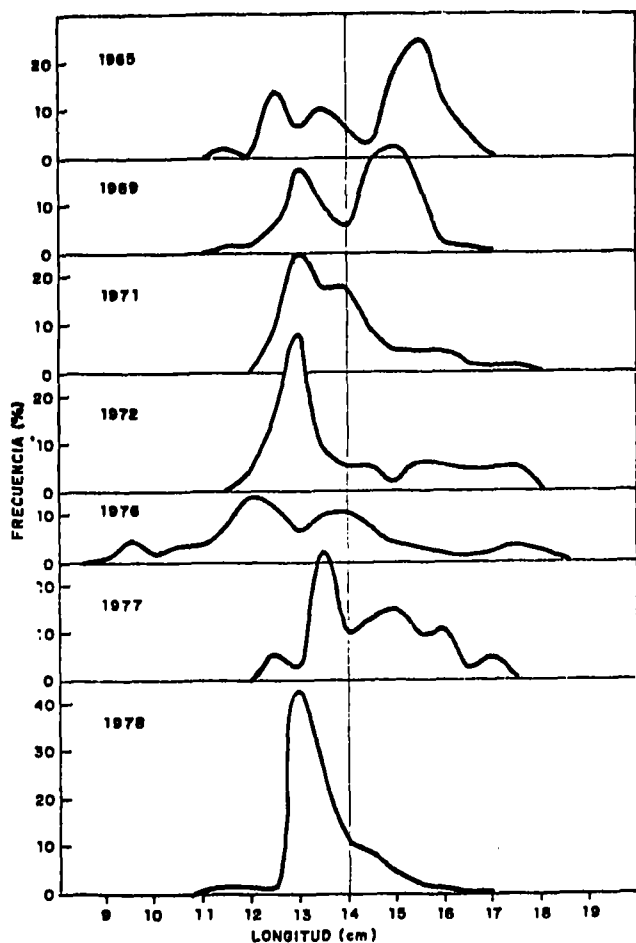


Figura 2a. Estructura por tamaños del stock desovante, durante períodos no calientes

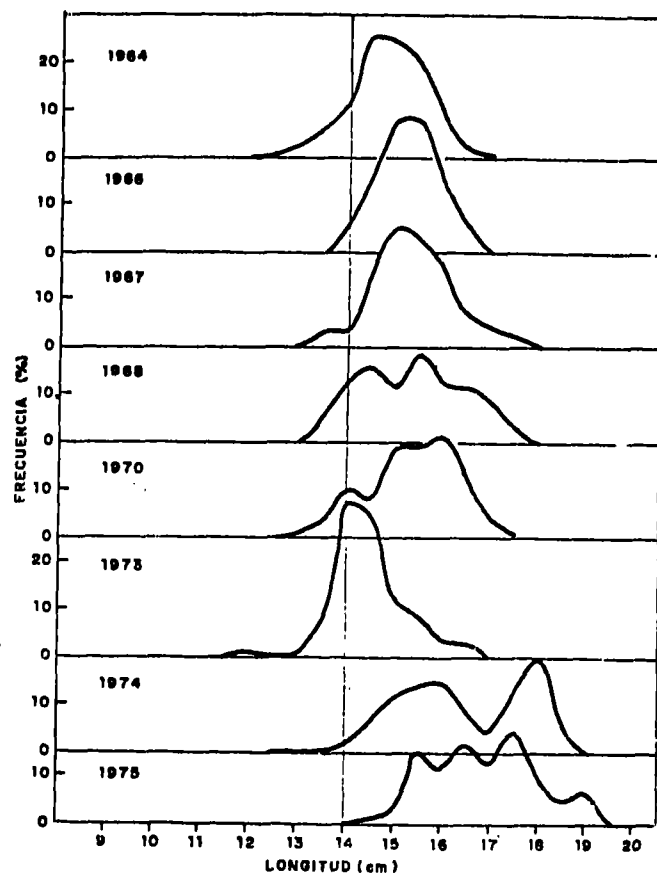


Figura 2b. Estructura por tamaños del stock desovante, durante períodos calientes

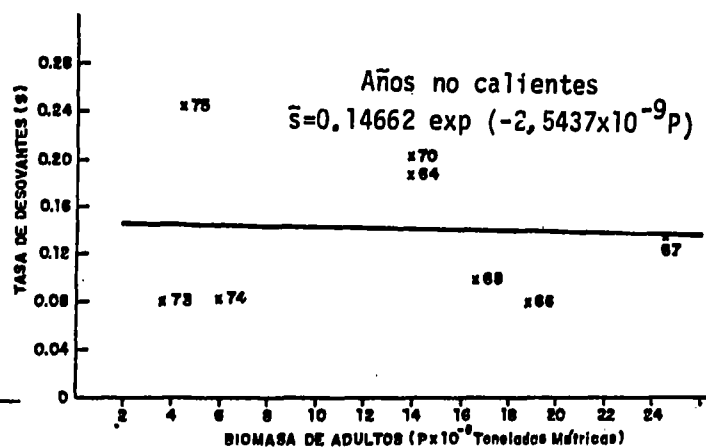
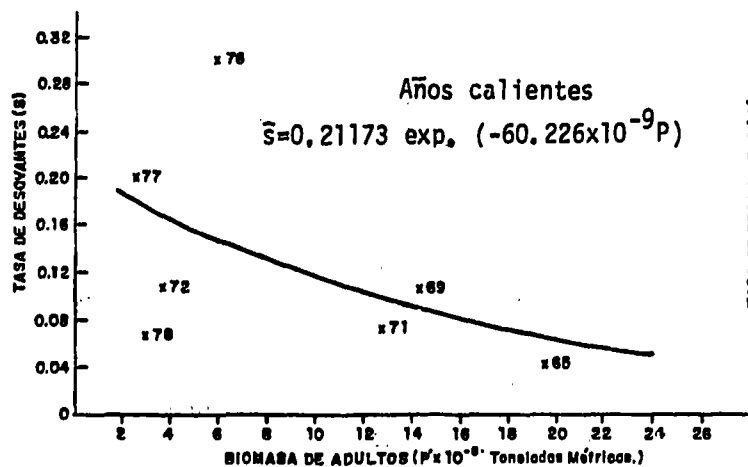


Figura 3. Tasa de desovantes (S) y su dependencia con la biomasa de adultos (P) durante los ciclos reproductivos de primavera

Sobre estas consideraciones, la variación en la tasa de desovantes debería reflejar en gran medida, un índice que relaciona el tamaño de la población y la disponibilidad de alimento necesaria, en función a sus requerimientos energéticos. La relación funcional que describe las variaciones en la tasa de desovantes, S , como dependiente de la población adulta P , y cuyas gráficas se muestra en la Fig. 3 es:

En años no calientes: $S = 0,146619 \exp (-2,543742 \times 10^{-9}P)$

En años calientes: $S = 0,211732 \exp (-60,226 \times 10^{-9}P)$

Se puede apreciar que en períodos no calientes la tasa de desovantes mantiene una tendencia casi constante a través de un amplio rango de población adulta, en cambio en años calientes la tasa de desovantes declina notoriamente a altos niveles de población.

Las implicancias de estos resultados nos están indicando que la temperatura es un indicador primario que refleja la interacción de elementos bióticos y abióticos en el ecosistema en que habita la anchoveta, por lo que al ocurrir calentamientos apreciables perturban su condición fisiológica con la consecuencia probable de producir menor cantidad de huevos por hembra y/o huevos menos viables. Es conocido también de los mapas de distribución y concentración de cardúmenes obtenidos de las prospecciones tipo "Eureka" y de los cruceros acústicos pesqueros de evaluación del stock, que durante períodos de calentamiento las agregaciones de anchovetas se concentran en áreas muy reducidas, conformando núcleos con altas densidades lo que conllevaría a una mayor competencia por alimento y mayor desgaste metabólico.

Bagenal (1969) arguye que la restricción del alimento conduciría indirectamente a una disminución de la fecundidad al producir mayor tensión en los peces por la mayor competencia y que esta tensión a su vez, produce disminución de la fecundidad a través de cambios en la actividad endocrina. Asimismo argumenta que la fecundidad jugaría un rol significativo en el control de las fluctuaciones de la población puesto que se esperaría que los peces en una situación de apiñamiento o sobresaturación y déficit de alimento produzcan menor cantidad de huevos.

AGRADECIMIENTOS

Expresamos nuestro agradecimiento a los Sres. José Pellón y Augusto Haro del grupo de Monitoreo de Anchoveta del IMARPE por su eficiente ayuda en el tratamiento de las muestras de distribución por madurez de todo el material disponible. Al Sr. Alec Mac Call del Department of Fish and Game de La Jolla, California, por sus valiosos comentarios.

REFERENCIAS

- BAGENAL, T.B. 1969. The relationship between food supply and fecundity in brown trout *Salmo trutta* A.J. Fish Biol. 1:167-182
- CSIRKE, J. 1979. El reclutamiento en la anchoveta peruana y su dependencia de la población adulta en los años 1961-1976 Bol.Inst.Mar Vol.4 (1)
- INSTITUTO DEL MAR DEL PERU. 1972. Informe sobre la Segunda Reunión del Panel de expertos en dinámica de población de la anchoveta peruana. Bol.Inst.Mar. Vol. 11 (7)
- INSTITUTO DEL MAR DEL PERU. 1973. Operación Eureka XXVIII (12-13 de noviembre de 1973) y diagnóstico del estado del stock de anchoveta en noviembre de 1973. Sr.Inf.Esp.Inst.Mar Perú. IM-146
- INSTITUTO DEL MAR DEL PERU. 1976. La situación de la población de anchoveta y el clima marino a octubre de 1976. Informe al Ministro de Pesquería
- INSTITUTO DEL MAR DEL PERU. 1977. La situación de la población de anchoveta y sardina a principios de 1977. Informe al Ministro de Pesquería

- INSTITUTO DEL MAR DEL PERU. 1977. El recurso anchoveta, el medio ambiente, la regulación de su pesquería desde 1960-1977 y sus perspectivas. Informe al Ministro de Pesquería
- JOHANNESSON, K. y R. VILCHEZ. Application and some results of echo integration methods in monitoring Peruvian anchovy resources, USA/USSR Meeting on Acoustic, M.I.T., June 1979 MS
- JORDAN R., J. CSIRKE e I. TSUKAYAMA. 1978. Situación de los recursos anchoveta, sardina, jurel y caballa a junio 1978. Inf.Inst.Mar Perú. No.56
- TSUKAYAMA I. y J. ZUZUNAGA. 1974. Crecimiento de la anchoveta en base a distribución por tamaños, MS
- WARE, D.M. 1980. Bioenergetics of stock and recruitment. Can.J.Fish.Aquat.Sci., 37:1012-1024
- ZUTA S. y W. URQUIZO. 1972. Temperatura promedio de la superficie del mar frente a la costa peruana período 1928-1969. Inst.Mar Perú. Vol. 11 (8)

FITOPLANKTON Y DESOVE DE LA ANCHOVETA
(*Engraulis ringens* J.)

por

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Phytoplankton and Spawning of Anchoveta

by

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and

Noemí Ochoa López

Abstract

The Peru Current is characterized by high productivity. The highest productivity is found within 60 n mi of the coast associated with upwelling. Phytoplankton is ingested directly by several of the major species of pelagic fishes in the Peru Current, anchoveta (*Engraulis ringens*); sardine (*Sardinops sagax sagax*); Pacific menhaden (*Ethmidium maculata chilense*) and others, accounting for the very high relative production of fishes in the system. This study examines the distribution, composition and abundance of phytoplankton in the coastal waters of Peru.

A total of 40 cruises and 2 225 sampling stations were examined. For studies of relations between phytoplankton abundance and spawning the stations in the area of Chimbote were selected as being representative. Phytoplankton was sampled at 10 m with Nansen bottles. The egg and larva data were gathered from plankton samples of the water column from 50 m to the surface. The numbers of eggs and larvae were proportional to the zooplankton and general secondary production at the time of sampling.

The density and composition of the phytoplankton varied with the season. The major density of phytoplankton observed was in autumn (1 764 cells/ml) and this was predominantly *Chaetoceros*. In the winter the density is low and few foci of abundance were observed. In the spawning the density foci increase in distribution and abundances ranging as high as 1 228 cells/ml of *Sahroderella* were observed. In the summer the highest concentrations are very near the coast, with station averages ranging from 1 to 913 cells/ml. Also large latitudinal phytoplankton variations are observed within and among seasons.

Larval fish appear to prefer to eat species which do not form tight aggregations or those which are mobile. To examine the relation between phytoplankton production and spawning, three representative cruises were selected and graphics were prepared showing the densities of phytoplankton, eggs and larvae of anchoveta, and densities of phytoplankton species eaten by anchoveta larvae.

Cruise 6108 (August, 1961) encountered a large concentration of phytoplankton off Chimbote which coincided with spawning foci. The food species for the larval anchoveta were abundant assuming high survival of this year class in this region.

Cruise 6211 (November, 1961) encountered a broad (60 n mi) band of phytoplankton off Peru, with the major concentrations and foci of spawning centred off Pimentel. There were, however, few of the preferred food species in this concentration, perhaps leading to the poor recruitment in 1963.

Cruise 6511 (November, 1975) encountered phytoplankton close to the coast from Pimentel to Huarmey. The principal spawning area and general phytoplankton coincided but the major abundance areas of the preferred food species were not within this region. The following year a good recruitment was observed. On the one hand we have question of whether the food organism abundance was well estimated from only 10-m Nansen bottles samples, and on the other hand we have the observation that the numbers of larvae were lower than those in previous studies from which one might infer that, due to lack of competition, survival was increased. Considering the numerous possible answers no conclusive explanations can be given for these events.

In general the relation between phytoplankton abundance and anchoveta spawning centres is strong. This association may not be only for feeding of the adults, but may be an adaptation assuming availability of food for the first feeding larvae.

Starting in December 1965 and continuing through the first half of 1966 there was a bloom of *Gymnodinium splendens* which is not a normal source of food for anchoveta (post-larvae) and the juveniles were noticed to be severely affected in having decreased size at age. As they matured the fat content did not rise to normal levels, and size at maturity was low, resulting in poor spawning. However, the survival of larvae during this period was quite high resulting in very high recruitment as the juvenile and adults failed.

INTRODUCCION

Las aguas de la corriente peruana se caracterizan por su gran productividad, encontrándose los valores más altos dentro de las 60 millas de la costa asociados a los procesos de afloramiento. El conocimiento de la producción de fitoplancton en la costa peruana es de gran importancia porque es el eslabón principal dentro del complicado proceso de la vida en el mar.

El fitoplancton, por ser una comunidad compleja, sus patrones de distribución en el tiempo y espacio no son expresión del conjunto, sino de las fluctuaciones de las poblaciones específicas que responden a las variaciones del ambiente.

Determinadas especies fitoplanctónicas son de considerable importancia como alimento ya que al parecer los herbívoros no consumen el fitoplancton al azar, sino que toman en cuenta su medida, calidad y cantidad.

En la costa peruana, varias especies de peces como la anchoveta (*Engraulis ringens* J.), la sardina (*Sardinops sagax sagax* J.) y el machete (*Ethmidium maculata chilense* H.) a determinadas longitudes se alimentan directamente del fitoplancton; la coexistencia de estos peces dentro de una misma área de distribución supone la competencia por determinadas especies fitoplanctónicas que constituyen su alimento. El conocimiento de las especies fitoplanctónicas del mar peruano, es fundamental porque en ella se apoyan diferentes cadenas alimentarias, por lo que el objetivo principal de este trabajo es dar a conocer la composición, distribución y densidad del fitoplancton de la costa peruana y su relación con las áreas de desove y su significado en la sobrevivencia de las larvas.

MATERIAL Y METODOS

Para este estudio se han considerado las muestras de fitoplancton colectadas a lo largo de la costa peruana durante los años 1961 a 1970 utilizando los barcos de investigación BAP Bondy (1961-1963), BAP Unanue (1964-1968) y SNP-1 (1969-1970) con un total de 40 cruces y 2 225 estaciones de muestreo. Para la comparación entre fitoplancton y desove se consideró el área de Chimbote por ser la principal área de desove de la anchoveta.

Las muestras de fitoplancton fueron colectadas con Botellas Nansen, a la profundidad de 10 m y preservadas con lugol. Desde 1966 se utilizó formalina neutralizada al 4 por ciento.

En el laboratorio se hicieron los análisis cualitativos y cuantitativos de las muestras utilizando un microscopio invertido y siguiendo la técnica de Utermohl.

La densidad de la población fitoplanctónica se expresa en número de células por mililitro.

Los huevos y larvas de anchoveta fueron separadas de las muestras de plancton colectadas con Red Hensen en una columna de 0 a 50 m de profundidad y fijadas en formalina neutralizada al 10 por ciento. Se expresan en No/m². El número de huevos y larvas fue proporcionado por el área de zooplancton y producción secundaria.

RESULTADOS Y DISCUSION

Distribución horizontal del fitoplancton

Las estaciones de muestreo fueron separadas por cuadrados Marsden de un grado y los datos del total de fitoplancton para cada cuadrado Marsden, fueron promediados.

Con estos datos promedio se prepararon los mapas de distribución de fitoplancton, trabajándose separadamente cada estación del año.

Verano (Figura 1). Las mayores concentraciones de fitoplancton se encuentran en las estaciones muy pegadas a la costa, los promedios por cuadrados Marsden variaron entre 1 y 913 cells/ml. Este último se encontró entre Pisco y Punta Doña María. Las especies predominantes fueron *Rhizobolenia delioatula* (908 cells/ml) y *Thalassiosira subtilis* (329 cells/ml).

Otro foco importante se presenta en El Callao (846 cells/ml) que se debió en gran parte a la presencia de un parche de *Olisthodiscus luteus* (44 555 cells/ml Est. 121-6402). Las especies predominantes en esta área fueron *Rh. delioatula* (336 cells/ml) y *Th. subtilis* (290 cells/ml). Entre San Juan y Atico se observa otro foco (593 cells/ml) con predominancia de *Thalassionema nitzschioides*.

Otoño (Figura 2). La mayor densidad promedio (1 764 cells/ml) se presentó entre Salaverry y Chimbote en estaciones muy pegadas a la costa con predominancias de diferentes especies de Chaetoceros (*Chaetoceros socialis*, 864 cells/ml). Otro foco, con 560 cells/ml se observó frente a Callao, predominando *Skeletonema costatum* (194 cells/ml) y *Nitzschia delioatissima* (138 cells/ml).

Esta estación se caracteriza por la presencia de focos de concentración frente a Talara que no se observa en otras épocas del año, con predominancia de *Chaetoceros*.

Invierno (Figura 3). La distribución fitoplanctónica es más dispersa, con pocos focos de concentraciones y densidades bajas. La mayor concentración se observa frente a Pimentel (714 cells/ml) y las especies predominantes fueron: *Sk. costatum* (522 cells/ml) y *Schroderella delioatula* (241 cells/ml). Otro pequeño foco se encuentra frente a Callao (325 cells/ml) con *Rh. delioatula* (93 cells/ml) y *Sch. delioatula* (79 cells/ml) como predominantes.

Primavera (Figura 4). El área de abundancia se extiende de Callao a Punta Doña María con un foco de concentración frente a Tambo de Mora (939 cells/ml) con predominancia de *Sch. delioatula* (1 228 cells/ml) y *N. delioatissima* (489 cells/ml).

La gran riqueza que se observa en esta área sería el resultado de los afloramientos que se presentan en San Juan durante el invierno.

Otro foco se observa en Pimentel con 868 cells/ml y con predominancia de *Th. subtilis* (754 cells/ml) y *Asterionella japonica* (380 cells/ml).

En general, el fitoplancton se presenta en mayor densidad durante la primavera extendiéndose como una faja continua desde Punta Aguja a Punta Doña María. Los focos de mayor densidad de fitoplancton se presentan en los bordes de los centros de afloramientos.

Variación latitudinal y estacional de la densidad del fitoplancton

La pesquería en el Perú, tanto pelágica como demersal, está mayormente concentrada en una faja de 60 mi paralelas a la costa conociendo además que la anchoveta, se distribuye principalmente dentro de las 60 mi y que ésta, al estado adulto, se alimenta preferentemente de fitoplancton. Se consideró importante mostrar la variación latitudinal de la densidad del fitoplancton en esta área.

Con este propósito se preparó la Figura 5 que muestra la variación latitudinal del fitoplancton por estación del año y la curva de variación latitudinal del promedio anual de fitoplancton.

La estación del año de mayor densidad fitoplanctónica dentro de las 60 mi corresponde al verano y la de menor densidad al invierno, existiendo diferencias en la densidad según la latitud en las diferentes estaciones del año. En el verano se observa la mayor densidad (1 142 cells/ml) entre los 14°-15° LS, en el otoño entre los 8°-9° LS (648 cells/ml); en el invierno entre los 6°-7° LS (667 cells/ml) y en la primavera la mayor densidad (907 cells/ml) se observa entre los 13°-14° LS.



Figuras 1-4. Variación estacional del fitoplancton

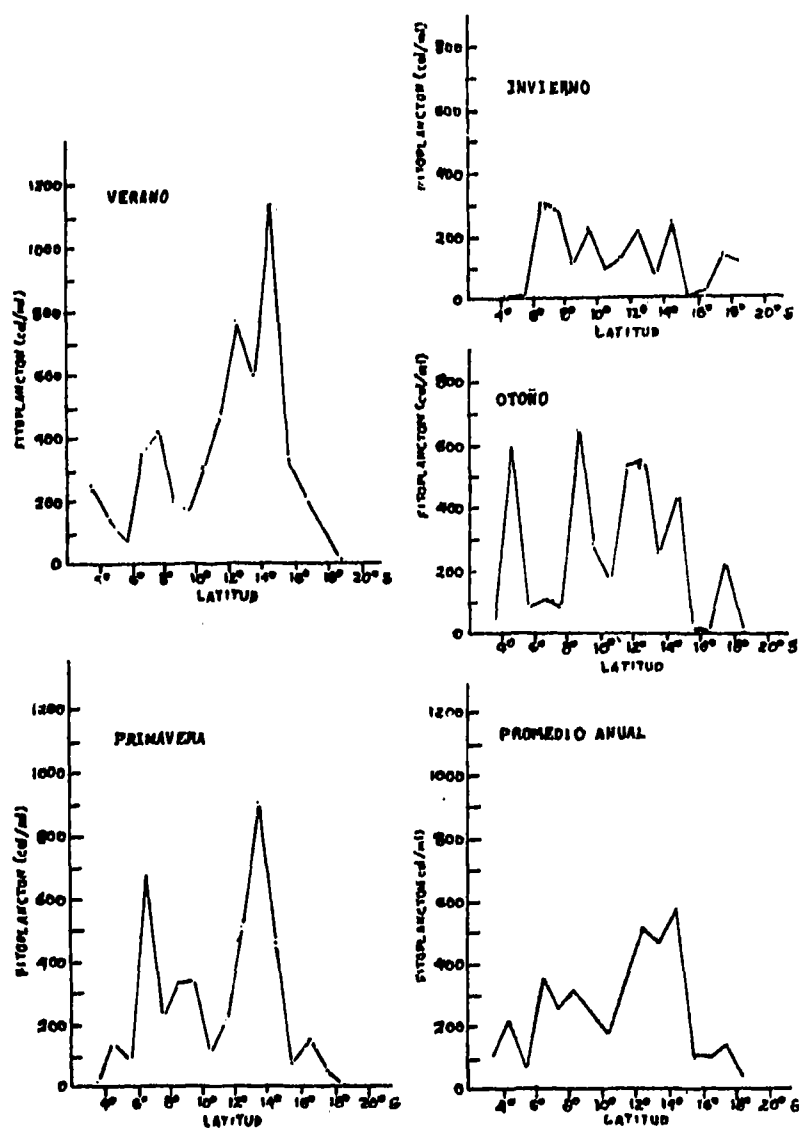


Figura 5. Variación latitudinal del fitoplancton

Este mismo gráfico muestra la curva de variación latitudinal del promedio anual de densidad de fitoplancton que presenta dos máximos: una entre los 60-90 LS y otra entre los 120-150 LS que coinciden con las dos principales áreas de afloramientos de diferente magnitud y comportamiento. Zuta y Guillén (1970) indican que el afloramiento típico y permanente se presenta entre los 140-160 S, aunque también ocurren afloramientos durante gran parte del año entre los 40-60 S, 70-80 S y 110-120 S.

Fitoplancton versus desove

Las larvas muestran preferencia por especies que no forman cadenas o que poseen un relativo movimiento propio. Entre ellas tenemos a las diatomeas como *Aotinoonyalus*, *Roperia*, etc. y a los dinoflagelados como: *Gymnodinium splendens*, *Gyrodiniumillum*, *Diplopsalis lenticula*, etc., y algunos organismos del zooplancton como huevos de copépodos y pequeños copépodos (Rojas de Mendiola y Gómez, 1980).

Por motivos de comparación entre la densidad del fitoplancton y densidad de desove, se han seleccionado sólo 3 cruceros que se consideran representativos y se han preparado gráficos con la densidad de fitoplancton, densidad de huevos y larvas de anchoveta, y densidad de los organismos fitoplanctónicos que se consideran que constituyen el alimento de las larvas.

Agosto 1961 Crucero 6108 (Figura 6)

Se observa una gran concentración de organismos fitoplanctónicos frente a Chimbote, que coincide con los focos de desove, la concentración de larvas y las especies que constituyen el principal alimento de las larvas, lo que aseguró una buena sobrevivencia de las larvas resultando en una buena clase anual 1962 (Valdivia, 1980).

Noviembre 1962 Crucero 6211 (Figura 7)

Hay una gran abundancia de fitoplancton que se extiende en toda el área hasta las 60 mi, principalmente frente a Pimentel, donde se encuentra también el mayor foco de desove, pero no existe coincidencia entre el alimento disponible y la concentración de larvas. Esto probablemente influyó en el bajo reclutamiento observado en 1963 (Valdivia, 1980).

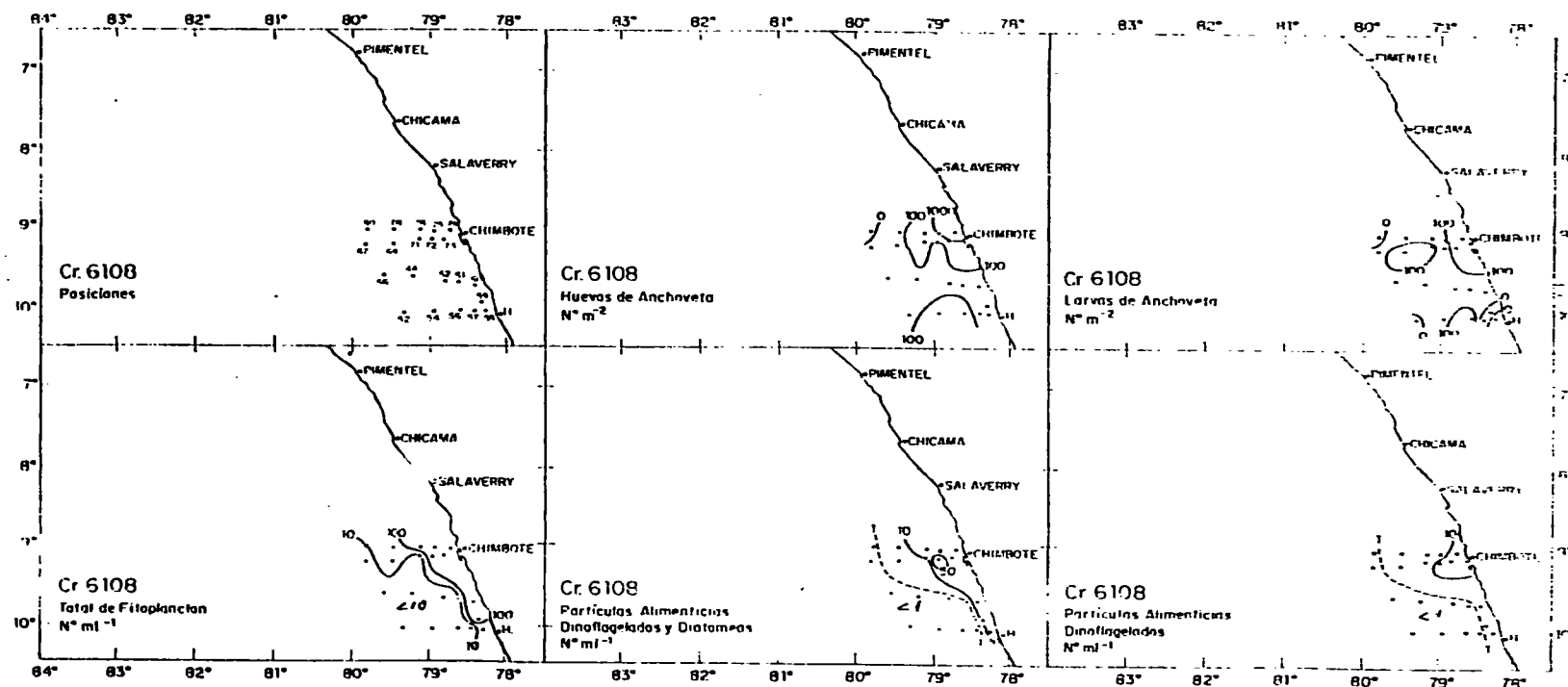
Noviembre 1965 Crucero 6511 (Figura 8)

El fitoplancton se encuentra distribuido cerca de la costa de Pimentel a Huarmey. Existe coincidencia entre los principales focos de desove y la mayor concentración de fitoplancton pero la disponibilidad de las partículas que podrían servir de alimento a las larvas pequeñas recién eclosionadas, no fue buena.

Sin embargo, según lo observado por Valdivia (1980) el reclutamiento proveniente de este ciclo de desove fue alto. Una posible explicación sería que el alimento no estuvo disponible a los 10 m, nivel al que se colectó el fitoplancton, pero su mayor densidad posiblemente coincidió con el nivel donde se encontraban las larvas lo que permitió la sobrevivencia de las mismas.

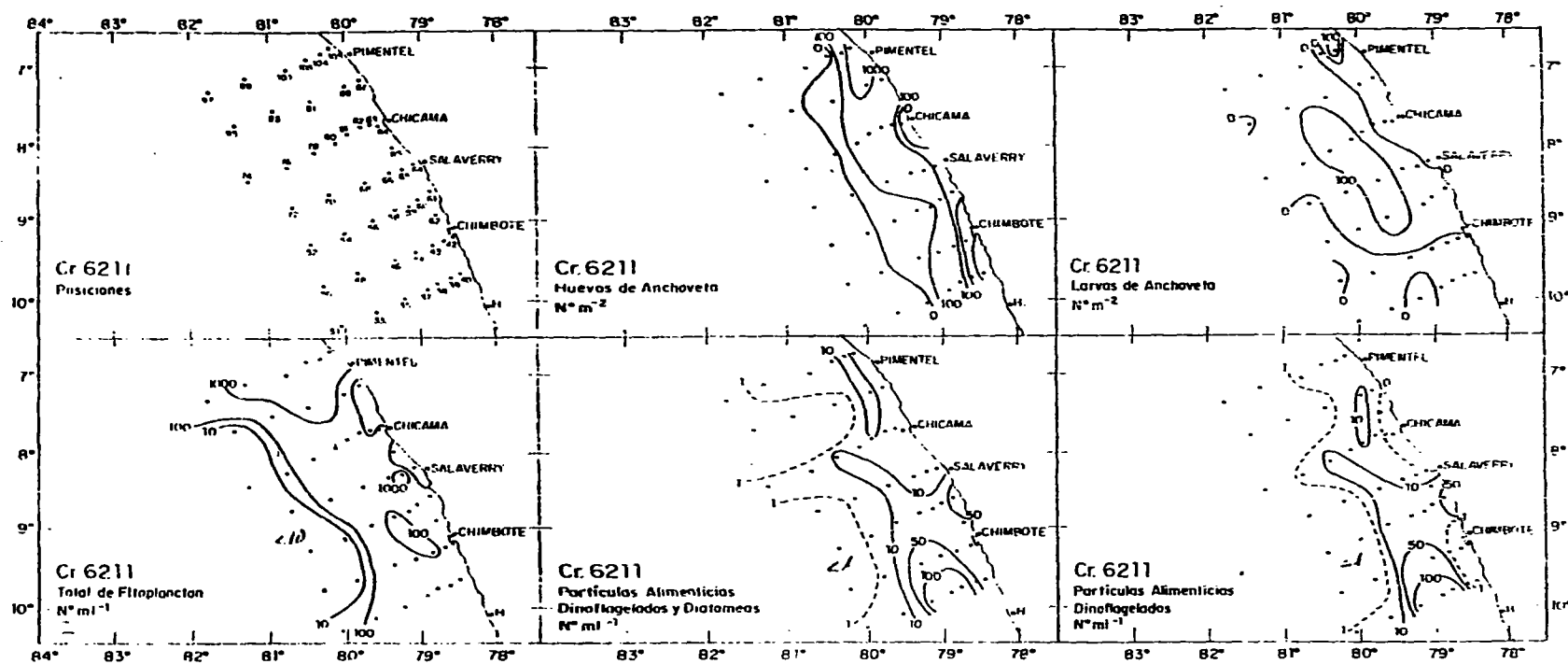
Por otro lado, este desove, considerando el número de huevos por m^2 , fue bajo, (Santander y S. de Castillo, 1969). Esto posiblemente permitió una mayor sobrevivencia de las larvas debido a la poca competencia por alimento entre ellas.

En general, se observa una relación directa entre los focos de desove y la densidad de fitoplancton, lo que nos indica que la anchoveta adulta frecuenta las áreas de abundancia de fitoplancton constituido por diatomeas, no sólo para alimentarse sino también para desovar, como una posible forma de asegurar una buena disponibilidad alimenticia para las larvas en el momento de su primera alimentación.



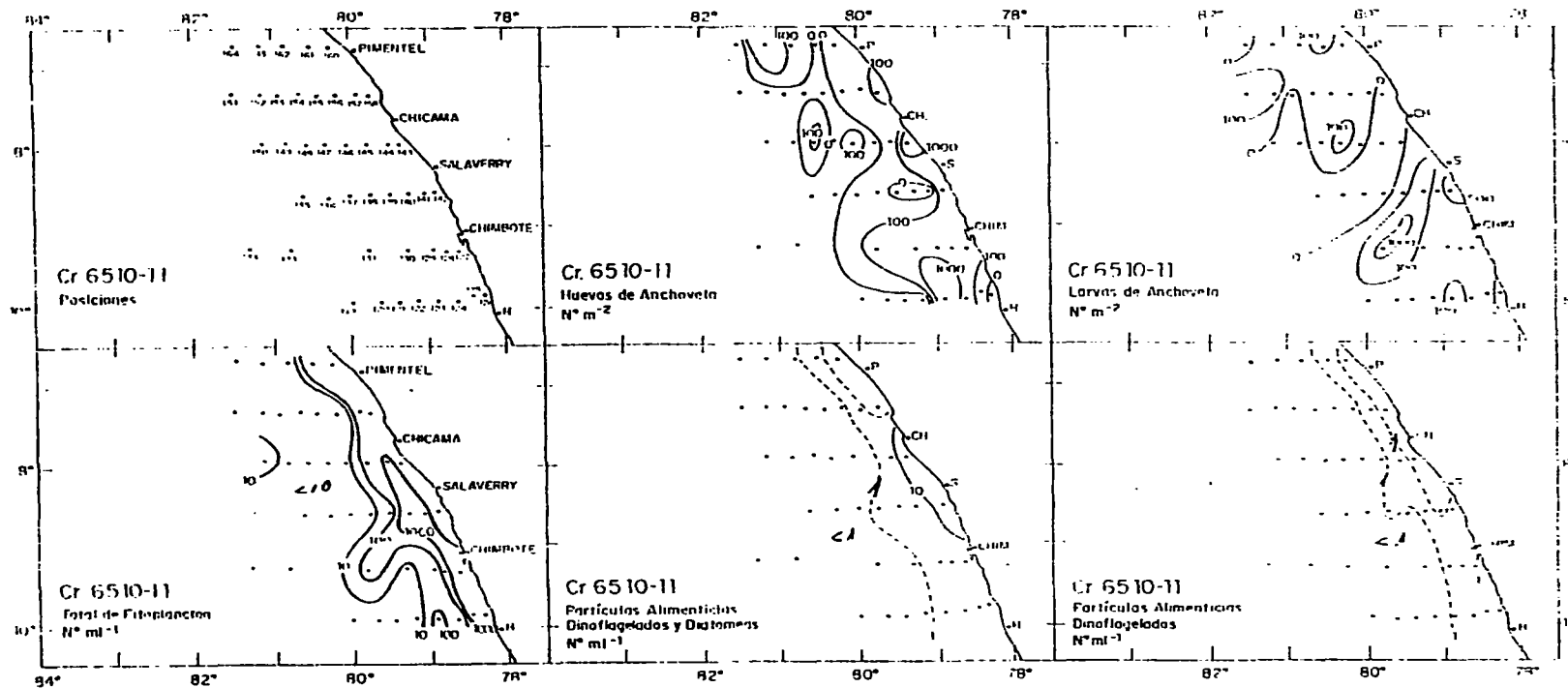
Huevos, larvas y alimentos de anchoveta en Agosto de 1961

Figura 6



Huevos, larvas y alimentos de anchoveta en Noviembre de 1962

Figura 7



Huevos, larvas y alimentos de anchoveta en Noviembre de 1965

Figura 8

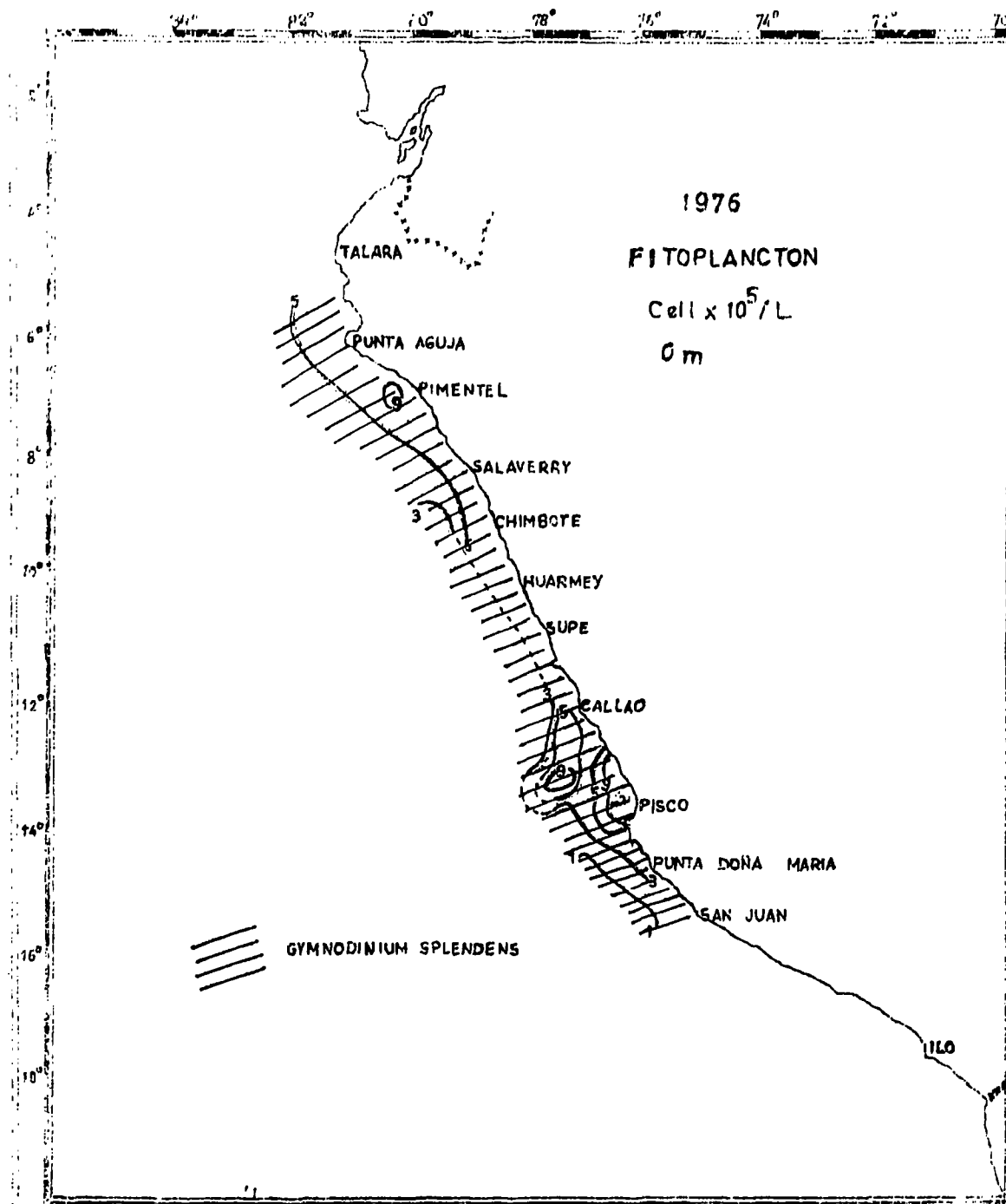


Figura 9. Distribución del fitoplancton

Los cambios en la composición específica del fitoplancton con dominancia de *Gymnodinium splendens*, que no es normal fuente de alimento de la anchoveta, se iniciaron en diciembre de 1975 y se incrementaron gradualmente durante todo el primer semestre de 1976 (Figura 9) teniendo efectos negativos sobre la anchoveta. Se observó una reducción en la tasa de crecimiento de la clase recluta 1976 hasta niveles de 70 y 100 mm para las anchovetas de 6 meses y un año de edad respectivamente.

La normal tasa de crecimiento es de 80 y 110 mm (Chumán de Flores, 1978). Otros efectos fueron la caída en el contenido graso, reducción del tamaño al que la anchoveta alcanza la madurez sexual y una baja en la densidad del desove en agosto de 1976 (IMARPE, 1976). Sin embargo, la presencia de *G. splendens* en los últimos meses de 1975, antes de que adquiriera las condiciones de "bloom", se puede considerar como una situación favorable para la sobrevivencia de las larvas que sí se alimentan de *G. splendens*, resultando en el alto reclutamiento que fue observado en 1976 (Valdivia, 1980).

REFERENCIAS

- CHUMAN DE FLORES, E. 1978. Análisis comparativo del crecimiento de la anchoveta *Engraulis ringens* J. en la región central durante 1976 y 1977. IMARPE (En prensa)
- EINARSSON, H. y B. ROJAS DE MENDIOLA. 1966. An attempt to estimate annual spawning intensity of the anchovy (*Engraulis ringens* Jenys) by means of regional egg and larval surveys during 1961-1964. California Cooperative Oceanic Fisheries Investigations. Reports Vol.XI, 1 July 1963 to 30 June 1966
- IMARPE. 1976. Operación Eureka XXXVI, Informe Especial No.I-M-185
- ROJAS DE MENDIOLA, B. 1966. Relación entre la cosecha estable de fitoplancton, el desove y la alimentación de la anchoveta *Engraulis ringens* J. Memoria del Primer Seminario Latinoamericano sobre el Océano Pacífico Oriental. Lima, Perú
- ROJAS DE MENDIOLA, B. y OLGA GOMEZ. 1980. Alimento, sobrevivencia y tiempo de inactividad de las larvas de anchoveta *Engraulis ringens* J. Taller de Trabajo "Sobrevivencia de huevos y larvas de peces pelágicos y sus relaciones con el ambiente". IMARPE
- ROJAS DE MENDIOLA, B. 1980. Variaciones del fitoplancton a lo largo de la costa peruana. IDOE International Symposium on Coastal Upwelling, CUEA, Los Angeles, California, USA
- SANTANDER, H. y O. SANDOVAL DE CASTILLO. 1969. El desove de la anchoveta *Engraulis ringens* J. en los períodos reproductivos de 1961 a 1968. Informe Especial No.IM-40
- VALDIVIA, J. 1980. The Peruvian Anchoveta. Taller de Trabajo Sobrevivencia de huevos y larvas de peces pelágicos y sus relaciones con el ambiente. IMARPE
- ZUTA, S. y O. GUILLEN. 1970. Oceanografía de las Aguas Costeras del Perú. Boletín, Vol.2 No.5 IMARPE Callao, Perú

FLUCTUACIONES DEL DESOVE DE ANCHOVETA
Y ALGUNOS FACTORES RELACIONADOS

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Fluctuations in Spawning of Anchoveta
and some Related Factors

by

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Abstract

This contribution is a summary of Peruvian anchoveta spawning cycle and egg and larval abundance data and their relation to ambient condition fluctuations in the years from 1965 to 1979. In the past a typical cycle of anchoveta spawning would begin in July and increase well into the winter with a peak in September; finally spawning would cease in the summer month of March. April, May and June were periods of rest. The general area of the major spawning was between 6° and 14° S, a region with a unique shelf configuration, as well as hydrographic and weather characteristics. The winds in this region in general are most strong in winter and weakest in summer, but are quite different within the region at various seasons and locations. These differences have significant consequences on the patterns of food production for larval anchoveta in the spawning areas.

The major occurrences of eggs and larvae do not coincide with the major areas of upwelling. Oxygen is an important element to larval anchoveta survival, and is influenced by the upwelling processes, as well as subsurface current flow. Embryonic development time is influenced by temperature of the water in which the eggs are shed. Their transport and subsequent survival are directly attributable to the dynamics of these spawning areas.

The spawning areas are apparently selected by the adults for survival of the eggs and larvae. The adults can also apparently sense the characteristics preceding the advance of unfavourable superficial equatorial or oceanic waters into their normal habitat and either move southward or into the narrow coastal sanctuary zones for subsequent reproduction.

The phytoplankton and zooplankton are also most abundant some distance from the foci of upwelling. Subsurface current movements affect changes in distribution and abundances of phytoplankton, zooplankton, anchoveta eggs and larvae, and this is often reflected in the sample variation from the spawning regions.

The maximum observed spawning occurred in the years 1966 and 1967. No great oceanographic anomalies were observed and upwelling was continuous in the southern area (below Pisco) and to a lesser extent throughout the spawning area. By 1968 the abundance of eggs had begun to decline. This continued into 1969 when the level of spawning appeared to be about 25 percent of that observed in 1967. Spawning reached a minimum in 1971 and 1972. In 1973 and 1974 there was an increase to levels approximating those observed in 1969.

Up to 1971 the spawning peak or maximum egg abundance was in September. In 1972 there were changes in the behaviour of the spawning stock, some of which are likely attributable to the El Niño phenomenon. The spawners occurred concentrated within 20 miles of the shore in contrast to up to and beyond 60 miles in past years, and where these high densities were observed, the spawning was also noted to be quite poor. The pattern of the spawning cycle also changed such that the normal onset and peak spawning were offset by about three months and ended in February, about one month earlier than usual. These adults were observed to have very high fat content, probably resulting from a physiological change which impeded the fat's transposition to gonadal development. The cause is not known for this impeded process, although in previous years the decline in fat content coincided with egg development.

In the second half of 1973 there was an obvious cooling trend which again resulted in a different cycle from the pattern of years prior to 1972. A spawning peak was observed in February 1974, following a continuous increase from the winter months through to summer.

In 1974-1975 the spawning cycle was observed from August to February, with the peak again occurring in the "normal" September period. The 1975-1976 cycle appeared to have a normal form also, although a poorer summer spawn was observed than in preceding years back to 1972. Also an encroachment of superficial subtropical water right up to the coast and general reductions in phytoplankton concentration and distribution were observed.

The pattern of peak spawning appear to be related to production cycles. These patterns were unusual in the 1972-1973, 1973-1974 and 1976-1977 cycles when ambient conditions were markedly altered, resulting in changes in occurrence of maximum production from spring to summer. It is not known what causes these anomalous conditions, but the changes in spawning cycles are obviously responses which are intended to improve the chances of larval survival during the anomalous ambient conditions.

Anchoveta are not the sole species in the Peruvian system and some attention should be given to some of the other species, in particular to the sardine. From 1961 to 1964 the anchoveta was the dominant species in the ichthyoplankton with 85 percent of the eggs encountered being anchoveta and the rest from other species. In 1965 this decreased to 65 percent in a year of moderate oceanographic anomalies. From 1966 to 1971 the proportion fluctuated between 80 and 90 percent. In 1972 and 1973 the values were 50 and 47 percent respectively. Since 1974 the proportion of anchoveta eggs has been about 20 percent of the total.

In contrast sardine eggs were absent from 1966 samples and not abundant in 1967 and 1968. From 1969 a slow increase in their abundance was observed. In 1970 and 1971 their spawning was limited to a few small areas in the northern region. With the 1972 "El Niño" the area of abundance of sardine eggs and larvae increased to include the entire coastline in a fringe area about 35 miles from the coast. The area inside was occupied by anchoveta. From 1973 to 1977 the sardine spawning cycle was inverse with respect to that of the anchoveta. Since 1977 the sardine spawning indices have surpassed those of anchoveta, and they have been well distributed up to the coast in many areas.

Both ambient oceanographic conditions and the fluctuations of the anchoveta population appear to have benefited the sardine. There are clear implications that in the final stages of the increase of the sardine population to dominance there is competition between the two species.

INTRODUCCION

Desde 1972 a 1980, las poblaciones de peces pelágicos frente al Perú, anchoveta, sardina, jurel y caballa, principalmente, han variado en diferente sentido. Fluctuando la anchoveta en forma inestable con tendencia al descenso de la población, y del incremento de las otras especies. Pero estos incrementos de las otras especies, no alcanzan los niveles de la población de la anchoveta de la década del sesenta.

Uno de los procesos fundamentales en la renovación de los recursos, la reproducción, refleja a través de las fluctuaciones del desove en forma general los cambios o tendencias que ocurren en las poblaciones. Pero esto no se presenta en una forma directa y simple. Excluyendo la abundancia poblacional de la especie, que debiera influir directamente en el volumen del desove, el ambiente como conjunto de elementos condiciona en diferente sentido a la población desovante y en algunos casos parece determinar la producción del desove.

Al parecer la anchoveta a través del tiempo ha logrado adaptarse a las condiciones existentes en las costas peruano-chilenas ($03^{\circ}30'$ a $25^{\circ}40'$ S) y seleccionar para el desove áreas y períodos relacionados con el sistema de afloramientos costeros.

Siendo el desove uno de los procesos de vital importancia en su ciclo biológico, la presente contribución resume la información sobre los ciclos de desove, desde 1965 hasta 1979, tratando de analizar las relaciones de sus fluctuaciones con las condiciones ambientales.

DESOVE DE ANCHOVETA

El desove principal se inicia en el mes de julio y aumenta de intensidad gradualmente para llegar a su máximo generalmente, a fines de invierno, en septiembre y finalizar al término de verano, en marzo. Entre abril y junio es el período de reposo.

La anchoveta desova a lo largo de toda la costa del Perú, a partir de las proximidades de Cabo Blanco ($03^{\circ}30'$ S). La distribución vertical alcanza hasta 70 m, aunque principalmente ocupa los 30 m superficiales y una mayor concentración se localiza en el nivel de 30 m (Santander y S. de Castillo, 1973).

Frente al Perú, el área Norte-Central es la más importante para el desove de anchoveta y está situada entre Punta Aguja y Pisco (06° - 14° S), aunque al sur también se presentan algunos focos de desove, son de menor intensidad y extensión que al norte de 14° S.

El desove se realiza principalmente en áreas próximas a la costa, asociado a los bordes fríos de los frentes hídricos, costeros en el verano y más débiles y distantes en el invierno.

La extensión del desove ha variado mucho. La mayor densidad del desove hasta 1970, se localizaba en la zona costera comprendida en las 60 mi. En los años de gran intensidad del desove, septiembre de 1967 y 1966 (Figura 1) se localizaron altas concentraciones hasta 120 mi de la costa, con densidades mayores a 1 000 y hasta 40 000 huevos por m^2 .

En los tres últimos años (1977-1979) la pobreza del desove es tal, que sólo alcanza hasta alrededor de 20 mi de la costa (Figura 2).

La ubicación de la principal área de desove y consecuentemente de crianza, entre 6° y 14° S, reúne características muy particulares. Es la región de mayor amplitud de la plataforma, delimita por la isobata de 100 brazas, principalmente de 7° a 10° S, con un ancho máximo de 65 mi a los 9° S.

La pendiente más suave del talud coincide con el área de mayor extensión de la plataforma y hasta 14° S, mientras que al norte de 7° S y sur de 14° S, ésta se hace más pronunciada.

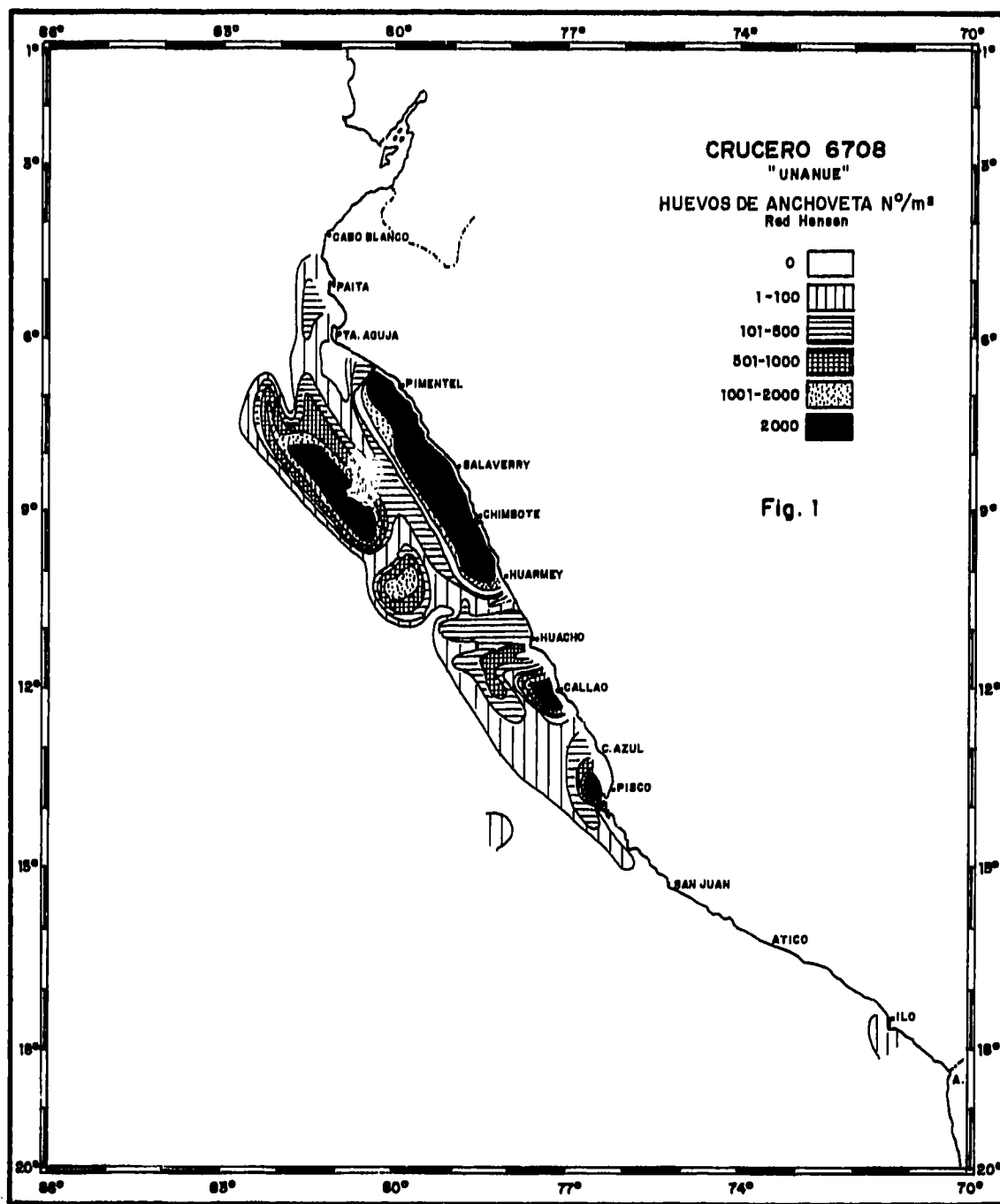


Figura 1. Crucero 6708 "UNANUE"

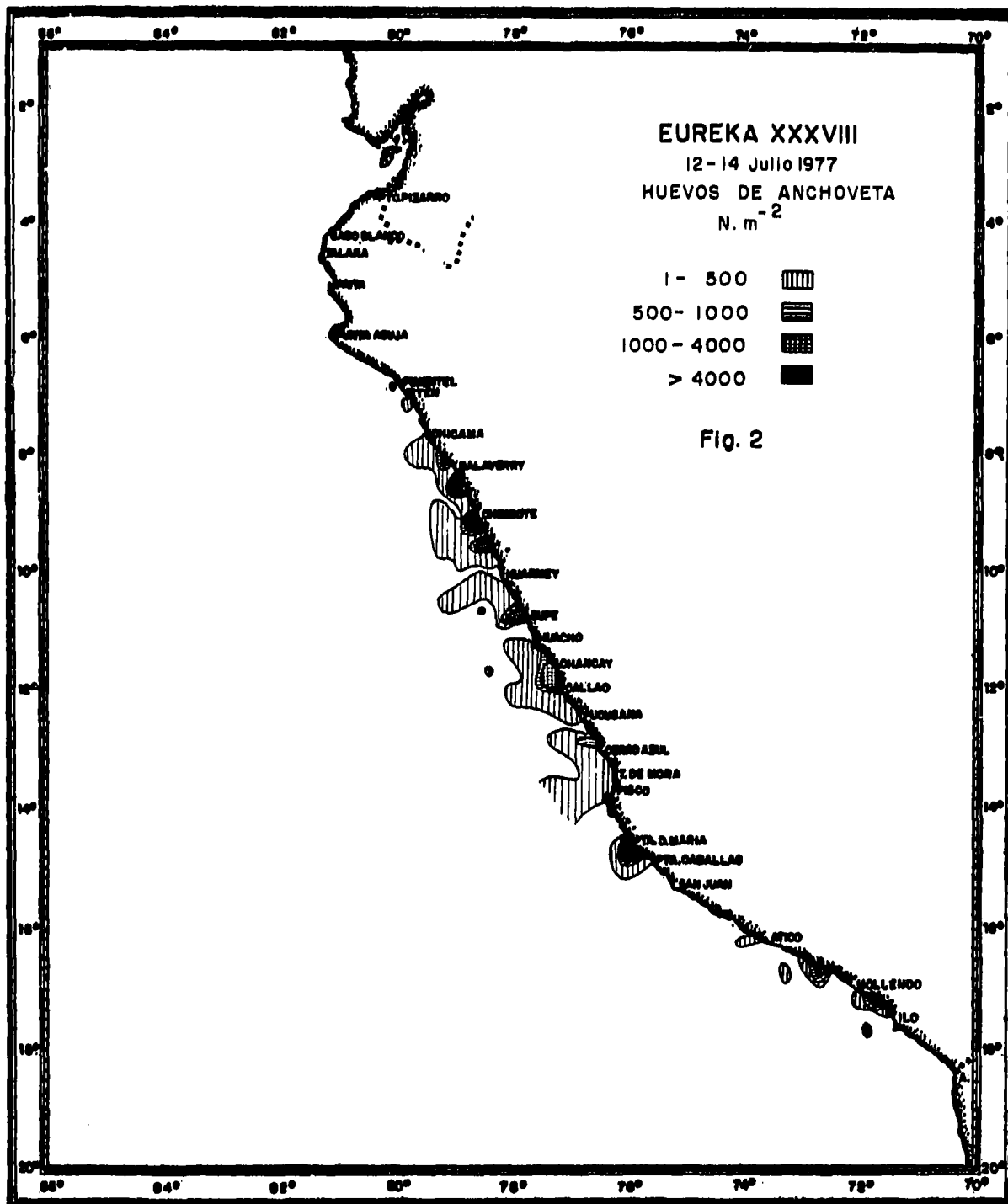


Figura 2. EUREKA XXXVIII
24-14 julio 1977

La línea costera entre 6° y 14° S, está orientada SSE (150°). Al sur de 6° S, la línea costera es aproximadamente paralela a la dirección predominante de los vientos alisios de SE.

La zona entre Punta Aguja-Pisco, no es zona de gran divergencia, como las áreas Talara-Punta Falsa y Pisco-San Juan; ni son frecuentes los remolinos entre Pimentel y Callao, como al norte y sur de esta área (Zuta y Guillén, 1970).

Los vientos en general son más fuertes en invierno y más débiles en verano, pero no se presentan con la misma intensidad en los diferentes períodos y áreas. Frente a Chimbote son más débiles en agosto y octubre, y frente a Callao, en enero y octubre.

Al sur de 14° S, especialmente frente a San Juan, los vientos son más intensos y más persistentes; y al norte de 6° S, los vientos son más variables, con direcciones de S y SW en las cuatro estaciones del año. Uno de los procesos de especial significancia en la secuencia de la producción y disponibilidad del alimento de larvas, es el afloramiento. Frente al Perú, como carácter común para las tres principales áreas, norte, centro y sur, se produce este proceso en forma casi permanente. Son de mayor intensidad en invierno y están limitados principalmente a la capa de 100 m. Se diferencian dos centros de gran intensidad donde la gradiente horizontal es más pronunciada, al norte de 6° S y principalmente entre 14° y 16° S, donde una lengua de agua fría se proyecta lejos de la costa en todo o gran parte del año. Otras áreas importantes son: Callao (12° S), Atico (16°20' S) y Mollendo (17° S). Y en tercer término, los afloramientos moderados de Pimentel (6°50'), Chicama (7°40'), Salaverry (8°20'), Chimbote (9°) y Supe (10°50'), (Zuta y Urquiza, 1972), correspondiendo estos últimos al área principal de desove y de distribución larval de anchoveta.

Las mayores concentraciones de huevos y larvas no co-ocurren con las áreas (Pisco-San Juan) de máximo afloramiento.

Según Zuta y Guillén, los afloramientos se hacen más intensos en algunas localidades de acuerdo a las estaciones del año:

Primavera	7°, 12°, 15° S
Verano	9°, 12°, 15° S
Otoño	5°, 7°, 10°, 15° S
Invierno	5°, 7°, 9°, 14°, 16° S

El pico del desove a inicios de la primavera, parece corresponder con la secuencia en cadena de los procesos de producción biológica. Máximos afloramientos en invierno, máximo de fitoplancton (Calienes, 1973) y de copepodos en primavera, (Santander, 1974), en el área norte-central.

Tanto en invierno como en otoño las concentraciones de fitoplancton (Guillén et al., 1971) y zooplancton decrecen comparadas con la abundancia de primavera y de verano secundariamente.

Un elemento muy importante en la vida de los organismos es el oxígeno y valores hasta de 2 ml/L en superficie están relacionados con las áreas de afloramiento (Zuta y Guillén, 1970). Como el área de 6° a 14° S, es de afloramientos moderados, se supone que valores mínimos de oxígeno son menos frecuentes que en otras áreas donde el afloramiento es más intenso. Sin embargo el área frente a Supe (11° S) es señalada como un área de bajo contenido de oxígeno (3 ml/L) en otoño, invierno y primavera; Pacasmayo (7°30' S) en primavera y Salaverry-Chimbote en verano (Zuta y Guillén, 1970), en áreas próximas a la costa.

Frente al Callao, la isolínea de 0,25 ml/L aparece mayormente por debajo de los 75 m, haciéndose más superficial en las áreas costeras, profundizándose en febrero y septiembre. Y en general, una capa de mínima (< de 0,5 ml/L) se localiza por debajo de 50 m, y se hace más superficial cerca de la costa y hacia el sur (Zuta y Guillén, 1970).

En San Juan, $15^{\circ}22'$ S, un conspicuo mínimo de oxígeno se desarrolla bajo 100 m, éste es dominante de octubre a marzo y es asociado con el fuerte flujo hacia el sur, de la subcorriente peruano-chilena. A este respecto el área costera de máximo afloramiento (14° - 16° S) en general es eludida para el desove de peces.

En las Figuras 3, 4 y 5, se muestra una secuencia de mayores concentraciones de desove; temperaturas superficiales, cuyas mínimas se podrían considerar indicadoras de afloramientos; distribución superficial de oxígeno, las mínimas concentraciones relacionadas con los focos de afloramientos; transparencia, indicativa de concentración de fitoplancton; mayores concentraciones de zooplancton (Volumen) y máxima concentración de larvas. En la mayor parte de los casos, los desoves no se localizan en los focos de afloramientos, siendo el área de larvas todavía más excéntrico. En el caso de larvas, su localización se debería al efecto del transporte por la dinámica del agua, pero en el caso de los huevos, la duración del desarrollo embrionario implica que el área donde se localizan es mayormente donde fueron desovados. De la misma forma que la ocupación del área de 6° a 14° S, como principal área de desove, debe ser consecuencia de la selección de las condiciones favorables para la sobrevivencia de huevos y larvas, por la especie.

Durante los períodos irregulares de avance de aguas ecuatoriales superficiales y de aguas oceánicas (1972-73 y 1976) la especie parece detectar elementos desfavorables en el ambiente que determinan su avance hacia el sur y/o el repliegue de su área de desove a escasas millas de la costa. Sin embargo, aún cuando esto le es desfavorable, más nocivo parece ser el efecto de las aguas ecuatoriales y oceánicas con comunidades completamente opuestas a las prevalecientes antes de los cambios.

En el caso de las concentraciones de fitoplancton y zooplancton, éstas también se localizan principalmente por fuera de los focos de afloramiento.

En primavera de 1964 (área de 12° - $18^{\circ}30'$ S) cuando la abundancia del fitoplancton fue incrementada con respecto a la estación de invierno, las mayores concentraciones se localizaron al norte de los mayores focos de afloramiento (Guillén et al., 1973). Y en los años "El Niño", cuando se debilitan los afloramientos y la intensidad de las aguas subtropicales superficiales y las procedentes del frente ecuatorial aumentan, decrecen las concentraciones de fitoplancton y se acercan una gran variedad de zooplanctones oceánicos o ecuatoriales, hacia la costa y sur respectivamente.

Un aspecto no muy conocido en nuestro medio, es el de la dinámica de los sistemas de corrientes, factor que actúa directamente sobre organismos de ninguno o muy poco movimiento, como son los huevos y larvas de peces. El sistema de corrientes superficiales es el que debe dominar los cambios en distribución de huevos y principalmente de larvas, que además de las fluctuaciones irregulares en densidad del desove, relacionados con el nivel del stock desovante y/o con el desarrollo gonadal a través de la alimentación, muestra variaciones en la localización de las áreas de crianza.

Durante el período de desove las fuerzas interactuantes serían principalmente las que proceden de la corriente costera peruana, las aguas subtropicales superficiales y las que constituyen el frente ecuatorial. Las primeras fluyen hacia el noroeste, a lo largo de la costa, hasta aproximadamente 6° S. Las aguas subtropicales superficiales se manifiestan durante todo el año, por fuera de la costa, limitando los movimientos de las aguas antedichas, y en verano avanzan más hacia la costa. Usualmente su acercamiento es hasta alrededor de 50 mi. La intensidad varía de año en año y también estacionalmente, en relación inversa a la intensidad de los afloramientos.

Las aguas ecuatoriales superficiales que se presentan al norte de 6° S, alcanzan su mayor intensidad durante primavera y verano (Guillén, 1976). En invierno los afloramientos son más intensos y su límite puede llegar a 160 mi de la costa (Stevenson et al., 1970). La corriente costera es más intensa de abril a septiembre. Wyrski (1965) halló una velocidad promedio de 0,2 a 0,3 nudos a lo largo de la costa y hasta 0,5 a 0,7 nudos a 6° S, donde cambia de dirección hacia el oeste.

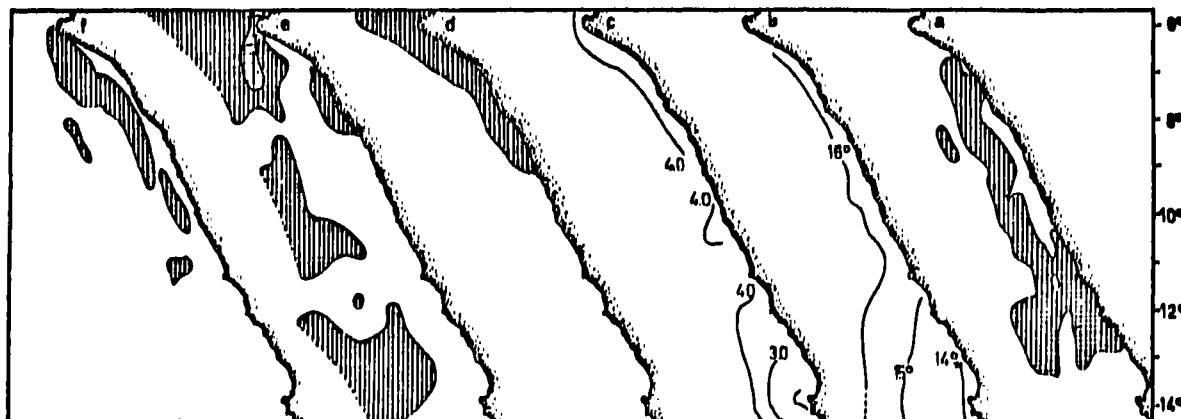


Fig.3. DISTRIBUCION HORIZONTAL DE: a) Huevos de anchoveta, b) Temperatura Om. (°C), c) Oxígeno Om. (ml./L), d) Transparencia, e) Zooplancton, f) Larvas de anchoveta en Setiembre de 1966.

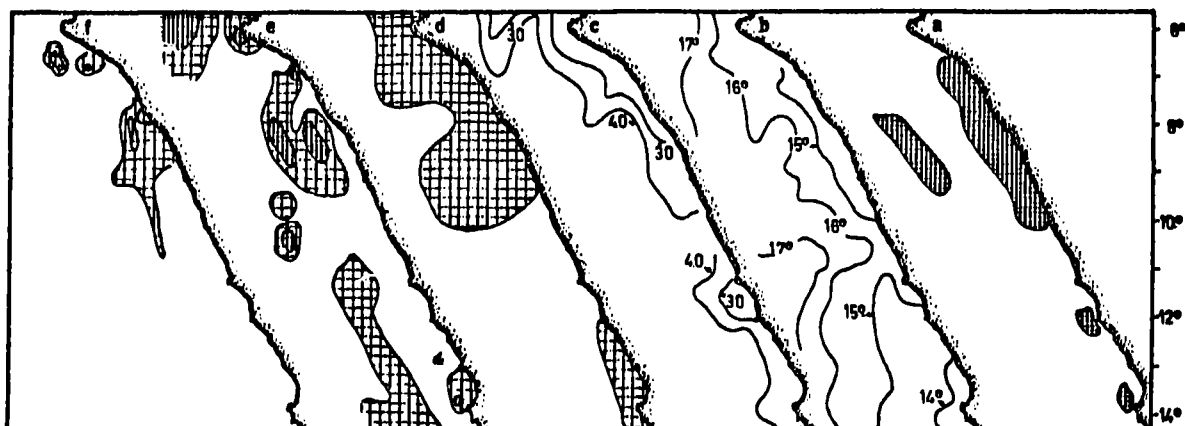


Fig.4. DISTRIBUCION HORIZONTAL DE: a) Huevos de anchoveta, b) Temperatura Om. (°C), c) Oxígeno Om. (ml./L), d) Transparencia, e) Zooplancton, f) Larvas de anchoveta en Setiembre de 1967

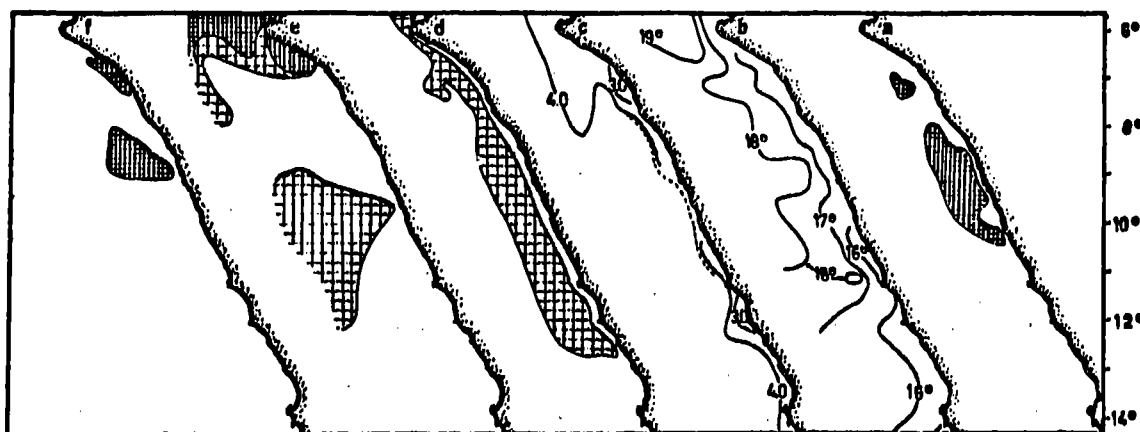


Fig.5 DISTRIBUCION HORIZONTAL DE: a) Huevos de anchoveta, b) Temperatura Om. (°C), c) Oxígeno Om. (ml. L), d) Transparencia, e) Zooplancton, f) Larvas de anchoveta en Setiembre de 1968.

FLUCTUACIONES DEL DESOVE DE 1965 A 1979

El desove de anchoveta ha tenido grandes fluctuaciones en el período 1965-1979. Para analizar estas variaciones consideramos el área de 6° a 14° S, por ser la principal área de desove (Figura 6).

Analizando el desove ocurrido en el mes de septiembre, período de mayor producción en el ciclo de desove, se observa que en los años 1966 y 1967 se obtuvieron los valores máximos, las distribuciones fueron las de mayor amplitud detectadas en todo el período estudiado y las de máxima densidad en áreas extensas.

En este período no se produjeron cambios oceanográficos drásticos en el ambiente, solamente fueron observadas en 1966, al norte de 5° S y hasta 120 mi de la costa, aguas ecuatoriales superficiales. Fuera de la costa se destacaron aguas subtropicales superficiales en verano las que se acercaron a la costa en otoño, invierno y primavera.

El afloramiento estuvo presente durante todo el año en el área sur de Pisco y secundariamente en las otras áreas. El acercamiento de las aguas subtropicales superficiales limitó la extensión de las mayores concentraciones de larvas a las áreas de desove (Figura 3).

El año 1967 fue más frío en general que 1966, con presencia de aguas de origen ecuatorial en verano y otoño al norte de Punta Falsa e influencia de aguas subtropicales superficiales durante todo el año, con diferentes intensidades en diferentes áreas de la costa, principalmente en primavera hacia la zona central. Los afloramientos costeros se desarrollaron durante casi todo el año, en las cuatro principales áreas, extendiéndose notablemente en invierno. La interacción de las aguas subtropicales superficiales y las de afloramiento permitió un desove bastante extenso entre Pimentel y Huarmey. La producción larval observada provino solamente del desove más costero, sugiriendo que la procedente del desove más distante de la costa no fue exitoso (Figura 4).

A partir de 1968 la abundancia del desove ha ido disminuyendo, en este año y en 1969, hasta alrededor de un cuarto del máximo que se produjo en 1967. Durante 1968, año ligeramente más caliente que 1967, se observaron aguas ecuatoriales superficiales al norte de Punta Aguja (6° S) hasta invierno, desapareciendo posteriormente y las aguas subtropicales superficiales se acercaron a la costa, principalmente al norte, entre Huarmey y Supe y al sur, en Pisco. Afloramientos moderados se presentaron en las áreas principales.

El año 1969 fue un año caliente, ocurriendo el calentamiento más notable entre los meses de abril y mayo, (período de desarrollo gonadal, previo al desove) que afectó las áreas costeras al norte de 10° S.

Los desoves llegaron a sus valores mínimos en 1971 y 1972. En 1973 y 1974 se nota un incremento en el desove, siendo el de septiembre de 1974 similar al de 1969.

Hasta 1971 el máximo del ciclo de desove se producía en septiembre, en la principal área de desove. Pero a partir de 1972, se produjeron diversos cambios en el comportamiento del stock desovante a consecuencia del fenómeno "El Niño". Este, se manifiesta como una lengua de agua superficial de elevadas temperaturas y salinidades bajas ($< 34,8$ por ciento), con desplazamientos rápidos sobre una termoclina fuertemente desarrollada, pegándose muchas veces a la costa y anulando o reduciendo notablemente el afloramiento en su avance hacia el sur. El borde de dicha lengua viene a estar constituido por el frente ecuatorial.

Estas condiciones anormales pueden surgir principalmente por desplazamientos pronunciados de aguas subtropicales hacia la costa y por el desplazamiento hacia el sur de los 6° S, de aguas tropicales superficiales y aguas ecuatoriales superficiales. El primer caso es más frecuente y de menor efecto.

Dos de los hechos constatados en 1972 fueron el desplazamiento del stock desovante hacia el sur y el acercamiento hacia la costa distribuyéndose dentro de las 20 mi.

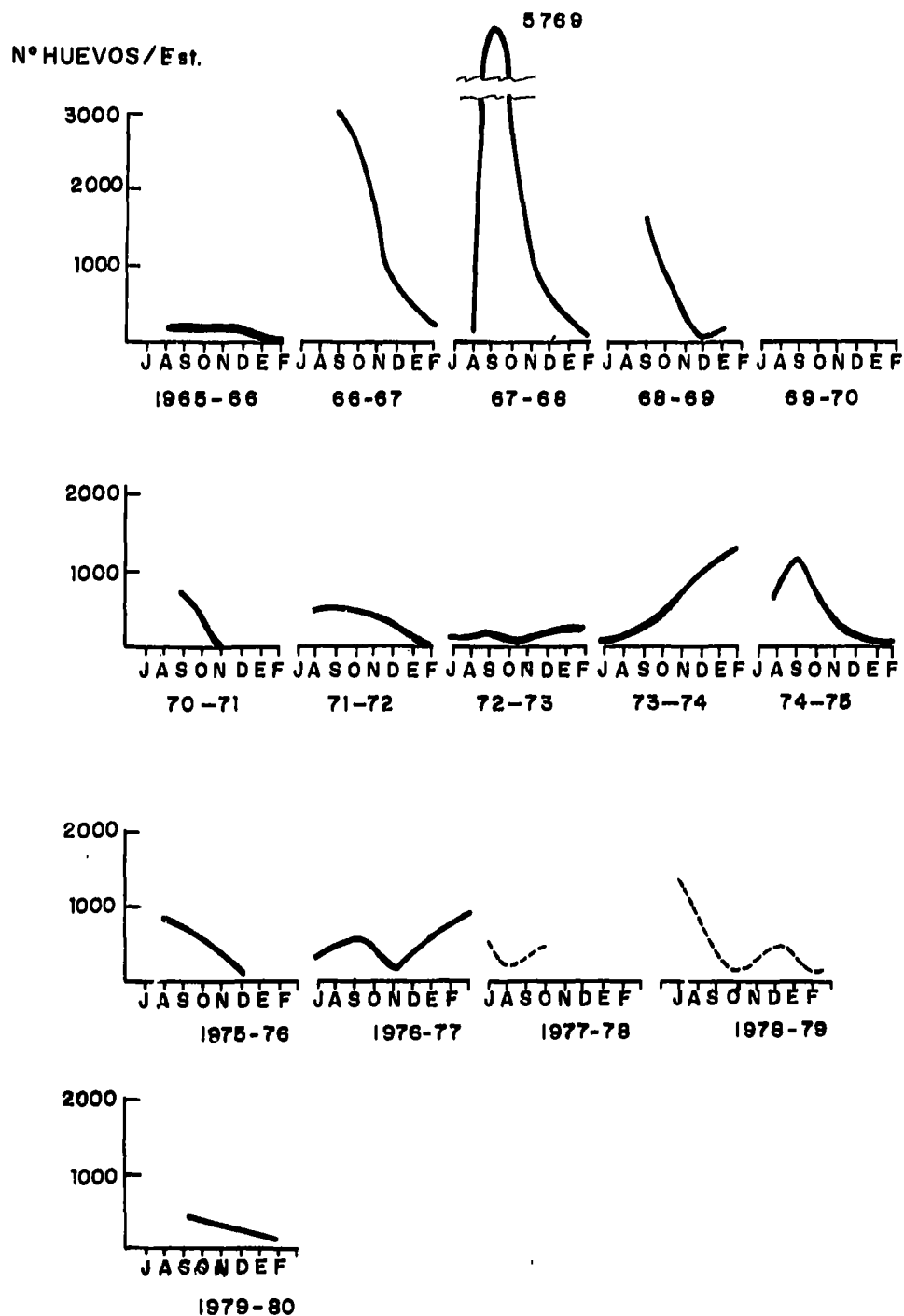


Figura 6. Valor promedio de huevos de anchoveta
en el área de 6° a 14° L.S. de 1965-1980

Estos dos hechos fueron comprobados por el desove que se produjo en las áreas central, principalmente, y sur, lo que regularmente se realiza en el centro y norte (Figura 7). En los meses que se observaron estas concentraciones de anchoveta de alta densidad en áreas reducidas los desoves fueron muy pobres.

Otro de los cambios observados en el comportamiento del desove es el referente al cambio del pico en el patrón del ciclo de desove (Figura 6). Durante el ciclo 1972-73, el modo estuvo en la estación de verano, lo que comúnmente ocurre a comienzos de primavera. Después de un pobre inicio del desove de julio, agosto, se obtuvo un discreto modo en septiembre para luego incrementar en forma ininterrumpida hasta febrero. Una posible explicación sería, el cambio en el mecanismo fisiológico de la reproducción, alterado por las inapropiadas condiciones para el desove en julio, agosto, septiembre, mejorando ligeramente de acuerdo a lo que ocurría en el ambiente en los meses posteriores.

Aunque esto no es totalmente conocido, se tiene evidencia de la pobre producción de huevos por individuo, pues una alta producción de grasa significaría que fue baja su utilización en la producción de huevos. En años regulares, previamente a la época de desove, los valores de grasa disminuyen, interpretándose, que es usada en la producción de óvulos.

Desde el segundo semestre de 1973, las condiciones ambientales a más de normalizarse, tendieron a enfriarse, dando por resultado un ciclo 1973-74 diferente al patrón regular que se venía produciendo hasta antes de 1972. En este ciclo el pico fue detectado en el mes de febrero de 1974 (verano), después de un incremento continuado, observado a partir de junio (invierno), agosto, septiembre y noviembre de 1973. Este segundo ciclo con alteración del pico hacia verano, podría haberse originado por incremento de desovadores de verano, procedentes del verano de 1973, si la sobrevivencia hubiera sido proporcional al desove.

El ciclo de desove 1974-75 fue observado a partir de agosto de 1974, hasta febrero de 1975, el ápice se detectó en septiembre con un índice semejante al de septiembre de 1969, por lo que se suponía, se retornaba al patrón regular de desove.

En el ciclo 1975-76, el desove se inició antes de agosto, según la tendencia de la curva, la mayor intensidad del desove se detectó en el mes de agosto y no en el de septiembre, como ocurría anteriormente, verificado por la presencia de juveniles de 7 y 7,5 cm, que procedían de desoves de junio, algo que generalmente no ocurre o con una mayor velocidad de crecimiento, como consecuencia de condiciones extremadamente favorables si procedieran de desoves posteriores a junio.

Al término de este ciclo ocurrió un pobrísimo desove en verano 1976, probablemente por el adelanto en el inicio de este ciclo que ha resultado ser el menor de todos los veranos de estos años desde 1972. Durante agosto de 1975, aguas subtropicales superficiales estuvieron próximas a la costa, entre Chicama y Huarmey y las concentraciones de fitoplancton se redujeron a pequeñas áreas muy próximas a la costa (IMARPE, 1976).

El desarrollo del ciclo 1976-77 no siguió el patrón normal de desove. En la primera parte del ciclo correspondiente al desove de invierno y primavera, éste fue menor al ocurrido en 1974 y 1975 y muestra un descenso consecutivo de 1974 a 1976, y solamente superior a la época correspondiente a los años 1972 y 1973. En la segunda parte del ciclo de desove, en verano, se observó la mayor producción del desove del ciclo.

Desde diciembre de 1975 se observaron parches de coloración marrón rojiza en diferentes áreas del litoral peruano, motivado por la presencia masiva del Dinoflagelado Gymnodinium splendens, que se fueron incrementando hasta cubrir extensas áreas, además de una fuerte proliferación de medusas, desde los primeros meses de verano hasta mediados de mayo. Aunque anualmente durante los meses de verano se presentan estos organismos planctónicos, no se tienen registros de las proporciones observadas en 1976.

Aún cuando organismos tales como G. splendens, en concentraciones suficientes constituyen alimento de larvas de peces, el período en que se desarrolló no co-ocurió en el pico del desove de anchoveta o de máxima producción larval de los ciclos 1975-76, 1976-77 (agos.-sept.).

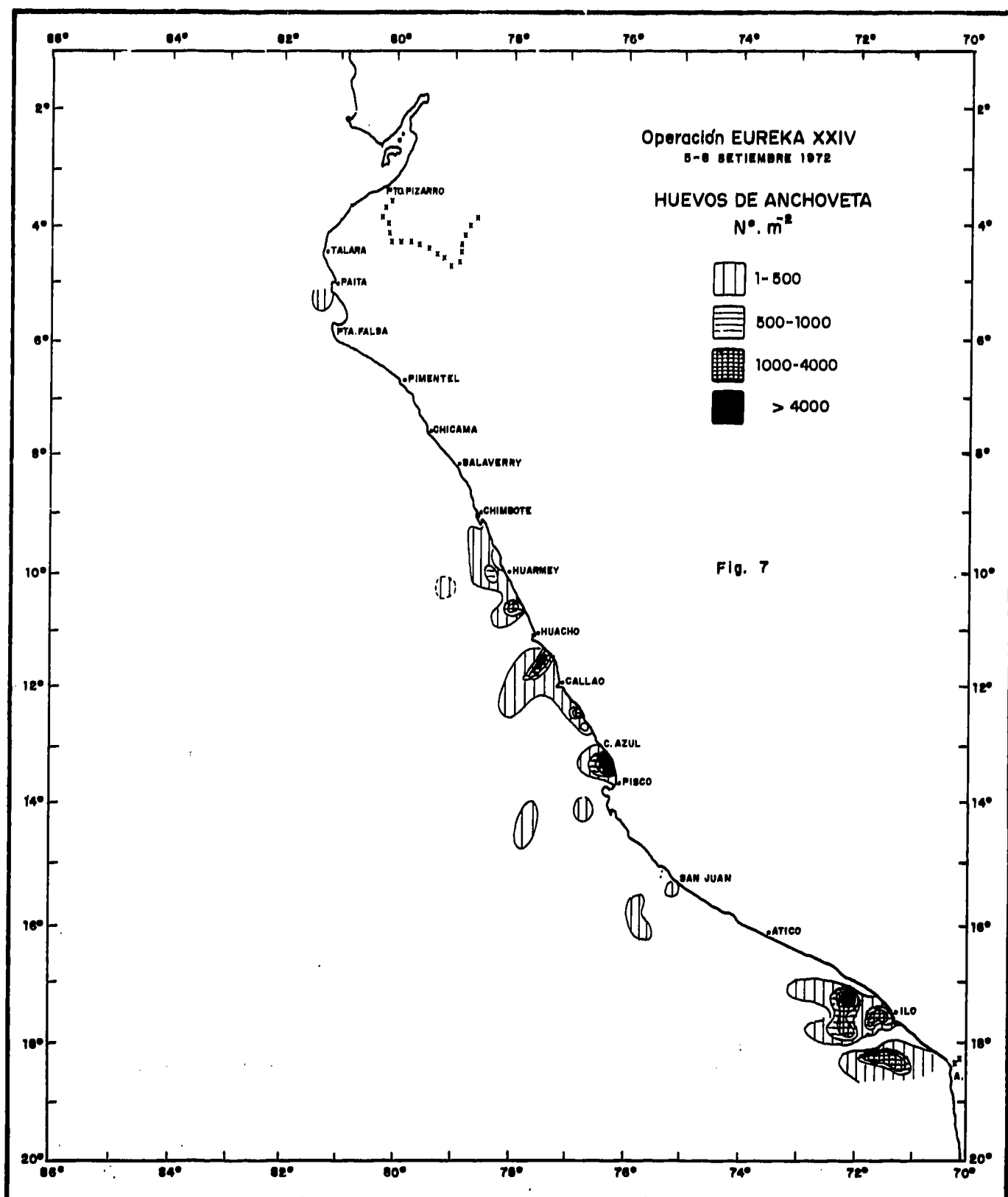


Figura 7. Operación EUREKA XXIV
5-8 septiembre 1972

Se correspondió con el período de desarrollo gonadal del ciclo 1976-77, lo que podría haber conducido a una pobre producción del desove, por la carencia de una mayor diversidad de fitoplancton.

Las variaciones temporales del pico de desove parecen estar en relación con los ciclos de producción. Durante los períodos 1972-73; 1973-74 y 1976-77, cuando las condiciones ambientales se mostraron aunque en diferente forma marcadamente alteradas, se modificó el patrón de desove. de máxima producción en primavera hacia verano.

La modalidad del desove con índices inferiores en primavera en relación a los de verano, no garantiza en general el éxito del desove en cuanto a condiciones de alimentación necesarias para la sobrevivencia de larvas, si se considera que la adaptación fisiológica de la especie responde a la secuencia del ciclo biológico del ambiente, el que parece ser más favorable en primavera. La reacción de reproducción de la anchoveta ante condiciones desfavorables ocurridas durante 1976, fueron los desoves pobres de julio a noviembre y un ligero mejoramiento de las condiciones en verano indujeron a un limitado incremento del desove.

Las condiciones durante el verano en períodos regulares no parecen ser los más convenientes para el éxito de la sobrevivencia de estos aionomorfos a juzgar por el reclutamiento consecuente siendo el precedente del desove de invierno-primavera el más sustancial. Sin embargo, no se conocen los cambios que se producen en los ciclos de producción, cuando ocurren anomalías como en los años 1972, 1973 y 1976, y si se produce una prolongada estación de "verano" por la permanencia de determinadas masas de agua en estos períodos, es probable que las traslaciones de máximos de desoves, o cambios en el patrón, se ajusten mejor a la sobrevivencia larval que, si se produjeran en un momento de mayor desarrollo del fenómeno.

Durante los ciclos posteriores de 1974 a 1980, los desoves han ido decreciendo hasta el último ciclo 1979-80, donde la densidad del desove y la extensión de las áreas son muy reducidas.

INTERRELACIONES DEL DESOVE DE ANCHOVETA CON EL DE SARDINA

En los primeros años estudiados, 1966-1971, las áreas de desove estuvieron ubicadas principalmente en el área norte y secundariamente central para la sardina. Desde Cabo Blanco hasta El Callao y a distancias entre 20 y 40 mi de la costa (Figura 8).

Sucesivamente en los años 1966, 1967 y 1968, los desoves fueron pobres. En 1966 la ausencia de huevos de sardina fue total. En 1969 se observó un ligero incremento del desove con respecto a los años anteriores, en enero y septiembre. Este fue un año caliente catalogado "Niño Pequeño", ocurriendo el calentamiento más notable en los primeros meses del año, afectando las áreas costeras al norte de 10°S y en otoño e invierno, el calentamiento abarcó toda la zona costera. En los años 1970 y 1971, las concentraciones del desove se limitaron a uno o dos puntos en el área norte.

A partir de 1972, cuando se produjeron los cambios ambientales por la ocurrencia del fenómeno "El Niño", se observó un incremento en el número de huevos y larvas, ampliándose su área de distribución a toda la costa. Las condiciones ambientales expresadas principalmente en la penetración de las aguas subtropicales superficiales, favorecieron los desoves, tanto en intensidad como en duración y extensión a lo largo de la costa.

La distribución de huevos de sardina en 1972 (Figura 9), se presentó en una franja ubicada por fuera de las 35 mi de la costa. Fue notorio que la franja costera no ocupada por el desove de la sardina estuvo cubierta por el desove de anchoveta, especialmente en las áreas norte y central.

El éxito de esta clase se relacionó con la prolongada alteración bio-oceanográfica y los cambios distribucionales de la anchoveta que se redujeron a áreas muy pegadas a la costa.

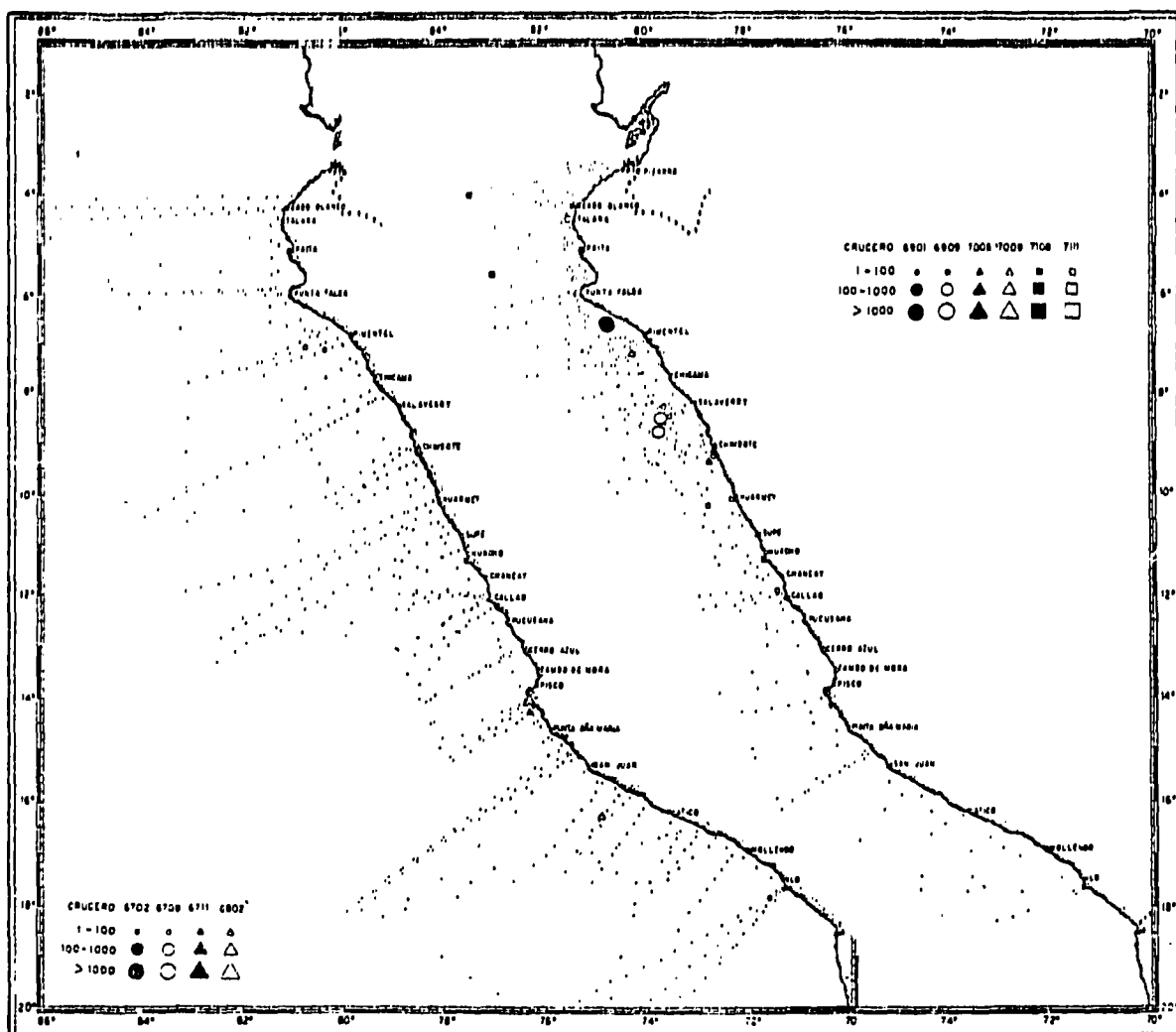


Figura 8. Huevos de sardina

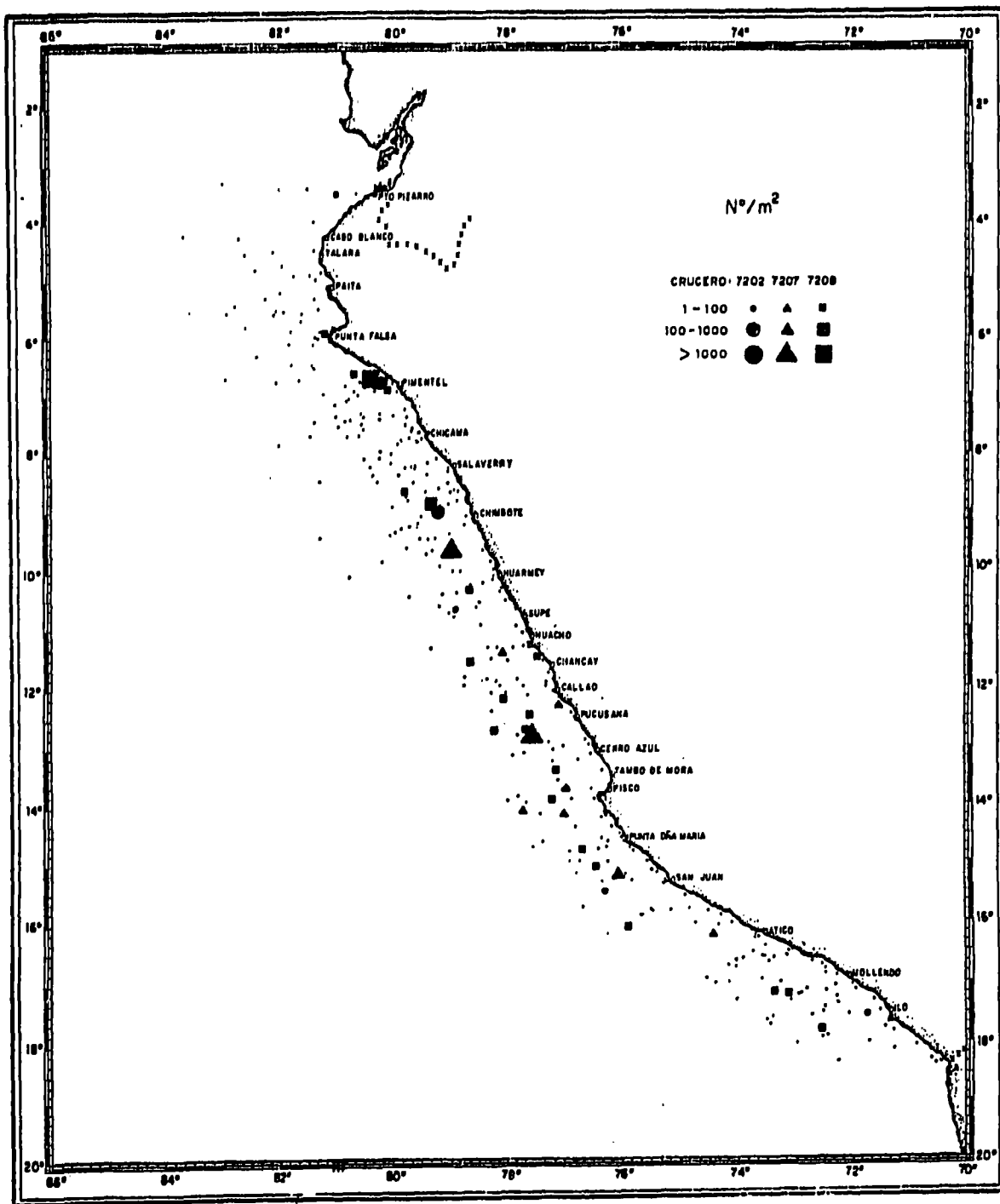


Figura 9. Huevos de sardina

Desde 1973 hasta 1977 los ciclos de desove fluctúan en forma relativamente inversa con los ciclos observados para anchoveta (Figura 10). Así en el ciclo 1973-74 el desove de sardina fue mínimo y aún cuando el desove de anchoveta fue irregular, con máximo en verano, la producción total de desove fue buena. En el ciclo 1974-75, la anchoveta retornó al patrón usual de desove, con máximo en septiembre, cuando se produjo un fuerte desove, resultando en 1975 en un buen reclutamiento. En el caso de la sardina, fue observado al inicio del ciclo, en agosto, un desove regular, superior al de 1972, pero en el resto del período, el desove fue muy pobre. En el año siguiente 1975-76, el desove de anchoveta fue algo inferior al año anterior, y el ciclo de desove de sardina se notó alterado, en cuanto al desarrollo de su máximo en verano y superior al año anterior. El ciclo 1976-77 de gran producción de huevos en septiembre, fue superior a todos los anteriores ciclos, aún cuando las condiciones ambientales fueron diferentes a los ocurridos durante "El Niño" 1972, pero igualmente desfavorables para la anchoveta.

Y en los tres últimos años, 1977, 1978 y 1979, principalmente este último, los índices de desove han incrementado hasta sobrepasar los de anchoveta.

Dos factores juegan papel muy importante en estas fluctuaciones de la sardina, las condiciones oceanográficas y las fluctuaciones poblacionales de la anchoveta. Inicialmente en 1972, afectaron los dos factores en la transgresión de la sardina hacia áreas no habituales para esta especie, posteriormente el decremento de la población de anchoveta en 1976-1979, favorecen aún más la acción de los cambios posiblemente leves de las condiciones ambientales, en los incrementos poblacionales de la sardina.

Hasta 1972 su distribución estuvo relacionada con aguas cálidas. Desde 1973 hasta 1979, los desoves fluctúan en forma relativamente inversa con los observados para anchoveta y solamente en los últimos períodos se viene observando un gradual avance en la ocupación de las áreas de anchoveta (Figura 11) pudiendo significar que una adaptación a estas condiciones está ocurriendo, que implica una real competencia entre estas dos especies.

FLUCTUACIONES DEL ICTIOPLANCTON

Desde 1961 hasta 1964 la anchoveta en sus fases de huevos y larvas, era la especie dominante en el ictioplancton y un 85 por ciento correspondió a los huevos de esta especie, mientras que el 15 por ciento restante estaba constituido por todo el resto de peces. En 1965 este porcentaje descendió a 65 por ciento, en un año de anomalías oceanográficas moderadas. A partir de 1966 y hasta 1974 se observaron cambios en la composición específica. De 1966 a 1971 la proporción de la anchoveta fluctuaba entre 80 por ciento y 90 por ciento y en los años 1972 y 1973, decreció hasta 50 por ciento y 47 por ciento respectivamente. Ocasionado por el decremento en el nivel del stock que ya se venía produciendo desde dos años anteriores por efecto de la pesca y como consecuencia de las alteraciones de las condiciones ambientales, tanto la producción desovadora de la anchoveta como de otros peces se alteró, disminuyendo la de anchoveta y aumentando en el caso de algunos peces, como sardina, caballa y melva principalmente. Desde 1974 a 1980, la proporción ha variado notablemente hasta quedar reducido en septiembre de 1979 al 20 por ciento del total de huevos de peces (Figura 12).

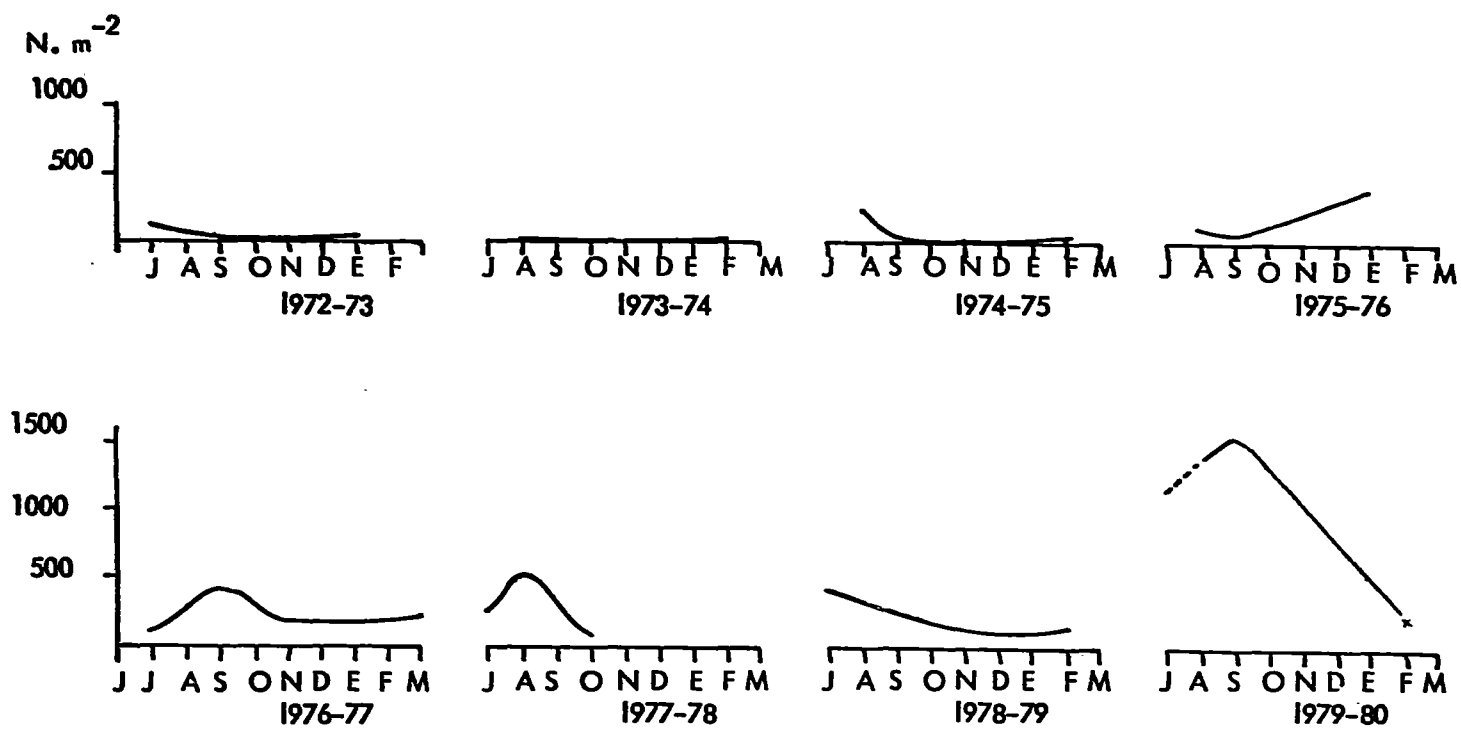


Figura 10. Huevos de sardina en el área de 6° a 14° S

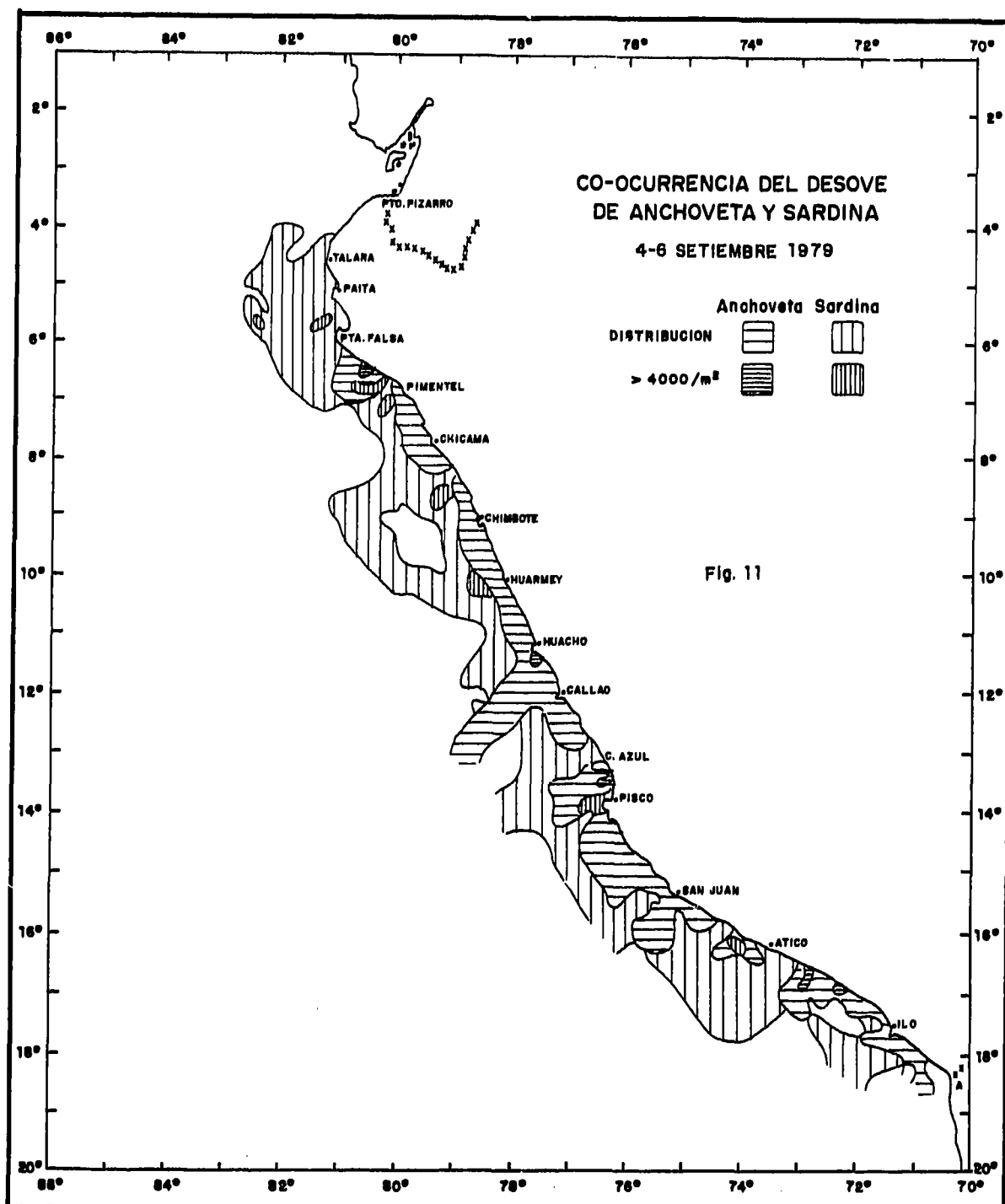


Figura 11. Distribución de desove de anchoveta y sardina
4-6 septiembre 1979

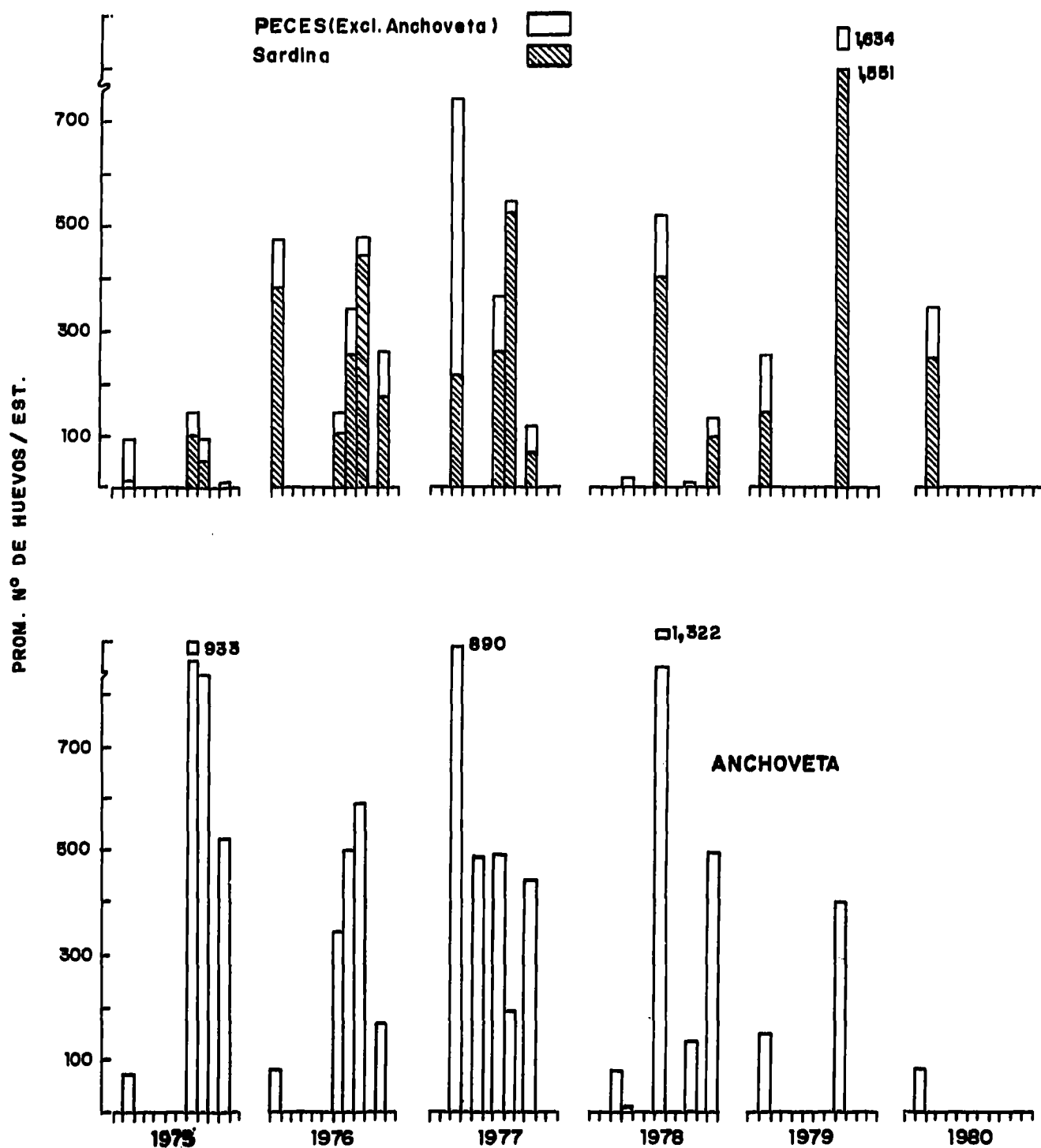


Figura 12. Número promedio de huevos de peces de 1975-1980
 en el área de 6° -14° S

REFERENCIAS

- CALIENES, R. 1973. Diversidad y asociación del fitoplancton en Callao. 1961-1973. Tesis. 84 p.
- GUILLEN, O., B.R. DE MENDIOLA y R.I. DE RONDAN. 1971. Primary productivity and phytoplankton in the coastal Peruvian waters. Fertility of the sea. (J.D. Costlow Jr., ed.) Vol.I:157-185
- _____. 1973. Primary productivity and phytoplankton in the coastal Peruvian waters. Oceanography of the South Pacific. 1972. Comp. R. Fraser. New Zealand National Commission for Unesco, 1973:406-418
- GUILLEN, O.G. 1976. El sistema de la corriente peruana. Parte I: Aspectos físicos. Reunión de trabajo sobre el fenómeno conocido como "El Niño. Guayaquil, Ecuador, 4-12 Diciembre 1974:243-284
- INSTITUTO DEL MAR DEL PERU (IMARPE). 1976. Operación Eureka XXXIII. Ser.Inf.Esp., Nº IM-178
- SANTANDER, H. 1974. Cosecha estable del zooplancton. Ser.Inf.Esp.Nº IM-148
- SANTANDER, H. y O.S. DE CASTILLO. 1973. Estudio sobre las primeras etapas de vida de la anchoveta. Inf.Inst.Mar Perú, Callao, Nº 41:1-30
- STEVENSON, M.R., O. GUILLEN y J. SANTORO DE ICASA. 1970. Marine atlas of the Pacific coastal waters of South America. University of California Press, 23 p.
- WYRTKI, K. 1965. The average annual heat balance of the north Pacific Ocean and its relation to ocean circulation. J.Geophys.Res.70:4547-59
- ZUTA, S. y O. GUILLEN. 1970. Oceanografía de las aguas costeras del Perú. Bol.Inst.Mar Perú, Callao, Vol.2, Nº 5:157-324
- ZUTA, S. y W. URQUIZO. 1972. Temperatura promedio de la superficie del mar frente a la costa peruana. Período 1928-1969. Bol.Inst.Mar Perú, Callao, Vol.2, Nº 8:462-486

ALIMENTO, SOBREVIVENCIA Y TIEMPO DE INACTIVIDAD
DE LAS LARVAS DE ANCHOVETA (*Engraulis ringens* J.)

por

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Food, Survival and Time of Inactivity of
Larval Anchoveta (*Engraulis ringens* J.)

by

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Abstract

The quality and quantity of available food are responsible for the concentration of schools, the development and migratory behaviour of anchoveta, and therefore is one of the principal factors that regulates the fisheries. There is evidence that the abundance of spawned eggs and subsequent recruitment are not directly related. Hjorth (1916, 1926) suggested that there were two major sources of larval fish mortality (1) an insufficient availability of food for the larvae, and (2) eggs and larvae could be transported by currents away from suitable areas favourable to their survival, resulting in high mortalities.

The distributions, qualities and quantities of food for larval anchovies need to be studied, and the first stages of study are the identification of anchoveta larva food and feeding behaviour. This began with studies in 1953 and continues today.

Experimental studies of larval anchoveta development and feeding were begun in 1977 under the direction and collaboration of Reuben Lasker and Dan Ware. The studies described herein relate information on first feeding, survival and activity of larval anchoveta.

Unlike (*E. mordax*), anchoveta larvae were not observed to have food in their gut 8 h after hatching. Their mouths do not fully develop until much later, and at 40 h, when their eyes were fully pigmented, they were observed to have fed to fullness on *Gyrodinium aureolum*. Others fed only natural plankton were not successful in feeding. The reasons which apparently account for this difference in feeding were that (1) appropriate food particles were not available in high enough concentrations to stimulate feeding, and (2) anchoveta larvae appear to prefer food organisms which are mobile and do not form aggregates.

Survival studies yielded poor results in that larvae fed at progressive intervals often did not survive as long as those not fed at all. This indicates that there is a cost associated with initial feeding, and that high food densities are required for long periods for the larvae to survive beyond this initial period of low feeding efficiency, and loss of condition. Half of the larvae survived up to 5 days and 80 percent had died by the eighth day.

These observations were also related to the activity changes in unfed larvae. Swimming activity increased from about 5 to 65 percent of the time from the ages of 2 to 6 days after hatching. From Day 7 onward, the activity decreased to initial levels again. Fed larvae had a similar pattern, but activity decreased to only 50 percent on Day 6 in comparison to the unfed larvae. Larval anchoveta clearly decrease their energy expenditure, and the survival rate changes in response. In some cases the proportional survival increased from Day 6 to Day 8 after hatching, suggesting that there is an inherent mechanism relating activity level and mortality, given poor food abundance. The egg yolk was no longer evident by Day 3 of the experiments. If feeding was not initiated on Day 3, then they were unlikely to survive, although their resistance time appears to be about one day more than *E. mordax*. If they are to survive larval anchoveta must begin feeding by 4 1/2 days after hatching.

Of the food particles offered in the experiments only the nude dinoflagellate, *G. aureolum* was of appropriate quality and quantity to stimulate feeding behaviour. In late 1975 and early 1976 a bloom of *Gymnodinium splendens* was observed off Peru. This corresponded with a dramatic increase in survival of the anchoveta larvae spawned in that period and a subsequent large recruitment of the juvenile population.

INTRODUCCION

La calidad y cantidad de alimento disponible, por su efecto en la concentración de cardúmenes, desarrollo y comportamiento migratorio, es uno de los principales factores que regulan las pesquerías.

Existen evidencias de una falta de correlación entre el número de huevos desovados y la magnitud del nuevo reclutamiento, lo que hace suponer que la mayor mortalidad se presenta durante la fase larval; Hjort (1916-1926) sugiere que la sobrevivencia de los estadios larvales puede ser afectada en dos formas: 1) por la falta de alimento al tiempo que la larva empieza a alimentarse; y 2) por las corrientes que pudieran transportar las larvas a áreas desfavorables para su posterior desarrollo, resultando en una alta mortalidad.

Hunter (1972) menciona que manchas de alimento en pequeña escala y la habilidad de las larvas para localizarlo y permanecer en la mancha, es crucial para la sobrevivencia de las larvas; Lasker (1979) menciona que aunque la idea de "Threshold-for-feeding" ha sido probada sólo para la anchoveta *Engraulis mordax*, esta idea se puede aplicar a otros peces en los que también puede determinarse que existe una mínima concentración de alimento que las larvas necesitan para iniciar su alimentación.

La anchoveta *E. ringens* es una de las principales especies de importancia económica para nuestro país y si el éxito de su pesquería depende de la sobrevivencia de las larvas y esta sobrevivencia es a su vez dependiente, principalmente de la disponibilidad de las partículas que le sirve de alimento (en tamaños, calidad y cantidad), el estudio de lo que constituye su alimento y hábitos alimentarios en la etapa larval es de gran importancia, porque permitiría explicar, si el colapso de la pesquería de esta especie se debió sólo a una sobre-pesca o fue debido a cambios en el ambiente que determinaron: una falla en la disponibilidad de las partículas que le sirven de alimento o una falla en tiempo y espacio de la coincidencia del tamaño de las larvas con el tipo de partículas disponibles como alimento.

Estudios sobre alimentación y hábitos alimenticios de adultos y juveniles de anchoveta *E. ringens* han sido realizados por R. Rojas (1953); F. De Buen (1958); Rojas de Mendiola (1966, 1969, 1971, 1973, 1978); pero con respecto a las larvas de *E. ringens* son pocos los trabajos que existen: Rojas de Mendiola (1974), Ware, Mendiola, Newhouse (1978), B. Mendiola y O. Gómez (1979).

Debido a la importancia que tiene el establecer los factores que controlan la sobrevivencia de las larvas, se realizaron por primera vez en el Perú, en 1977, estudios sobre la alimentación de larvas de anchoveta *E. ringens* criadas en el laboratorio.

El primer experimento sobre primera alimentación de larvas *E. ringens* se realizó entre el 5-9 de noviembre 1977 a bordo del CSS BAFFIN, este experimento se realizó, bajo la dirección y en colaboración con el Dr. R. Lasker (National Marine Fisheries Service, SWFC, La Jolla, Calif.).

Estudios experimentales sobre la tasa de desarrollo de los huevos de anchoveta y subsecuentes cambios en la morfología de la prolarva y postlarva en relación con el tamaño de las partículas que se le ofreció como alimento, así como sobrevivencia de las larvas, se realizaron en los acuarios especialmente contruidos en la Bahía de Samanco (9° LS), entre el 8 y 25 de noviembre de 1977 y bajo la dirección y en colaboración con el Dr. Dan Ware (Bedford Institute, Canada). Los resultados de este experimento han sido publicados (Ware, Mendiola, Newhouse, 1979).

El presente trabajo ofrece los resultados del experimento llevado a cabo en el CSS BAFFIN (5-9 noviembre 1977) y del experimento corrido en los acuarios del Laboratorio Central del IMARPE del 28 de agosto al 6 de setiembre de 1978, este último bajo la dirección y en colaboración con el Dr. Ware; el objetivo principal de este experimento fue confirmar los resultados obtenidos en Samanco y estuvieron referidos principalmente: a la primera alimentación de las larvas de anchoveta, sobrevivencia y actividad de las mismas.

MATERIAL Y METODOS

Durante la Leg. I del Crucero 7711 a bordo del CSS BAFFIN se hicieron colecciones de huevos de anchoveta en el área de Chimbote utilizando la red Neuston. Este material sirvió para realizar los experimentos sobre alimentación de larvas en la Leg. II (5 al 9 de noviembre de 1977).

Los huevos fueron separados de acuerdo a la fase de desarrollo en que se encontraban y colocados en recipientes con agua de mar.

El experimento se inició con la separación de las larvas con saco vitelino, las que en número de 100 fueron depositados cuidadosamente en cinco recipientes de experimentación de 8 litros de capacidad y que contenía agua de mar filtrada.

Los recipientes fueron cubiertos exteriormente con un plástico negro con el fin de que la luz penetrara por la parte superior y facilitara la observación de las larvas. Se les proporcionó aire superficialmente y la temperatura se mantuvo a 20°C.

El material de larvas fue observado en forma frecuente; después de tres días se observó que el saco vitelino se había reabsorbido completamente y que los ojos estaban pigmentados, lo que de acuerdo a experiencias realizadas con *E. mordax* significaba que estaban listas para ingerir su primer alimento (Lasker, 1975).

A las larvas de cuatro de los recipientes se les proporcionó alimento constituido de plancton natural, y a las larvas del quinto recipiente se les proporcionó alimento constituido por un cultivo puro de *Gyrodinium aureolum*, cuyo diámetro varía entre 14 y 20 micras, este recipiente serviría de control.

Para el examen del contenido intestinal de las larvas, éstas fueron separadas siguiendo la técnica descrita por Lasker *et al.* (1970).

Para el recuento de las partículas ofrecidas como alimento a las larvas, se utilizó el Coulter Counter Model TA II.

En los acuarios del Laboratorio Central del IMARPE entre el 28 de agosto y el 6 de setiembre de 1978, se efectuaron experimentos sobre alimentación, sobrevivencia y actividad de las larvas de anchoveta *E. ringens*. Para estos experimentos se utilizaron 10 recipientes conteniendo cada uno 10 litros de agua de mar filtrada y aireada, 100 huevos de anchoveta en la misma fase de desarrollo fueron depositados cuidadosamente en cada recipiente y la temperatura se mantuvo a 16°C.

Los recipientes se dividieron en cinco grupos por duplicado: las larvas de cuatro grupos recibirían alimento y un grupo se mantendría en estarcación, sirviendo éste de control.

Después de las 72 horas de la eclosión cuando las larvas habían completado la reabsorción de su saco vitelino y presentaban los ojos completamente pigmentados se les proporcionó en forma escalonada el alimento consistente de plancton natural.

Al primer grupo se le proporcionó alimento inmediatamente después de la reabsorción del saco vitelino, al segundo, tercero y cuarto grupo se les proporcionó el alimento uno, dos y tres días después de la reabsorción del saco vitelino respectivamente, al quinto grupo no se les proporcionó alimento.

De acuerdo a las experiencias obtenidas en Samanco, se decidió proporcionar a las larvas como primer alimento, plancton natural cuyo diámetro de partícula estuviera entre las 40 y 80 micras y en una concentración de 200 partículas por mililitro.

Con este fin el plancton natural colectado con red se pasó a través de una serie de tamices; 153 u, 102 u, 80 u y 40 u.

El tamaño de la partícula fue referida al diámetro de una célula simple (*Actinocyclus*, *Coscinodiscus*, dinoflagelados y huevos de invertebrados) o la longitud de la cadena (*Chaetoceros* y *Skeletonema* etc.) durante el conteo cada cadena fue considerada como una partícula.

Con el fin de identificar la calidad del plancton que se les estaba proporcionando como alimento así como la proporción en que diferentes especies se encontraban presentes, cada mañana se realizaron análisis cualitativos y cuantitativos del plancton en forma diaria, utilizando un microscopio compuesto y una cámara de recuento de 1 mililitro.

La concentración del alimento se mantuvo en 200 partículas por mililitro, agregando diariamente una fracción compensatoria, ya que el número de partículas, aún cuando no eran ingeridas, disminuía debido a que muchas de las especies presentes en el alimento que se les proporcionaba sedimentaban rápidamente.

El plancton sedimentado así como los huevos, las cáscaras y las larvas muertas se separaron utilizando una pipeta. Para preparar el gráfico de sobrevivencia, se consideró de cada recipiente sólo el número de larvas que eclosionaron y desarrollaron con éxito hasta la reabsorción del saco vitelino.

Para observar la actividad de las larvas se utilizaron 6 beakers de 1 litro de capacidad en los que se colocaron 25 huevos de anchoveta. El alimento fue proporcionado a las larvas de 3 beakers apenas terminó la reabsorción del saco vitelino; las larvas de los 3 beakers restantes se mantuvo en estarción. El alimento consistió de plancton natural, en una concentración de 50 partículas por mililitro.

Para las observaciones del tiempo de actividad se utilizó el material de larvas de todos los beakers, estas observaciones se realizaron dos veces por día, a las 10.00 y 14.00 horas.

RESULTADOS

Experimentos a bordo del CSS BAFFIN

Lasker (1975) menciona que las larvas de *E. mordax* presentan el intestino lleno después de las 8 horas de proporcionado el alimento; de acuerdo a estos resultados, a las 8 horas se separaron 5 larvas de *E. ringens* de cada recipiente y se observó bajo un microscopio el grado de llenura del intestino: el resultado fue negativo, los intestinos se encontraban vacíos, un examen más detenido de toda la larva utilizando mayores aumentos mostró que las larvas todavía no presentaban la boca abierta. Suponiendo que ésta era una de las razones por las cuales no habían ingerido ningún tipo de alimento, se continuaron con las observaciones, ya en forma más frecuente y es así como a las 40 horas de la completa reabsorción del saco vitelino, se observó que el intestino de las larvas criadas en el recipiente de control presentaban el intestino lleno de *G. fillum*.

Las larvas de los otros recipientes alimentados con plancton natural a pesar de presentar el mismo desarrollo morfológico no ingirieron ninguna de las partículas que formaban parte del plancton natural que se les ofreció como alimento, ni presentaban signos de que hubieran contenido alimento antes de la observación.

El plancton natural estuvo constituido principalmente por diatomeas que forman cadenas como: *Sk. costatum*, *Ch. socialis* y *Sh. delicatula*.

Los resultados del recuento de partículas del alimento ofrecido mostraron que éste se encontraba en una concentración de 80 partículas por mililitro en el recipiente de control y mayor de 200 partículas por mililitro en los recipientes con plancton natural. Los resultados de este experimento muestran: a) que las larvas de anchoveta comienzan a alimentarse 40 horas después de desaparecido el saco vitelino cuando los ojos están completamente pigmentados y la boca abierta; b) que la mínima concentración de alimento que la larva necesita para iniciar su primera alimentación es alrededor de 80 partículas por mililitro, cuando el

tamaño de la partícula varía entre 14 y 20 micras; c) las larvas no ingieren especies fitoplanctónicas que forman cadenas; d) que las partículas que le podrían servir de alimento no estuvieron presentes o no se presentaron en la concentración adecuada; e) que las larvas de *E. ringens* ingieren partículas con cierto movimiento como el dinoflagelado *Gyrodinium aureolum*, presente en el recipiente de control.

El resultado sobre el tiempo en que la larva inicia su primera alimentación, fue confirmado durante los experimentos llevados a cabo en Samanco por Ware, Mendiola y Newhouse (1979).

Acuario de IMARPE, Callao - agosto 1978

El objetivo de estos experimentos fue determinar el número mínimo de partículas, medida y calidad de la partícula que las larvas de *E. ringens* necesitan para iniciar su primera alimentación. Simultáneamente se hicieron observaciones sobre tiempo de inactividad de las larvas así como de sobrevivencia.

Primera alimentación

La observación diaria del intestino de las larvas con el fin de conocer si ellas se habían alimentado o no, mostró que estos se encontraban vacíos y sin signos de haber ingerido alimento previamente a la observación.

Los resultados del análisis cualitativo y cuantitativo del plancton natural ofrecido como alimento a las larvas y que se presentan resumidos en el cuadro 1, muestran que del total de 200 partículas por mililitro, sólo de 2 a 7 partículas por mililitro correspondió a: *Actinocyclus* sp.; de 2 a 8 partículas por mililitro a dinoflagelados, de 0,5 a 1 partícula por mililitro a nauplius de copépodos, de 0,5 a 5,5 partículas por mililitro a huevos de invertebrados y que alrededor del 85% del alimento estuvo constituido por diatomeas que forman cadenas en espiral como *Ch. debilis*, *Ch. curvicaetus*; forman estrellas como *Thalassionema nitzschiioides* o largas cadenas como *Leptocylindrus danicus* y *Sk. costatum*.

Estos resultados muestran que las especies que consideramos indispensables para que las larvas inicien su primera alimentación no estuvieron en la concentración mínima necesaria, a pesar que el alimento en número total de partícula fue suficiente, y que las larvas de anchoveta no se alimentan de especies que forman cadenas.

Estas evidencias nos llevan a enfatizar la importancia de la calidad y la concentración apropiada de las partículas que le sirven como alimento.

Sobrevivencia

En el gráfico N°1 se presentan las curvas de porcentaje de sobrevivencia de las larvas en cada uno de los recipientes y ellas muestran que a pesar de haberseles proporcionado el alimento en diferentes tiempos, todas las curvas presentan una tendencia similar incluyendo la curva del recipiente de control, alrededor del 50% de las larvas sobreviven hasta los cinco días y la mayor mortalidad (80%) se presenta al octavo día después de la eclosión.

En los experimentos realizados en Samanco, se encontró que la tasa de mortalidad, computada como la proporción del número inicial de individuos versus aquellos que mueren por día, fue más baja cuando las larvas fueron más grandes, independientemente de la concentración de alimento, ya sea fito o zooplankton.

Tiempo de inactividad

El gráfico No. 2 muestra los resultados obtenidos de la actividad motora de ambos grupos de larvas, con y sin alimento y se observa que las larvas aumentan su actividad progresivamente hasta el sexto día cuando muestra su máxima actividad para luego disminuir hasta los niveles de los primeros días indicando un estado de debilitamiento que termina con su muerte.

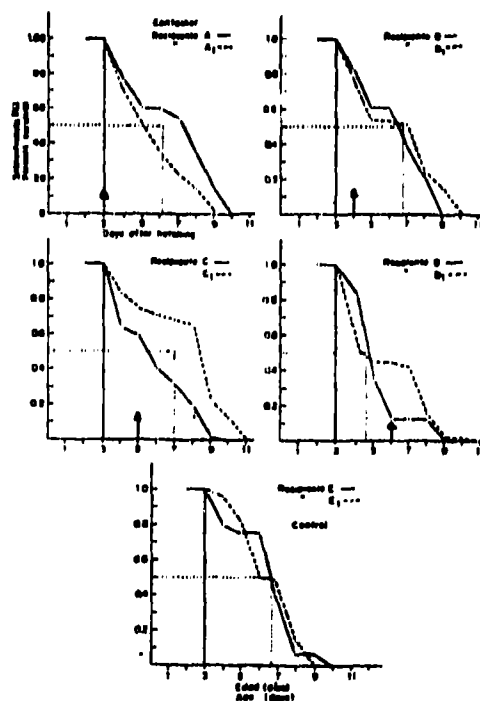
Cuadro 1

RELACION DE LAS PARTICULAS MAS ABUNDANTES EN PORCENTAJE, EN LA DIETA DE LARVAS DE ANCHOVETA

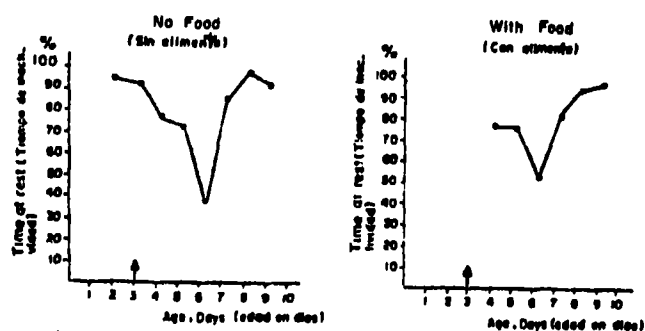
Table 1

ITEMS MORE ABUNDANT (%) IN THE FOOD OF ANCHOVY LARVAE, CALLAO

	29.8.79		30.8.79		31.8.79		1.9.79		2.9.79		3.9.79		4.9.79	
	%	Nº	%	Nº	%	Nº	%	Nº	%	Nº	%	Nº	%	Nº
<i>Thalassionema nitzschioides</i>	20		29		30		22		15		8		24	
<i>Chaetoceros debilis</i>	15													
<i>Chaetoceros</i> sp.	13		25		22		22		27		35			
<i>Ch. curvisetus</i>	7										25		10	
<i>Leptocylindrus danicus</i>			21		14		13		13				18	
<i>Skeletonema costatum</i>	8		11		8		3		4		1		4	
<i>Actinocyclus</i> sp.	4	7	3	3	2	3	0,2	2	7	4	5	4	2	2
<i>Thalassiosira</i>	1	2	1	1	2	3	3	3	5	3	0,2	0,2	0,5	0,5
Dinoflagelados. Otros	4	8	2	1	2	3	9	8	11	7	0,4	0,3	2	2
<i>Gymnodinium splendens</i>									0,3	0,2			0,2	0,2
<i>Diplopsalis lenticula</i>	0,2	0,3			0,7	1	1	1	3	2			0,3	0,3
Nauplios	0,5	1	0,5	0,5	0,4	0,5	0,6	0,5	1,6	1				
H. Invertebrados			0,5	0,5	0,7	1	2	1,5	1,6	1			5,2	5,5
Otros	27,1		7		18,2		24,2		11,5		25,4		33,8	
Total %	100		100		100		100		100		100		100	



Gr. 1 Percent survival of larvae fed at progressively later intervals in 10L experimental containers at 16°C. Vertical line at 3 days indicates approximate time of yolk absorption. Vertical arrow in each group is positioned at time food was added. Sobrevivencia de larvas en porcentaje. Línea vertical indica el tiempo de absorción del Yolk y la flecha el día en que alimento fue proporcionado. Temperature 16°C



Gr. 2 Tiempo de inactividad de las larvas en relación con la edad. La flecha indica la finalización del estadio prelarval. Time at rest of larvae, with age. Arrows indicate end of the prelarval stage

Estos mismos resultados fueron encontrados en los experimentos realizados en Samanco (Ware, *et al.*, 1979).

DISCUSION

Nuestros resultados sobre primera alimentación de las larvas de anchoveta *Engraulis ringens* J. muestran que éstas empiezan a alimentarse a los 4,5 días después de la eclosión, coincidiendo con lo hallado por Ware *et al.* (1979), quienes mencionan que la edad promedio de la larva para iniciar su primera alimentación es de 4,4 días después de la eclosión.

Con excepción de las larvas alimentadas con *Gyrodinium fillum* todas las larvas examinadas presentaron el intestino vacío. Este hecho estaría más relacionado con la calidad de las partículas ofrecidas como alimento que con la concentración de las mismas, ya que la concentración del plancton natural ofrecido como alimento en todos los experimentos siempre fue mayor de 100 partículas por mililitro.

El análisis cualitativo del plancton natural mostró predominancia de especies como: *Skeletonema costatum*, *Chaetoceros socialis*, *Leptocylindrus donicus* y *Thalassionema nitzschioides* que son especies de diámetro pequeño pero que forman cadenas, siendo éste posiblemente uno de los motivos por el cual no fueron ingeridos por las larvas.

Lasker (1975) menciona que las larvas de la anchoveta *Engraulis mordax* no se alimentan de *Chaetoceros* sp. o *Thalassiosira* sp. por ser diatomeas espinosas o que forman cadenas; por otro lado Lasker (1978), Arthur (1976) y Berner (1959) coinciden en que la anchoveta *E. mordax* necesita de un tamaño especial de partícula para iniciar su primera alimentación y que las pequeñas diatomeas sean en cadenas o en células simples, sin tomar en cuenta las concentraciones, usualmente no son lo suficientemente grandes para ser vistas o son ignoradas por las larvas por otras razones durante su primera alimentación.

En los experimentos realizados abordo del CSS BAFFIN, se encontró que las larvas de *E. ringens* se alimentaron de *G. fillum*, un dinoflagelado desnudo cuyo diámetro fluctúa entre 15 y 25 micras y que las larvas empezaron a ingerirlas cuando éstos se encontraban en una concentración de 80 partículas por mililitro, Lasker (1975, 1978), Bright (1978) mencionan que la anchoveta *E. mordax* requiere para su primera alimentación organismos cuyo diámetro varíe entre 30 y 50 micras y se encuentran en densidades que varíen entre 30 y 40 partículas por mililitro.

En el experimento realizado en los acuarios del IMARPE se utilizó como alimento el plancton natural, cuyo tamaño de partícula estuvo entre 40 y 80 micras y la concentración se mantuvo en 200 partículas por mililitro; sin embargo en ningún momento se observó alimento en el intestino de las larvas examinadas, debido posiblemente a que las concentraciones de lo que podría constituir su alimento como *Gymnodinium splendens* o *Aotinoocylus* se presentaron en concentraciones muy bajas no mayores de 4 partículas por mililitro. El 85% del total de las partículas correspondió a diatomeas que forman cadenas o son espinosas y ya hemos mencionado que las larvas de anchoveta no ingieren este tipo de partícula.

La presencia de nauplius y huevos de invertebrados en concentraciones de 1 y 2 partículas por mililitro, respectivamente, no motivó a las larvas a que iniciaran su primera alimentación lo que podría hacer suponer coincidiendo con lo expresado por Ware *et al.* (1979) que algunos fitoplanctones son especialmente necesarios en su primera alimentación sirviéndoles de sostenimiento primario y como fase de aprendizaje en su comportamiento antes de preñar sobre organismos del zooplancton útiles para continuar su crecimiento y desarrollo. Esta suposición no estaría apartada de lo hallado por Mendiola (1974) quien trabajando con material de larvas colectadas en cruceros realizados en la costa peruana encontró que las larvas mayores de 4 mm presentaban en el contenido intestinal predominancia de huevos de copépodos e invertebrados así como nauplius de copépodos, observándose todavía en el intestino la presencia de especies fitoplanctónicas así como diatomeas (redondas) y dinoflagelados. A medida que las larvas aumentan en longitud aumenta la predominancia de zooplancton en el contenido intestinal y es exclusivamente zooplanctófagas cuando las larvas llegan a los 9 mm de longitud total, Mendiola (1974).

Lasker ha demostrado en sus experimentos (1975) que el *Gymnodinium splendens* es un fitoplanctonte capaz de mantener el crecimiento de las larvas de *E. mordax* hasta la longitud de 6 mm, cuando este dinoflagelado, que tiene un diámetro de 40 micras, se encuentra en una concentración mínima de 30 partículas por mililitro. Sólo en una oportunidad hemos observado *G. splendens* en el intestino de las larvas de anchoveta, cuya longitud estaba alrededor de 3,1 mm, el intestino lo presentaba completamente lleno y el análisis de la muestra de plancton de las cuales fueron extraídas mostró que la concentración de las partículas era de 780 por mililitro, de las cuales: 1) 180 partículas por mililitro correspondían a *Aotinoococcus*; 2) 36 partículas por mililitro a *G. splendens* y 3) 12 partículas por mililitro a nauplius de copépodos; el resto de partículas estaba conformado por especies que forman cadenas; este resultado nos hace suponer que la larva de *E. ringens* prefirió para su primera alimentación *G. splendens*, no solamente por la concentración en que se encontraba sino también por su tamaño y movilidad, ya que parece que las larvas de *E. ringens* tienen un mismo comportamiento alimentario visual que las larvas de *E. mordax*, Hunter (1972).

Si nosotros aceptamos que las larvas de *E. ringens* también se alimentan en su primera alimentación de *G. splendens* como lo hacen las larvas de *E. mordax* (Lasker, 1975) que el valor calórico de *G. splendens* es de $4\,236 \times 10^{-5}$ cal. y es una fuente de alimento que permite a la larva de *E. mordax* crecer hasta los 6 mm de longitud (Hunter, in press, 1978) cuando ya son capaces de ingerir elementos del zooplankton que aseguren su desarrollo y sobrevivencia (Mendiola, 1974) podemos asumir que la presencia de *G. splendens* durante los últimos meses de 1975 y principios de 1976 antes de que adquiriera las condiciones de bloom, fue una condición favorable para las larvas de *E. ringens* en cuanto a disponibilidad de alimento, lo que permitió su sobrevivencia, explicando así el éxito de una abundante clase anual observada en el primer semestre de 1976 que incrementó el nivel de la población de esta especie.

Al analizar el gráfico de sobrevivencia encontramos que el 80% de las larvas murieron al octavo día y si nosotros consideramos que el tiempo en que la larva recién inicia su alimentación es a los 4,5 días, debemos suponer que la larva de *E. ringens* puede sobrevivir sin alimento por 3,5 días. Nosotros reconocemos que estos experimentos son iniciales y que necesitan de confirmación con mayor número de experimentos, pero si estos encuentros son ciertos nosotros podemos decir que las larvas de *E. ringens* tienen ventaja sobre las larvas de *E. mordax*, porque estas larvas morirán si no obtienen alimento apropiado después de 2,5 días (Lasker et al., 1970), mientras que las larvas de *E. ringens* morirán después de los 3,5 días. Para maximizar la sobrevivencia ambas especies tendrían que obtener el alimento un día antes, esto es, 1,5 para *E. mordax* (Lasker et al., 1970) y 2,5 días para *E. ringens*.

Aunque han sido pocas las observaciones sobre actividad de las larvas de anchoveta *E. ringens*, criadas en el laboratorio, ellas muestran que la actividad de las larvas es muy similar a la descrita para *E. mordax* (Hunter, 1972).

Durante nuestros experimentos en Callao encontramos que la actividad es máxima al sexto día después de la eclosión, pero que luego disminuía conforme la larva se iba debilitando, hasta morir, comparando con los datos de Hunter (1972) encontramos que existe un día de diferencia en la máxima actividad de las larvas, lo que podría significar que esta actividad se desarrolló más lentamente en *E. ringens* que en *E. mordax*. Similares encuentros fueron observados en los experimentos de Samanco; y Ware et al. (1979) sugirieron que este cambio regresivo en la actividad denotaría el "point no return" (Blaxter y Hempel, 1963). Si esto es cierto la muerte de las larvas de *E. ringens* sería una consecuencia inevitable si ellas no comienzan a alimentarse dentro de las 48 o 72 horas después del inicio del estado de postlarva.

Estos encuentros corroboran las asunciones mencionadas sobre el tiempo que la larva necesita para encontrar su alimento y sobrevivir.

CONCLUSIONES

1. Las larvas comienzan a alimentarse a 1,5 días (40 horas más o menos), después que ha completado la reabsorción del saco vitelino, presentan los ojos bien pigmentados y la boca abierta.

2. Las larvas muestran preferencia por especies que no forman cadenas, o que poseen un relativo movimiento propio.

3. Que la mínima concentración de alimento que la larva necesita para iniciar su primer alimentación es de alrededor de 80 partículas por mililitro, cuando el tamaño de la partícula varía entre 15 y 20 micras.

4. La ausencia del alimento en el intestino de las larvas estaría más relacionada con la calidad de la partícula ofrecida como alimento que con la cantidad.

5. Alrededor del 50% de las larvas criadas en el laboratorio sobrevivieron sin alimento entre 4 y 5 días, y el 80% sobreviven hasta el octavo día. Para maximizar la sobrevivencia de las larvas de *E. ringens*, éstas necesitan encontrar su alimento dentro de los 2,5 días después del tiempo en que inician su primera alimentación (4,5 días).

6. La actividad motora de las larvas incrementa del primer día después de la eclosión al sexto día, cuando manifiesta su máxima actividad, para continuar con niveles bajos de actividad similares a los observados los primeros días.

Este cambio regresivo al sexto día podría ser considerado como el "point no return" para las larvas de *E. ringens*.

REFERENCIAS

- ARTHUR, D.K. 1956. The particulate food and the food resources of the larvae of three pelagic fishes, specially the Pacific sardine, *Sardinops caerulea* G. Unpublished Doctoral dissertation, on file in the Library of Scripps Institution of Oceanography, University of California, La Jolla, 231 pp.
- BERNER, L. Jr. 1959. The food of the larvae of the northern anchovy, *Engraulis mordax*. Inter - Amer.Trop.Tuna Comm.Bull.(4):1-22
- HJORT, J. 1914. Fluctuations in the great fisheries of northern Europe Viewed in the light of biological research. Rapp.P.V.Réun.Cons.Perm.Int.Explor.Mer. 20:1-228
- _____ 1926. Fluctuations in the year classes of important food fishes. J.Cons.1:5-38
- HUNTER, JOHN. 1972. Swimming and feeding behavior of larval anchovy *Engraulis mordax*. Fish.Bull.,U.S., 70 (3):
- HUNTER, J.R. 1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull.,U.S., 75(1):81-88
- LASKER, R.H.M., G.H. FEDER, THEILACKER y R.C. May. 1970. Feeding, growth and survival of *Engraulis mordax* larvae reared in the Laboratory. Mar.Biol. 5:345-353
- LASKER, Reuben. 1975. Field criteria for survival of anchovy larvae: The relation between inshore Chlorophyll maximum layers and successful first feeding. Fish. Bull.U.S., 73(3):453-62
- _____ 1978. The relations between oceanographic conditions and larval anchovy food in the California Current: Identification of the factors contributing to recruitment failure. Rapp.Réun.Cons.Int.Explor.Mer 173:212-230
- _____ 1979. Factors contributing to variable recruitment of the northern anchovy (*E. mordax*) in the California Current: contrasting years, 1975 through 1978. ICES/ELH Symp. Woods Hole, Mass. April 2-5, 1979

- ROJAS DE MENDIOLA, B. 1974. Food of the larval anchovy *Engraulis ringens* J. in J.H.S. Blexter (Editor) the early life history of fish p.277, Springer-Verlag, Berlin
- SMITH, PAUL. 1977. Estimation of the effects of environmental variations on the eggs and larvae of the northern anchovy. Calif.Coop.Oceanographic Invert.Rep.19, 1977
- WALSH, J.J., T.E. WHITLEDGE, W.E. ESAIAS, R.L. SMITH, S.A. HUNTSMAN, H. SANTANDER y B.R. DE MENDIOLA. 1979. The spawning habitat of the Peruvian anchovy *Engraulis ringens* J. (in press)
- WARE D., ROJAS DE MENDIOLA B. y NEWHOUSE D. Behaviour of the first feeding Peruvian anchovy larvae *Engraulis ringens* J. (in press)

NOTE ON HYDROACOUSTIC OBSERVATIONS OF CHANGES IN
DISTRIBUTION AND ABUNDANCE OF SOME COMMON PELAGIC
FISH SPECIES IN THE COASTAL WATERS OF PERU,
WITH SPECIAL EMPHASIS ON ANCHOVETA

by

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INTRODUCTION

During the past five years, the Instituto del Mar del Perú (IMARPE), assisted by the Regional Acoustic Research Centre for Latin America (FAO/NORWAY) has conducted 11 bio-acoustic survey cruises as a part of a research scheme initially devised for monitoring the anchoveta resources. The surveys have generally covered a sampling area of 50,000-60,000 n.m² and yielded abundant hydroacoustic data in the form of echograms and integrals produced by analog echointegrators which were calibrated in units of absolute biomass density. These data, although primarily used for quantification of stock biomass, have also provided useful information on distribution, habitat and behaviour of the principal fish species in the area.

This note is intended to give a preliminary description of the large-scale features of observed changes in spatial distribution and abundance of anchoveta (*Engraulis ringens*). Likewise, an attempt is made to describe some variations in distribution and stock sizes of other common pelagic species such as: Pacific mackerel (*Scomber Japonicus peruanus*); Pacific jack mackerel (*Trachurus symmetricus murphyi*); saury (*Cololabis saira*); and pilchard (*Sardinops sagax sagax*). A more comprehensive description will be prepared when the required analyses of school parameters from echo and integrals has been completed.

The information presented in regard to variations in abundance and distribution patterns, is derived from analyses of integrator plots coupled with planimetric integration of related areas of fish distribution. The relevant methods are described in Jóhannesson and Vélchez, 1979. Information on packing densities and depthwise distribution of pelagic schools were obtained through geometric analysis of echograms in conjunction with analysis of discrete school echo-integrals following Jóhannesson and Losse (1977).

The coastwise distribution and density pattern of the observed anchoveta population(s), by year/season, and by degree latitude, is illustrated in the form of a series of bar-graphs. Likewise, annual and seasonal changes in the geometric characteristics of the stock distribution is portrayed by a series of density isopleth charts which also indicate variations in density levels. Observed fluctuations during a period of seven years in observed anchoveta biomass and mean stock density, concomitant with changes in area distribution of the species, is also presented in graphic form.

Finally, the main features of the abundance and distribution pattern of: pilchard, mackerel, jack mackerel and saury are described on the basis of the limited information available.

DISTRIBUTION AND ABUNDANCE

Geographic distribution

The largest concentrations of anchoveta are found outside northern and central Peru as shown in Fig. 1-C. Anchovetas are generally distributed in a coastwise band 10-14 miles wide extending from 7° (Lat.S) in the north to about 16° (Lat.S) in the south, a distance of approximately 700 nautical miles. Beyond these arbitrary boundaries the abundance falls off rapidly in the north while in the south it has a tendency to diminish gradually. Occasionally, anchovetas are found as far north as 5° (Lat.S), but then only in isolated areas and in very small quantities. Anchovetas are generally concentrated near-shore, so for practical purposes the shore-line itself is considered as the shoreward limit of the distribution. The average limit can range from roughly 10-40 miles, depending on season and stock magnitude. The basic characteristics of the geographical distribution pattern, based on four abundance levels, is presented in Figs. 2-11. It is noted that in an abundance year/season (Fig. 2), the stock exhibits almost a continuous distribution over a large sea surface area, with relatively frequent occurrences of high-density zones. In contrast, when the stock level is low, such as in March/April 1979, the distribution becomes discontinuous and forms separate, well defined sub-areas (sub-populations?) incorporating pockets of high density concentrations (Fig.4). A further decline in observed stock biomass, as the mapping of the 7708/10 cruise results shows, appears to be attributed to reduction in biomass density rather than change in area size (see Figs. 5-6).

Diurnal behaviour

Anchoveta behaviour differs greatly between day and night (Villanueva, 1970). During daytime the fish are concentrated in schools, while at night they are dispersed. The transition from schooling to scattering occurs usually at the onset of dusk. Conversely, the re-grouping in schools takes place during the dawn period. There are certain deviations from this general pattern which, apart from environmental factors, also might be influenced by variation in moonlight intensity.

Another day/night behavioural change which can be observed from echo records, is a vertical movement of the centre of gravity of the biomass. The bulk of the biomass is commonly observed to start ascending in the late afternoon or at onset of dusk, and in comparison with daytime hours remains 5-10 m closer to the sea surface until daybreak. Mathisen (1979) illustrates this from acoustic records made within the CUEA (Coastal Upwelling Ecosystem Analyses) programme, and offers an explanation by relating the vertical migration to diel feeding habits of the anchoveta. This vertical change in distribution is particularly pronounced in deeper water (depth > 50 m), while in shallow water depths (10-20 m) the vertical migration is clearly much smaller, if any. Echo-records taken from such shallow waters frequently show the anchoveta (schools or layers) occupying the entire water-column from surface to bottom.

Distribution and density of schools

Most anchoveta schools are found within the 40 m depth range. During summer and into the autumn season when particularly good weather conditions generally prevail, in the survey region, schools are frequently sighted by eye at surface level. Surface concentrations can either represent the upper end of compact (usually large) schools, or a thin, sometimes very dense, surface layer.

A typical depth frequency distribution of 1 042 pelagic schools (predominantly anchoveta) is shown in Fig. 11. The data, obtained from two cruises made in two consecutive years, April 1978 and March/April 1979, show that the vast majority of schools are detected within

DISTRIBUTION CHARACTERISTICS OF PERUVIAN ANCHOVY

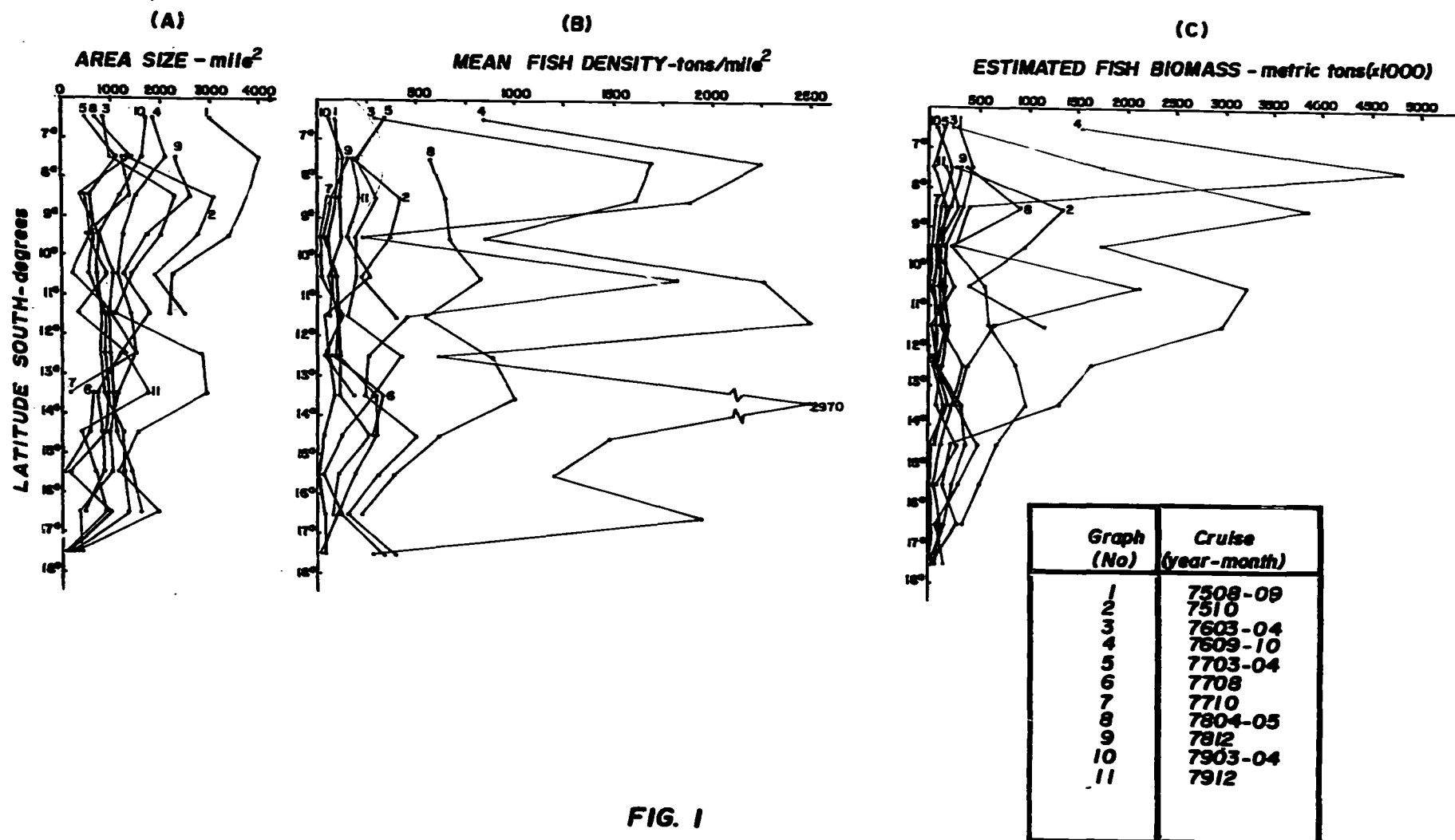


FIG. 1

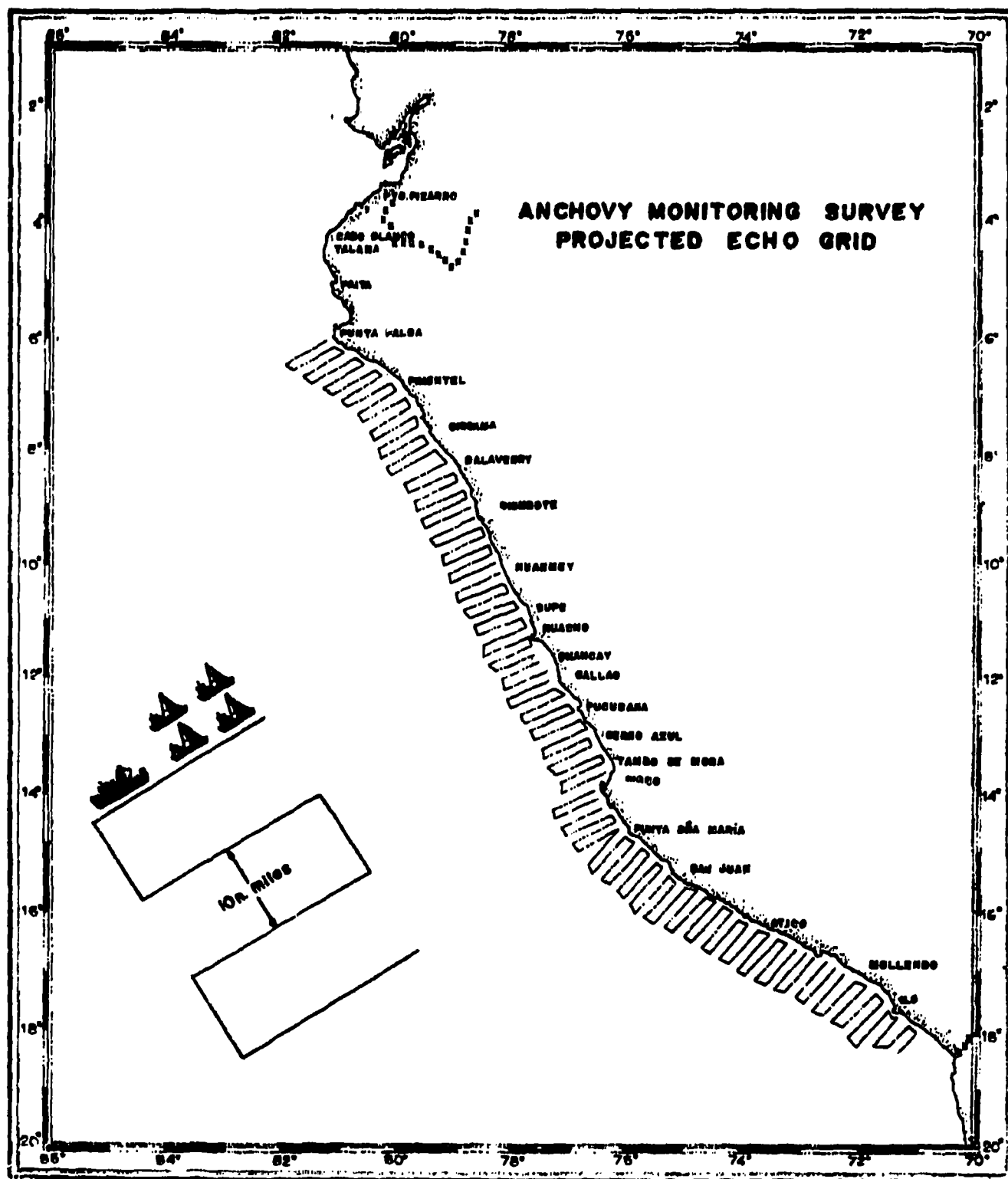


Fig.2A



FIG. 2B

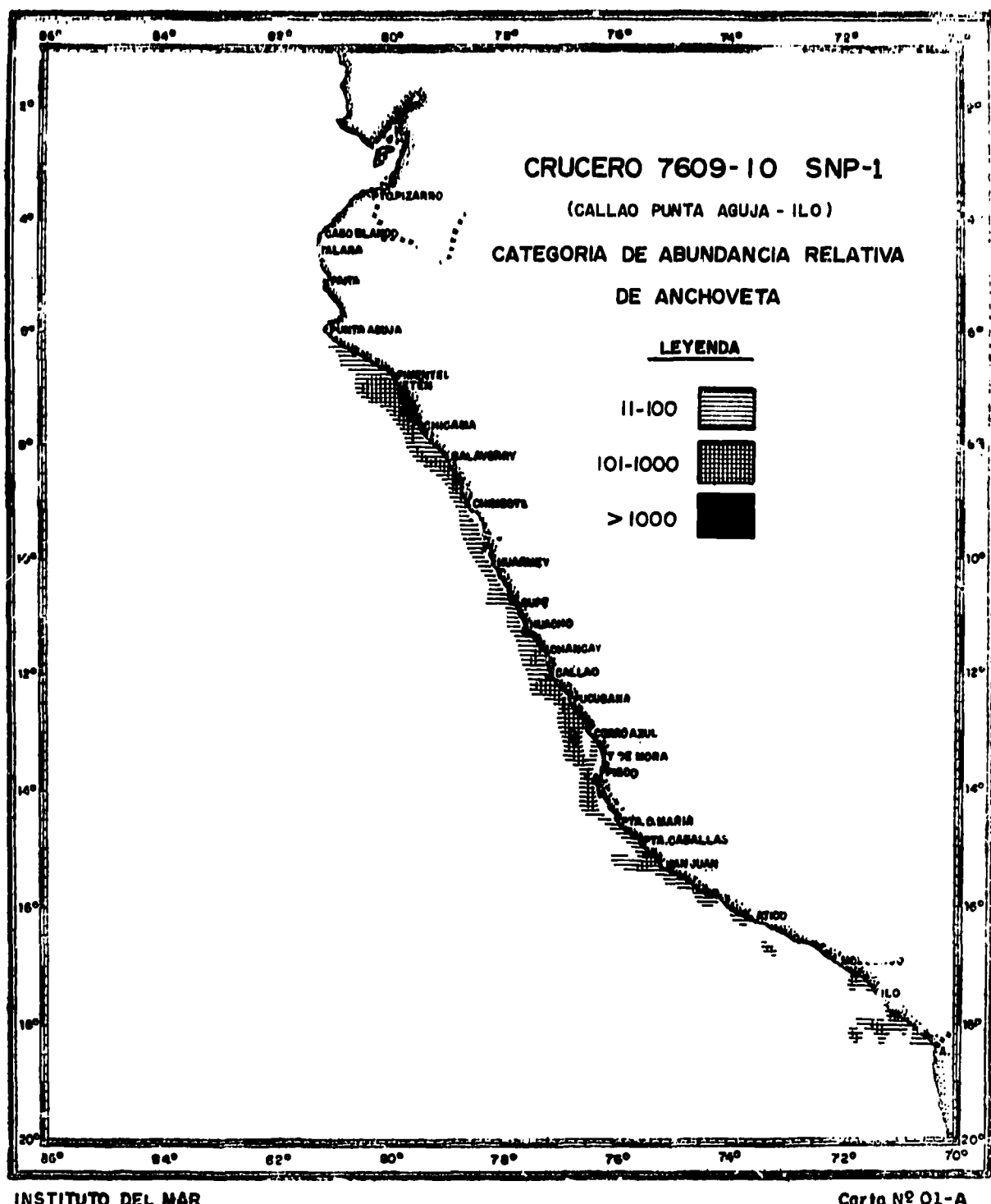


FIG. 3

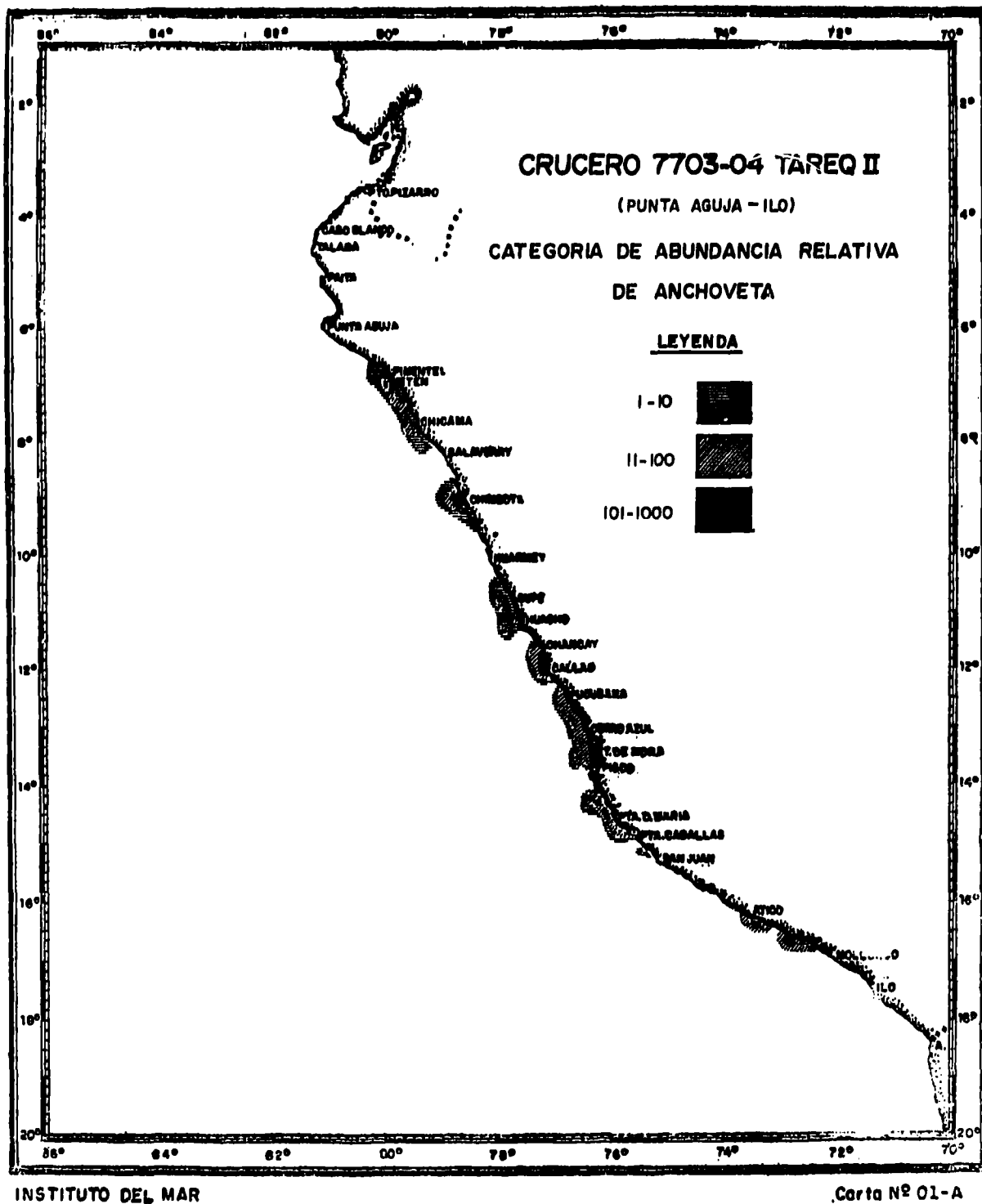
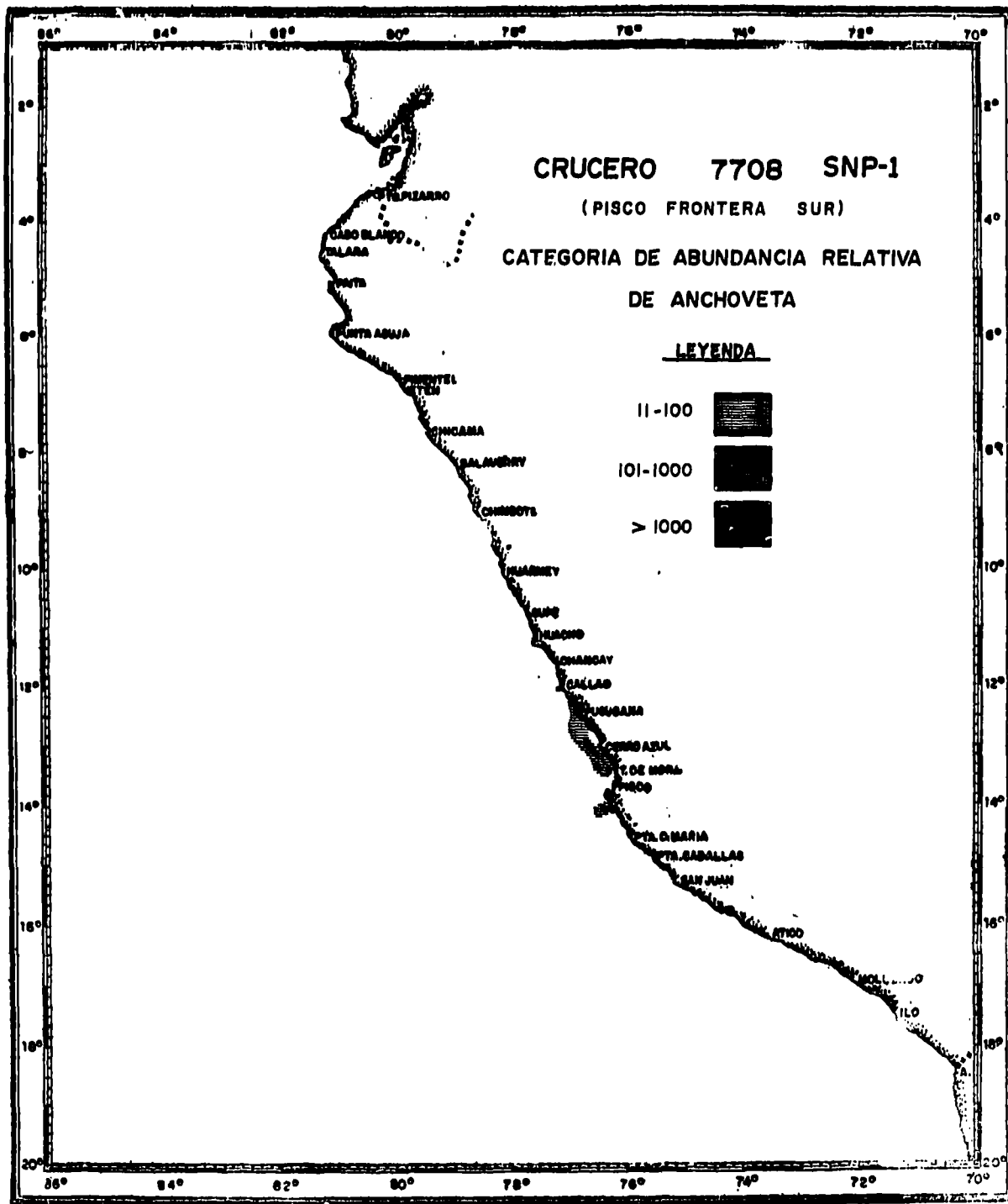


FIG.4



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FIG. 5

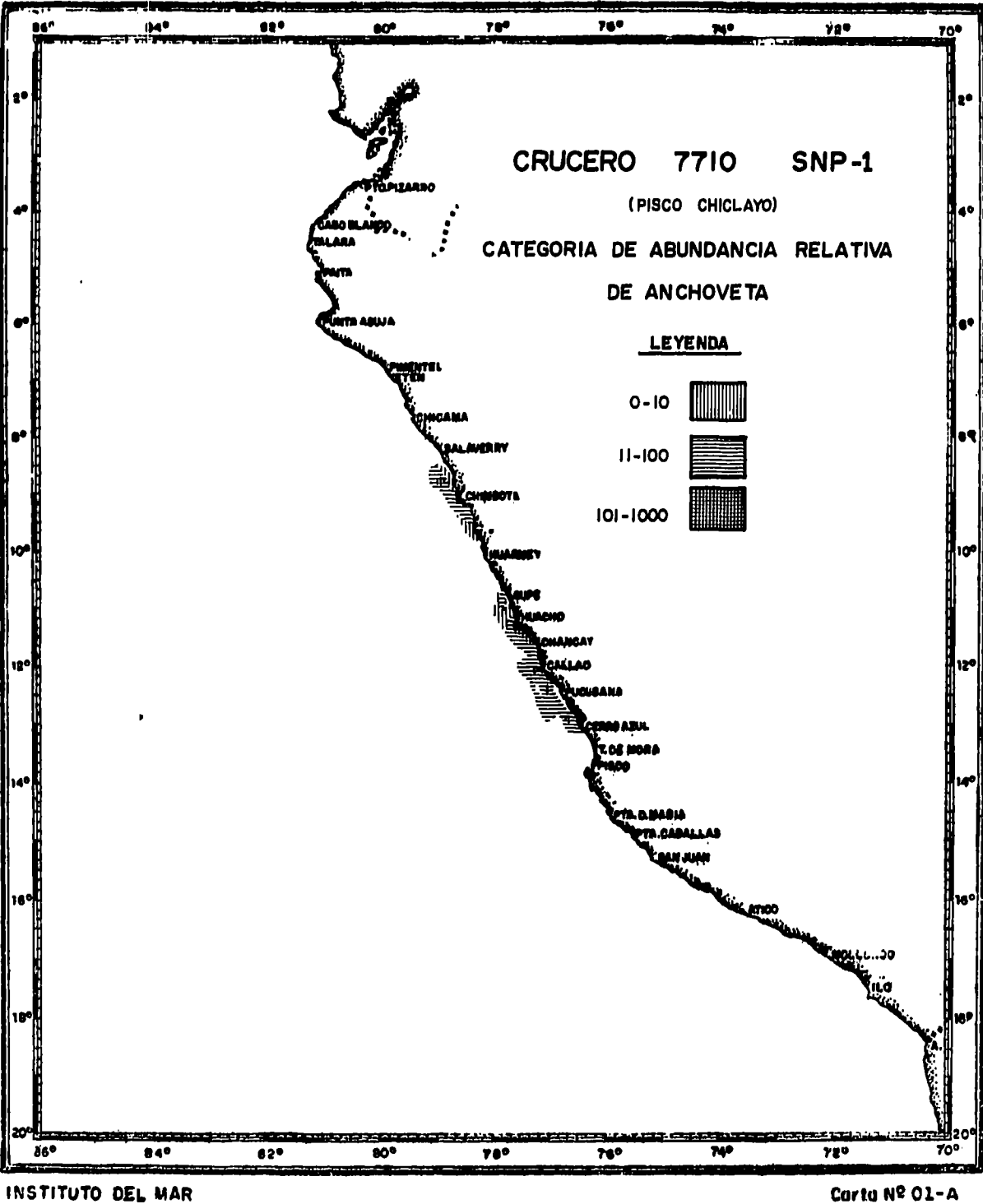
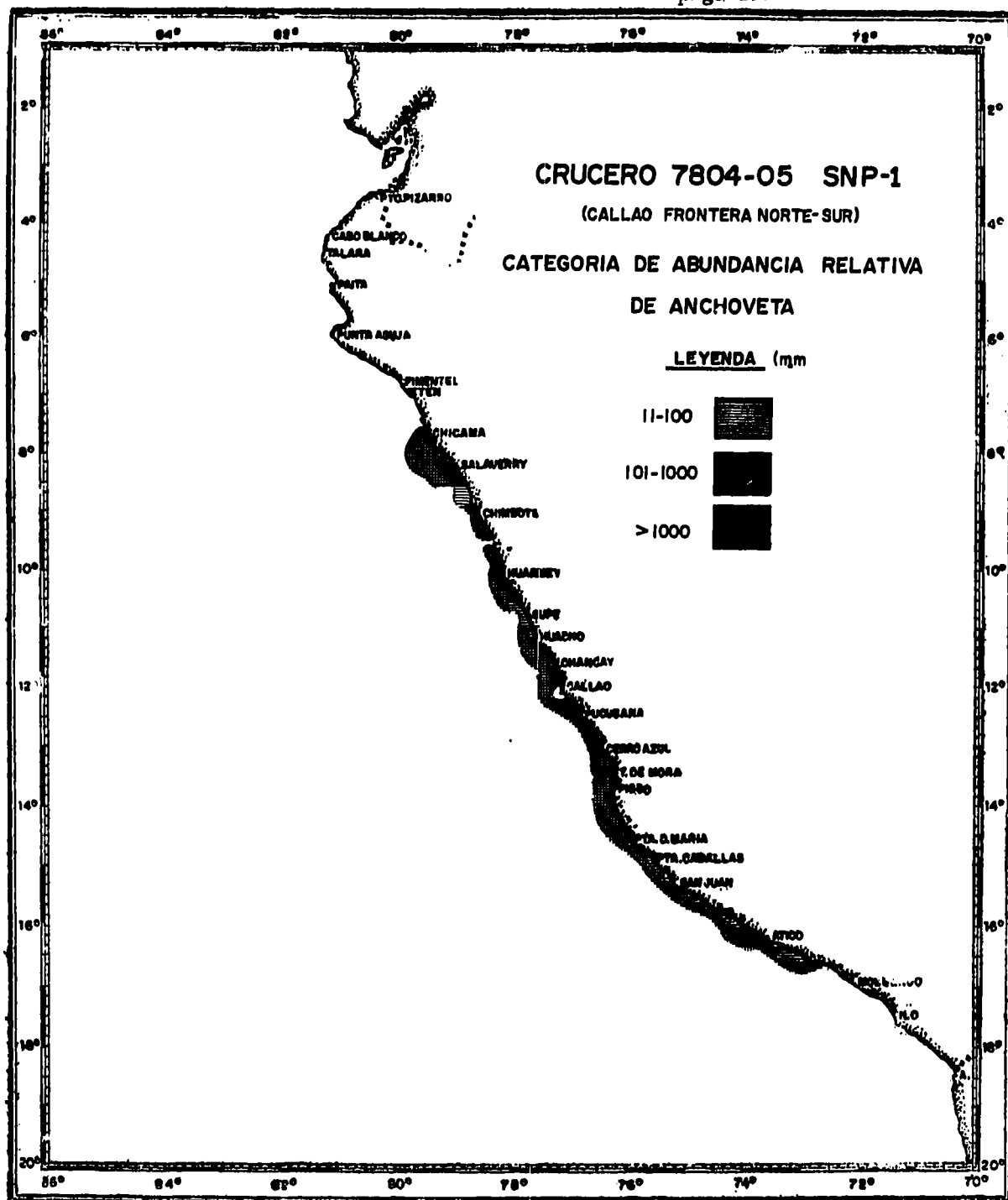


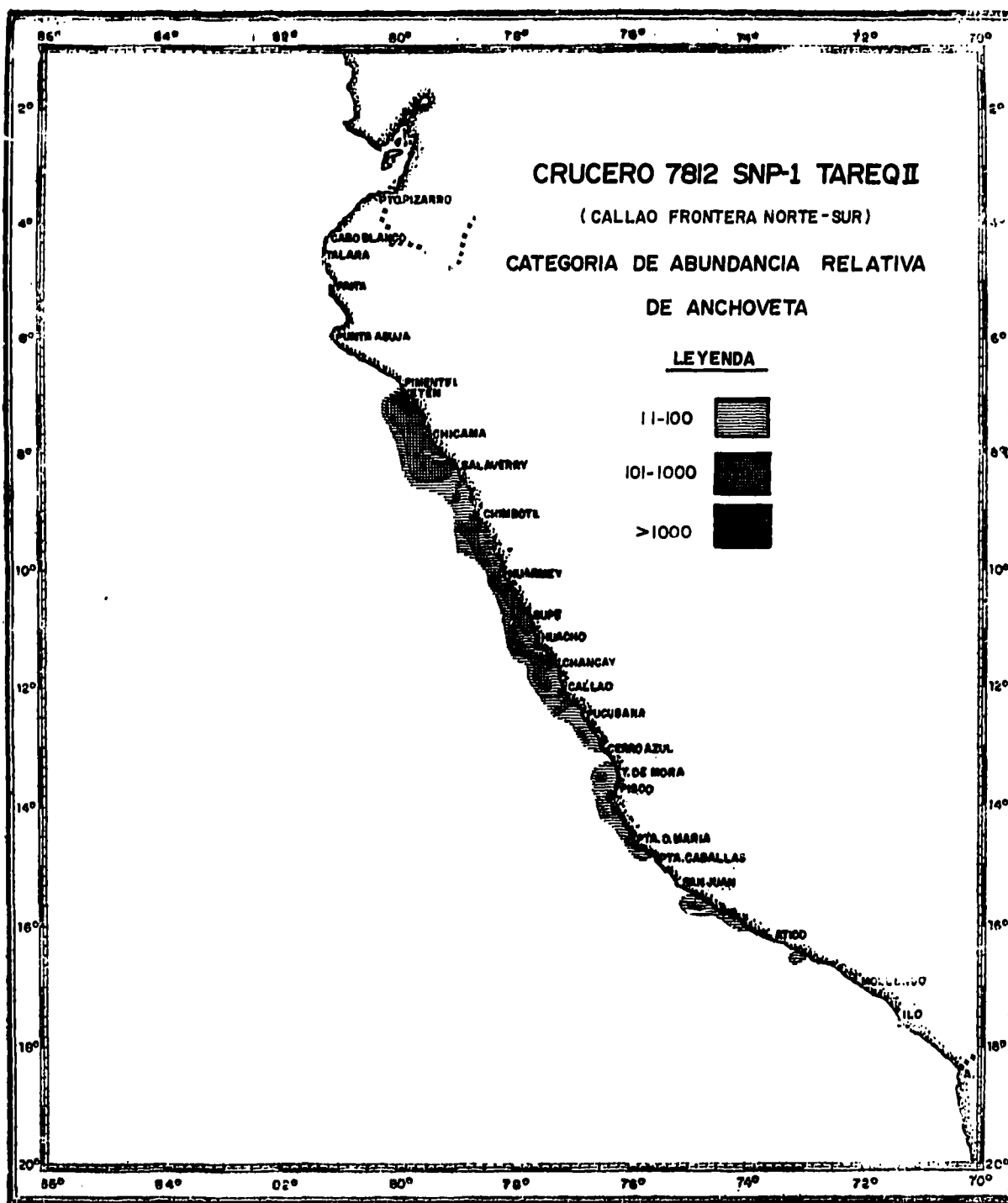
FIG. 6



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FIG.7



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FIG. 8

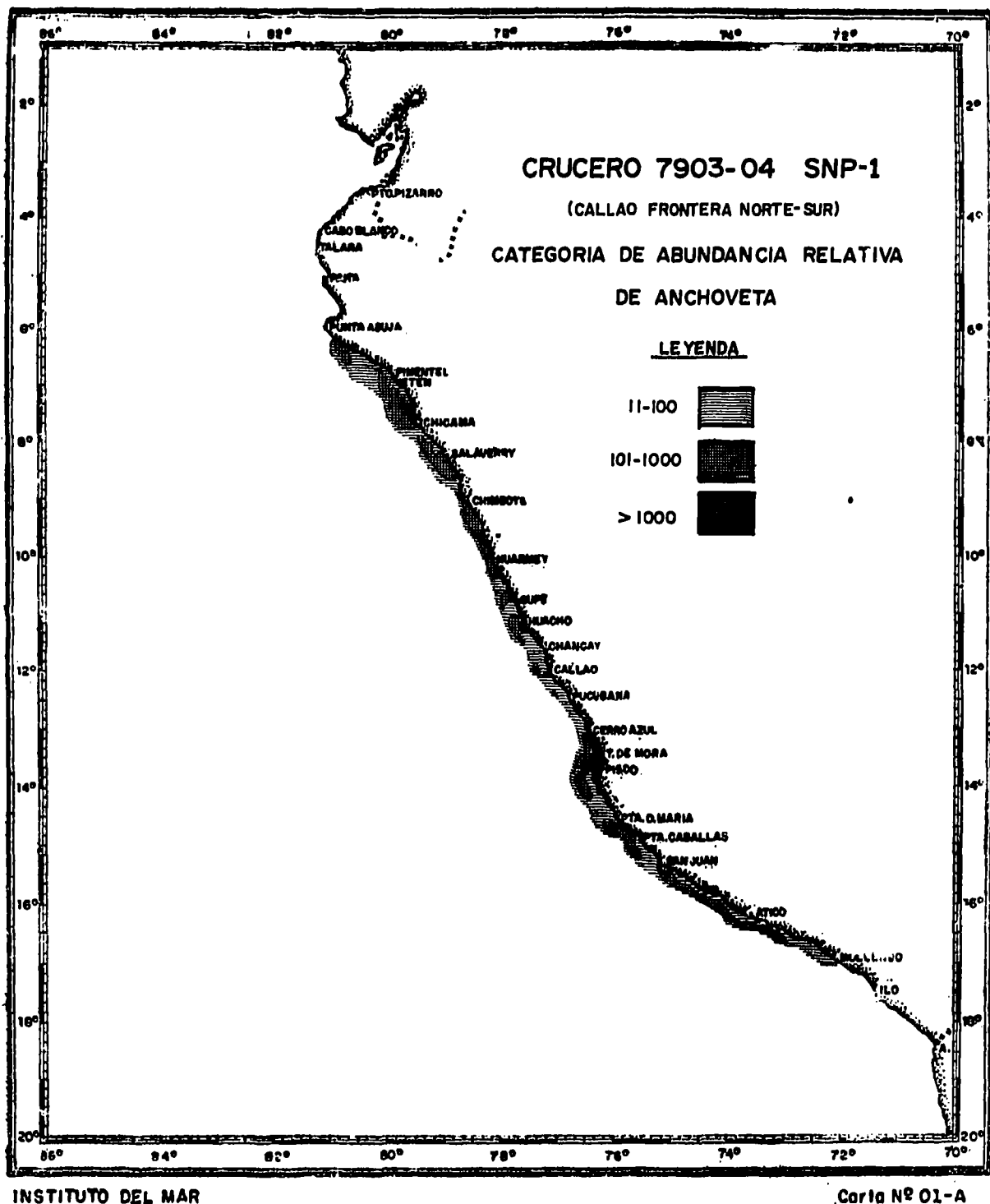


FIG. 9

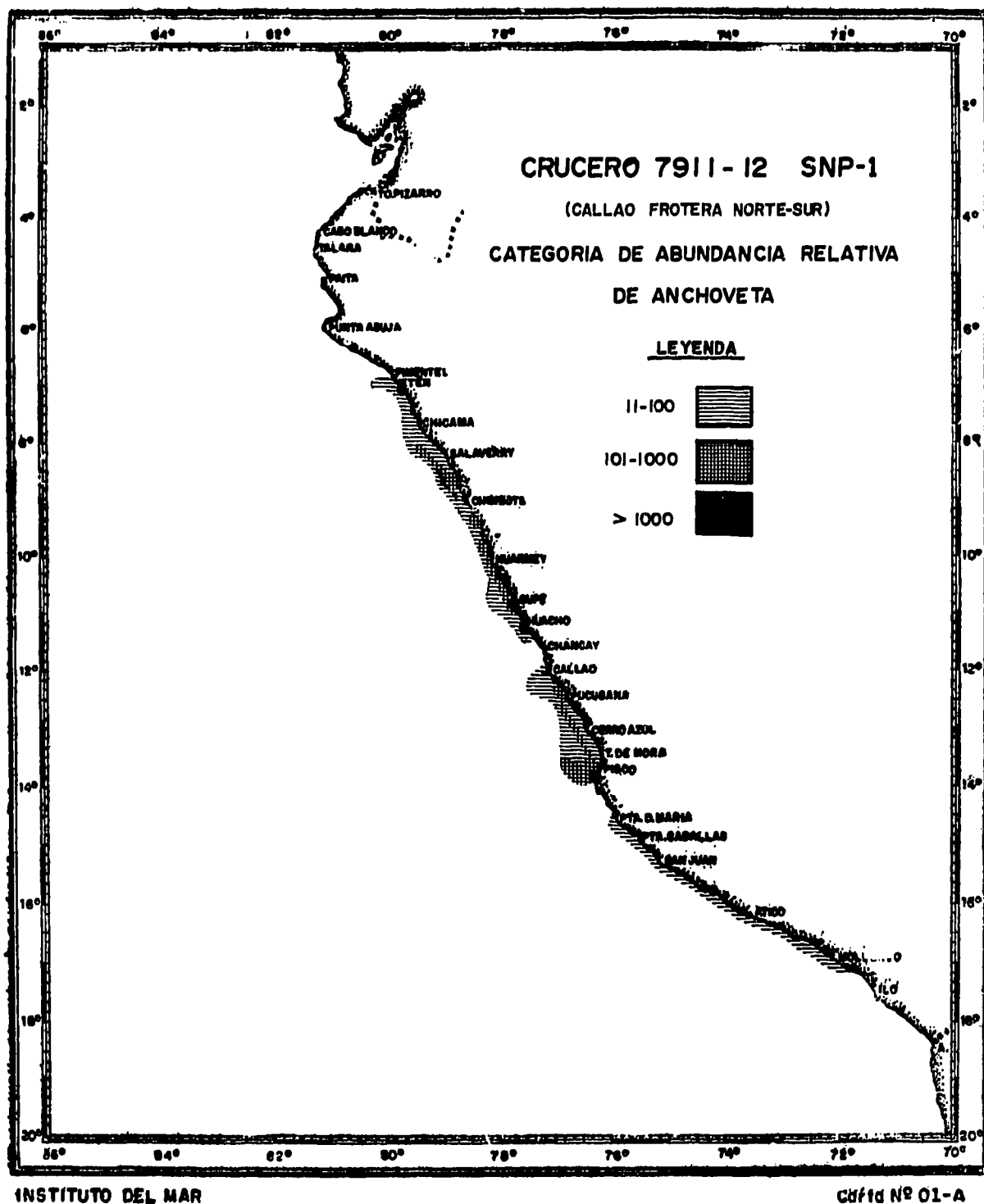


FIG. 10

the upper 40 m water column. Schools shown within the 40-100 m range do not have confirmed identity but subjective evaluation of related echo- and integrations strongly suggest that they can be assigned to mackerel and jack mackerel.

The compactness of the anchoveta schools as well as their shapes and sizes are highly variable factors when considering the survey as a whole. However, schools within a given area and time period tend to remain at uniform depths and exhibit physical similarities when recognized as acoustic targets.

The general variability in packing density of recorded pelagic schools, is illustrated in Fig. 12. The histogram, which relate to the same schools, whose depthwise distribution is given in Fig. 11, show a very wide range in estimated densities. The actual minimum/maximum densities are respectively 2 and 512 fish/m³. It should be noted that the methods used can only permit a density estimate to be given with reference to a specific fish size and weight. Thus, the above estimates are normalized to anchoveta 6.7 gr (10 cm). For the schools studied, the corresponding maximum volume and weight was respectively 2.8×10^6 m³ and 1 615 metric tons total school weight.

The distribution of the anchoveta schools within the total stock area, delineated by the hydroacoustic mapping, does not suggest a randomness but, to the contrary, a varying degree of localized and patchy features depending on season and/or year. Statistical analyses of the surveyed biomass during the 7603-04 cruise demonstrated a strongly contagious distribution. The tendency of the fish biomass to exhibit such a distribution is suggestively indicated in Fig. 13, which presents a probability distribution of occurrence of class-densities (echo-abundance levels) resulting from night and daytime observations, respectively. A total of 4 988 two-mile samples were obtained during survey cruises in 1978. Each sample represents a relative biomass density (M), measured by an echo-integrator as the average value over the corresponding two-mile survey track section. A comparison of night vs daytime values showed a statistically insignificant difference throughout the observed density (stratum) range. Hence, the integrator output used appears to be fairly independent of the spatial distribution pattern of the observed stock, and as such, does not provide information of a detailed nature on changes in the stock distribution pattern. To derive a more detailed description of these changes from the available acoustic records would require a joint analysis of echograms and integrations supported by information from concurrent catch data.

Coastwise variations in distribution and abundance

A graphical analysis was made to examine changes in distribution and abundance level along the coast. First, a set of bar-graphs showing relationship between density and area distribution of anchoveta by degree latitude, was prepared for each cruise as shown in Figs. 14-23. Secondly, a graphic summary of the data was made, also illustrated in Fig. 1.

An evaluation of these graphs shows that respective within-survey variations in density vs area size are inconsistent, i.e., an increase in density coincides either with positive or negative change in area size (Figs. 15, 16, 17 and 20). Also, the graphs suggest that a given change in direction ($\pm$) is independent of coastwise location (degree latitude). The rate of changes in area sizes is relatively rapid (e.g. Figs. 15 and 23), and on the scale considered, sharp density gradients are observed, notably when stock abundance is high (see Figs. 15 and 16). An interpretation of these changes, based on considerations of the interplay between biological factors and the nature of the Peruvian fishery, is given by Mathisen (1979). Comparison of the set of graphs resulting from the eleven surveys (Fig. 1-C) bears out three reasonably well defined abundance modes along the coast. The first mode occurs in the area between Pimentel and Chimbote (7° - 9°); the second one from Huarmey to Callao (10° - 12°), and the last mode, from Cerro Azul to San Juan (13° - 15°).

Fluctuations in stock abundance and distribution

Estimated variation in stock abundance and related parameters as a function of time are presented in the form of graphs in Fig. 24. The graphs which are largely self-explanatory show the annual, and to a lesser extent, the seasonal fluctuations. It should be noted

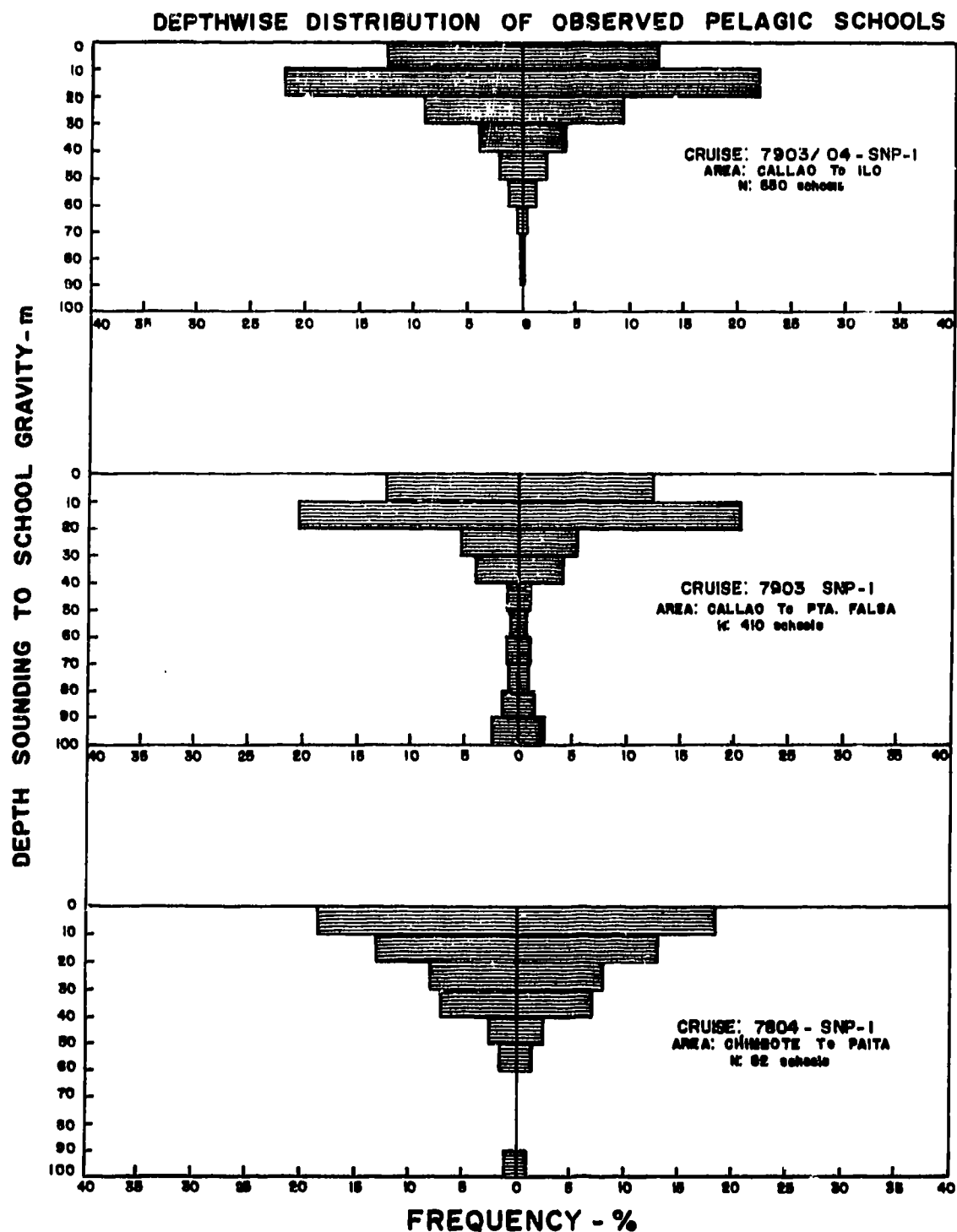


FIG. 11

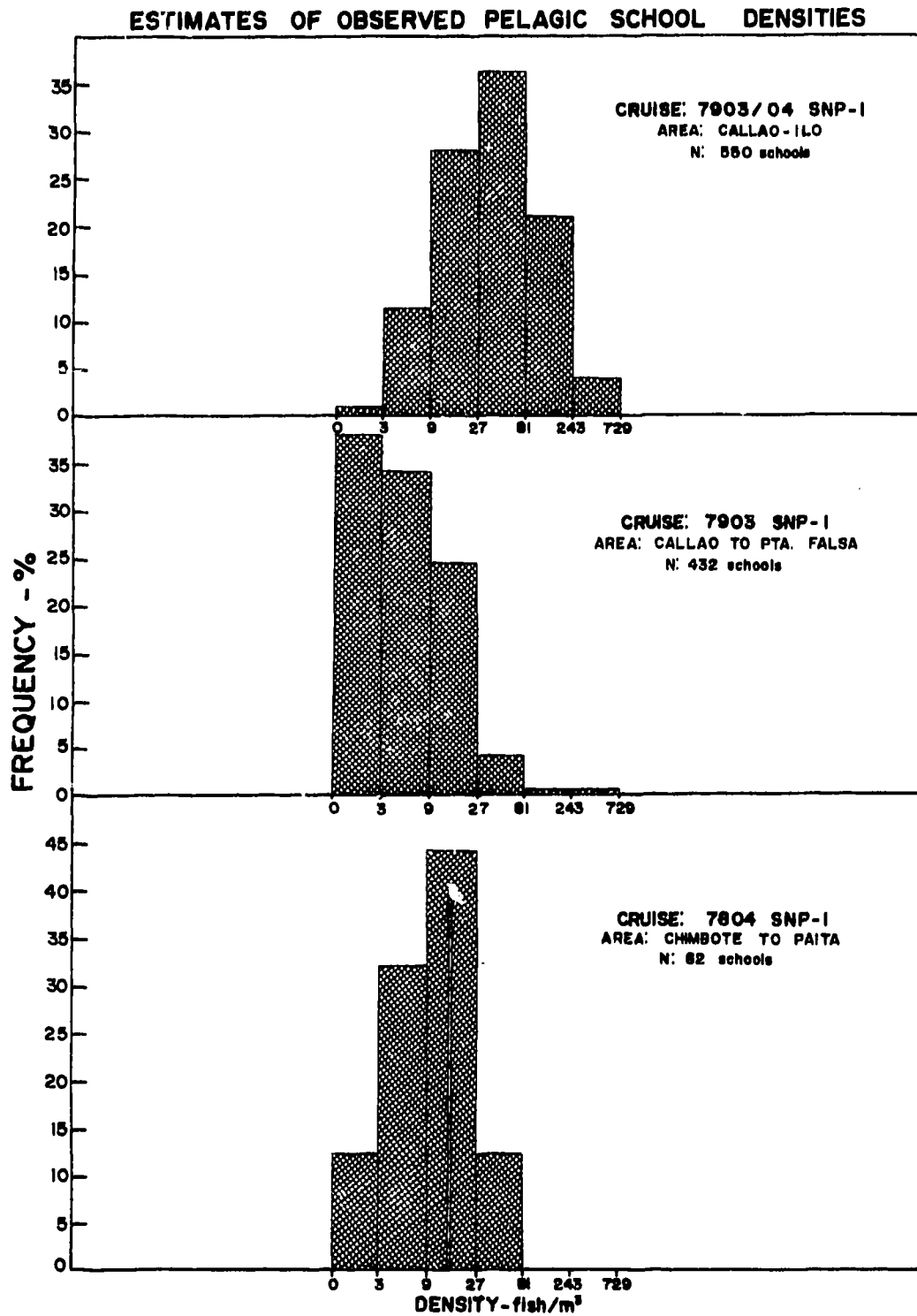


FIG. 12

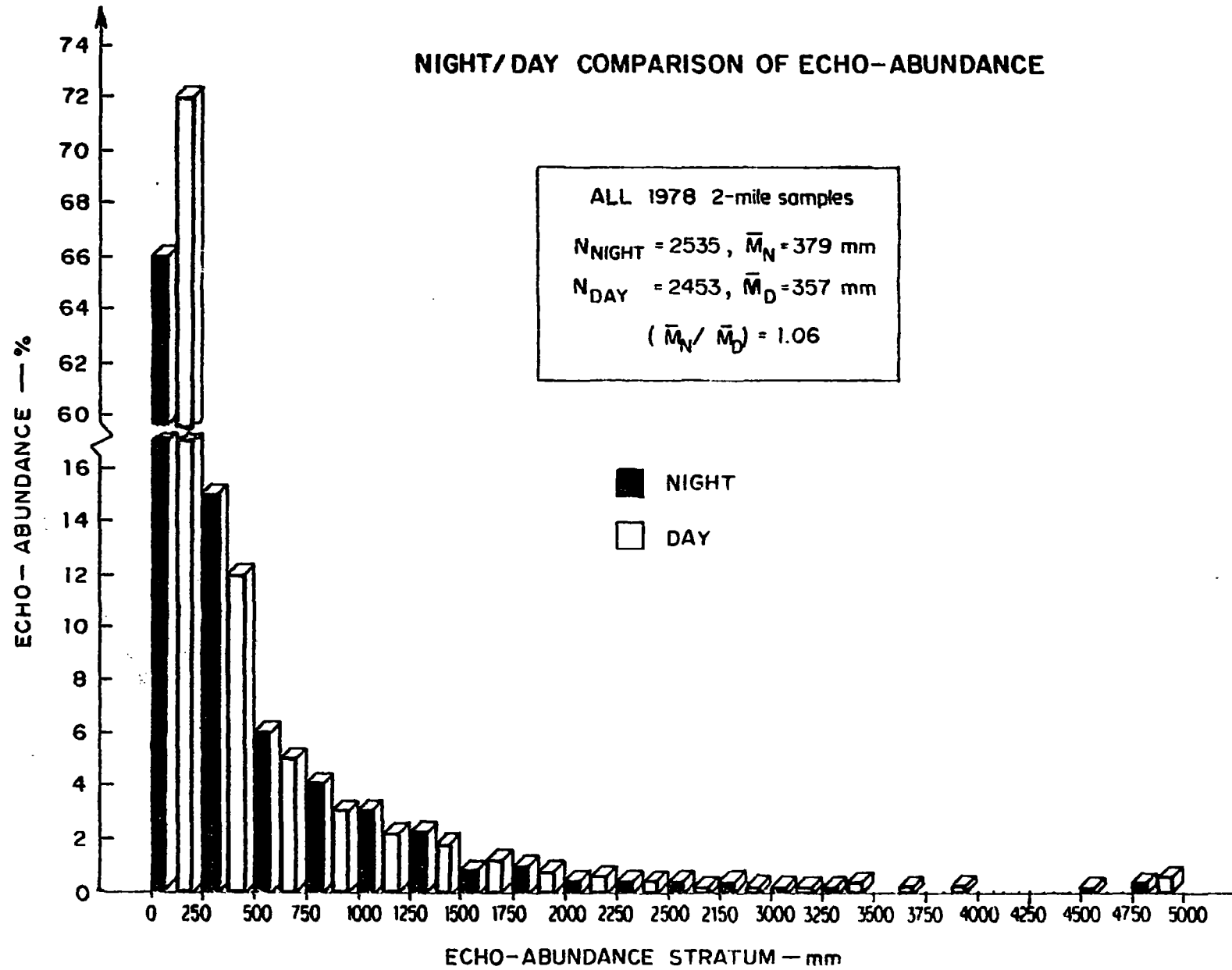


Fig. 13

CRUISE 7508-09 SNP-1

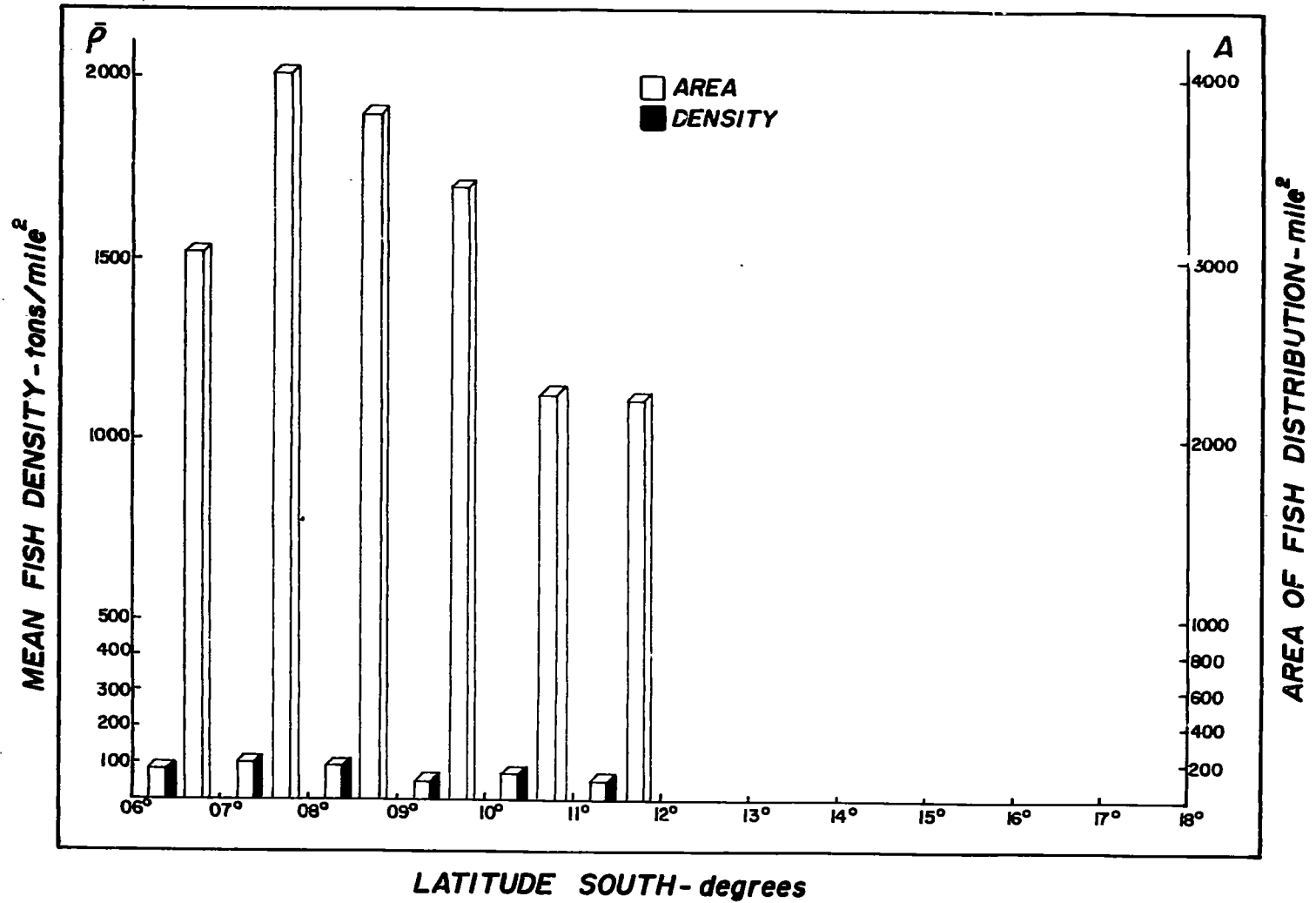
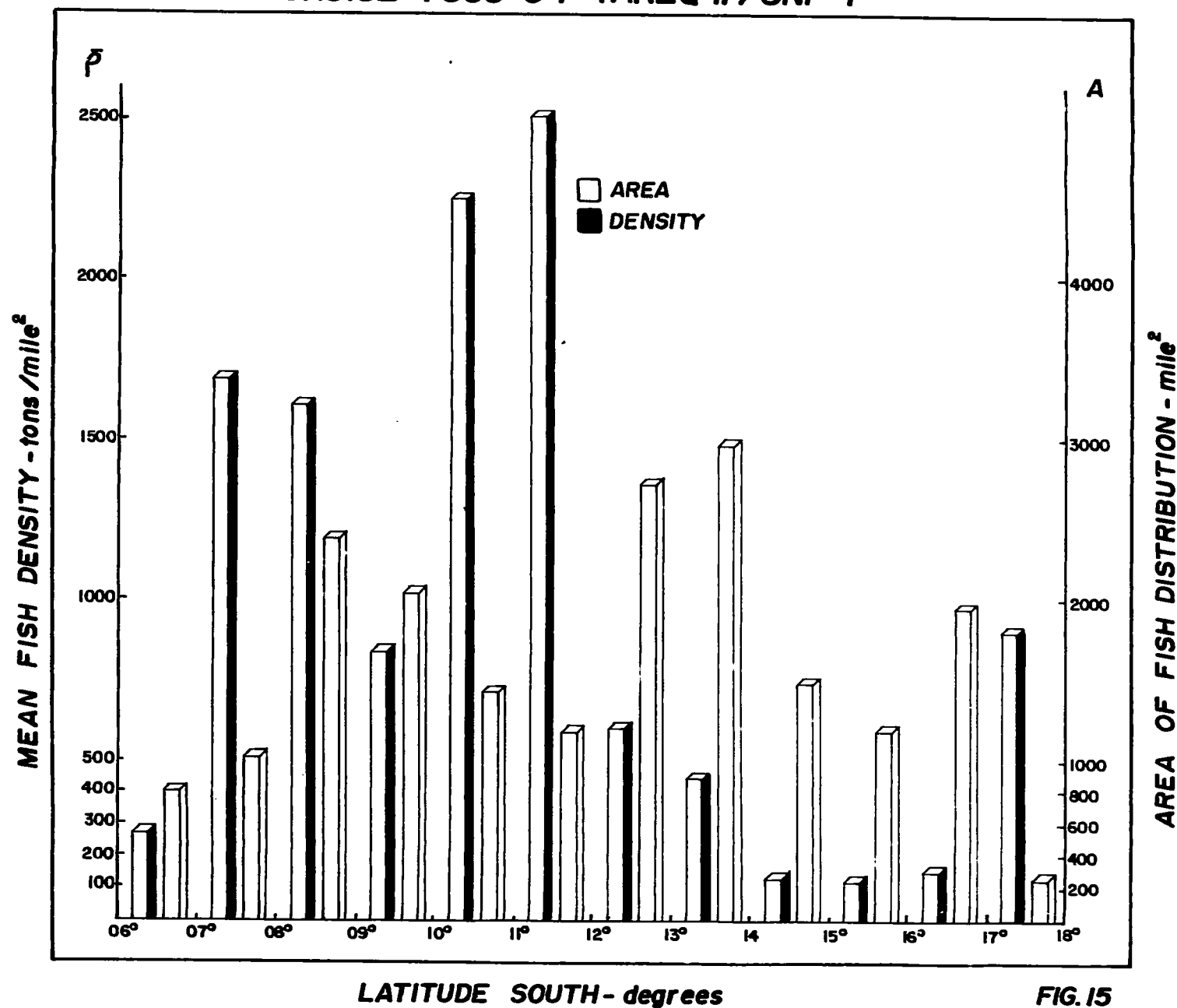


FIG. 14

CRUISE 7603-04 TAREQ II / SNP-1



CRUISE 7609-10 SNP-1

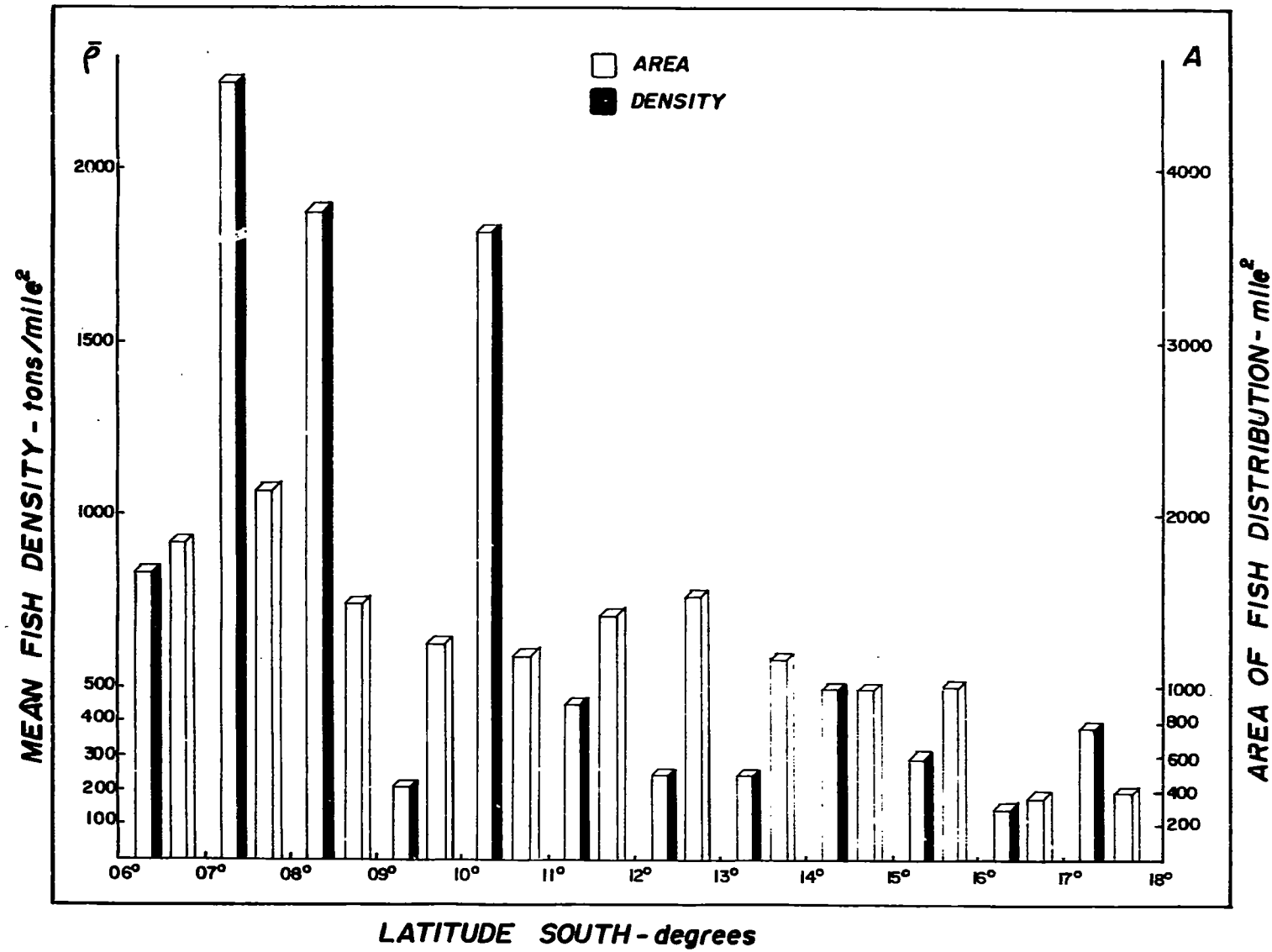


FIG. 16

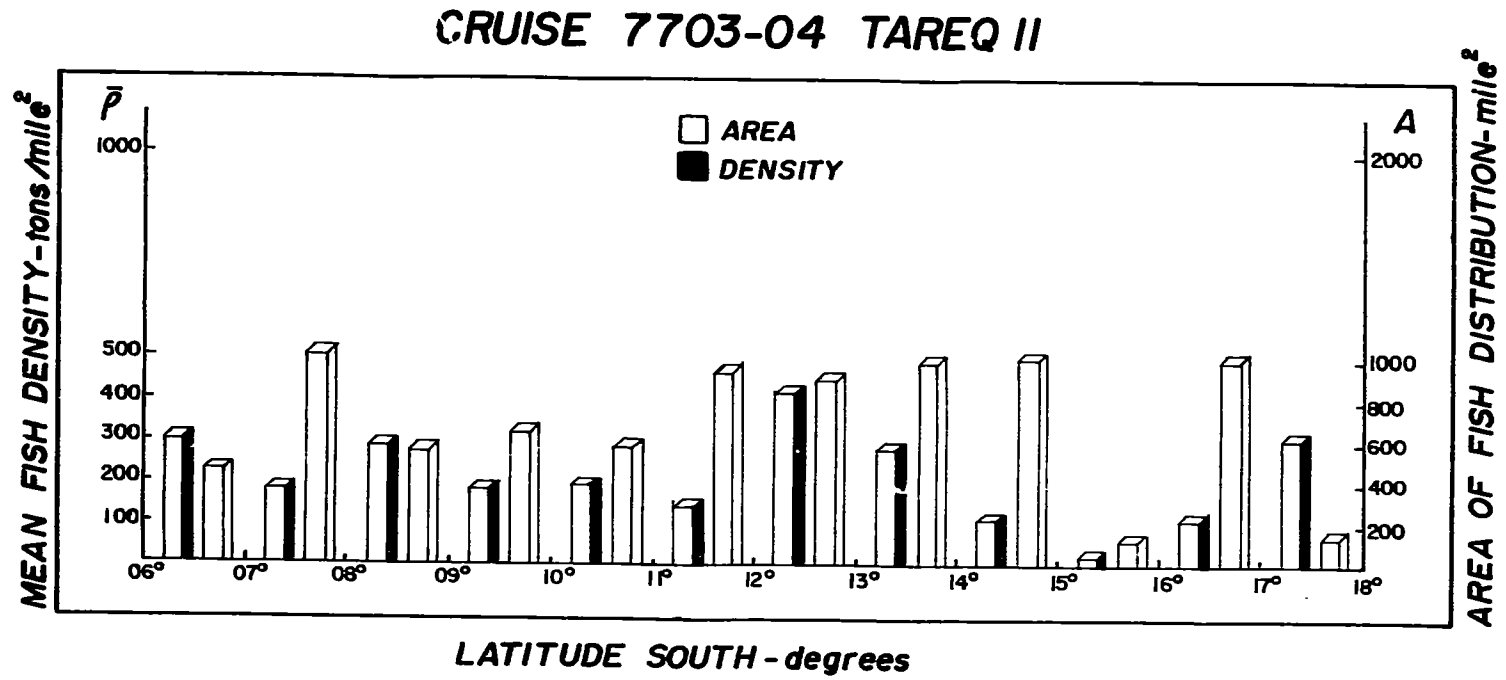


FIG. 17

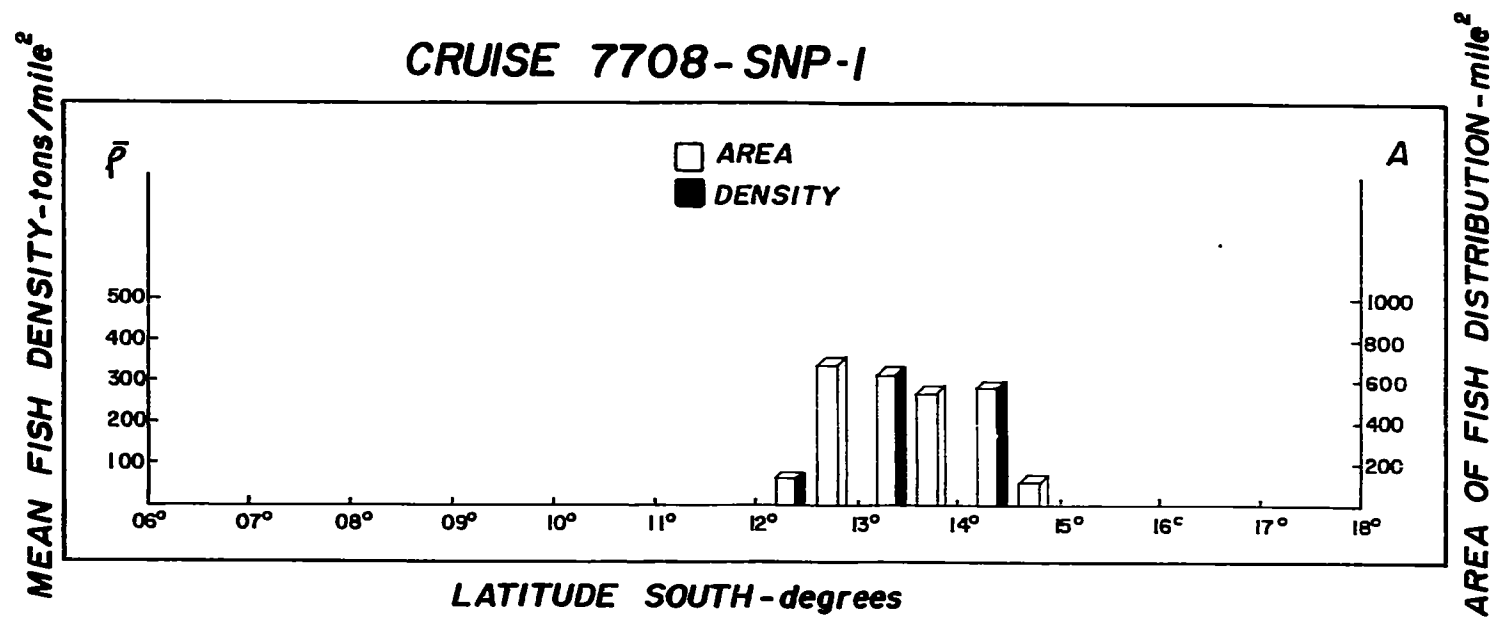


FIG. 18

CRUISE 7710 SNP-1

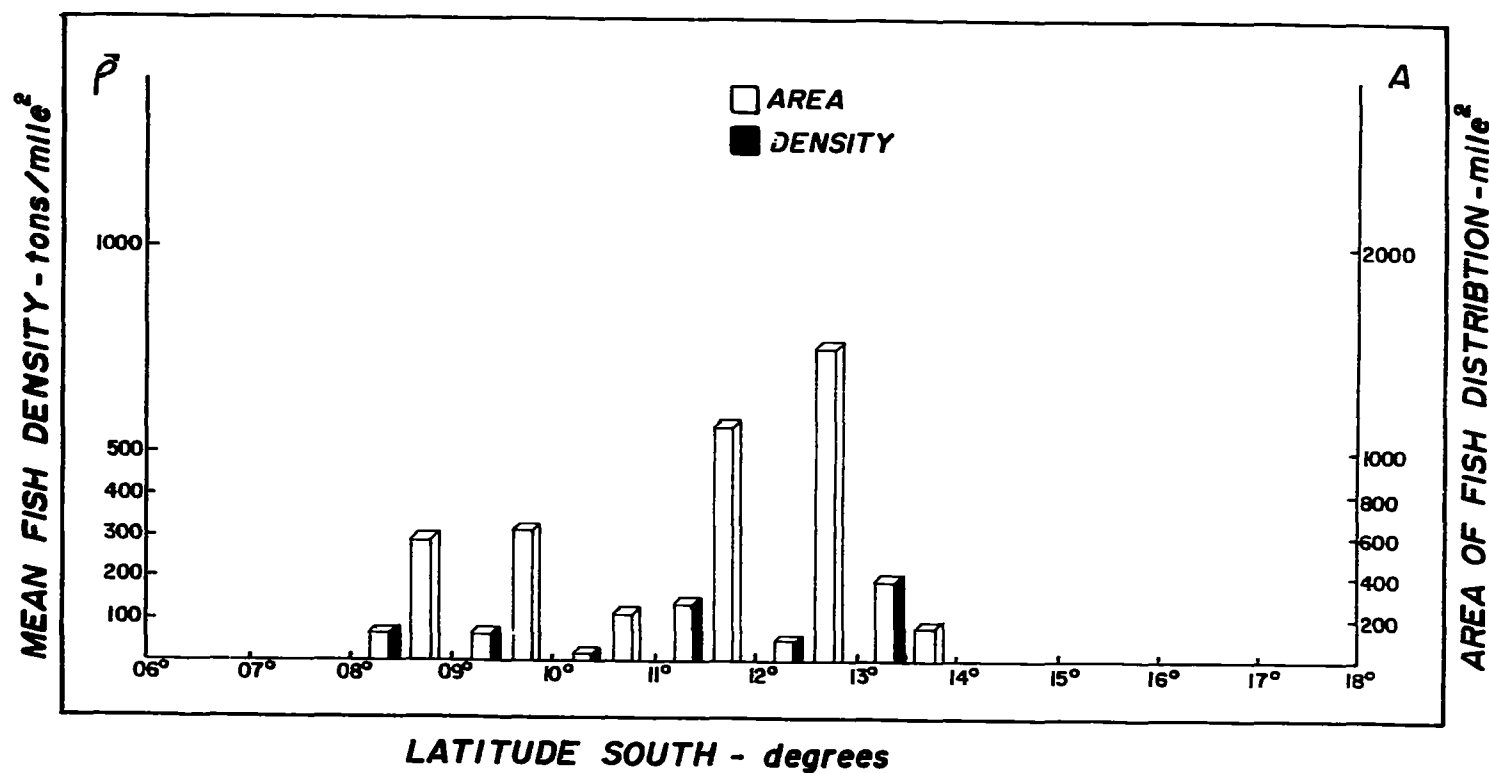


FIG. 19

CRUISE 7804-05 SNP-1

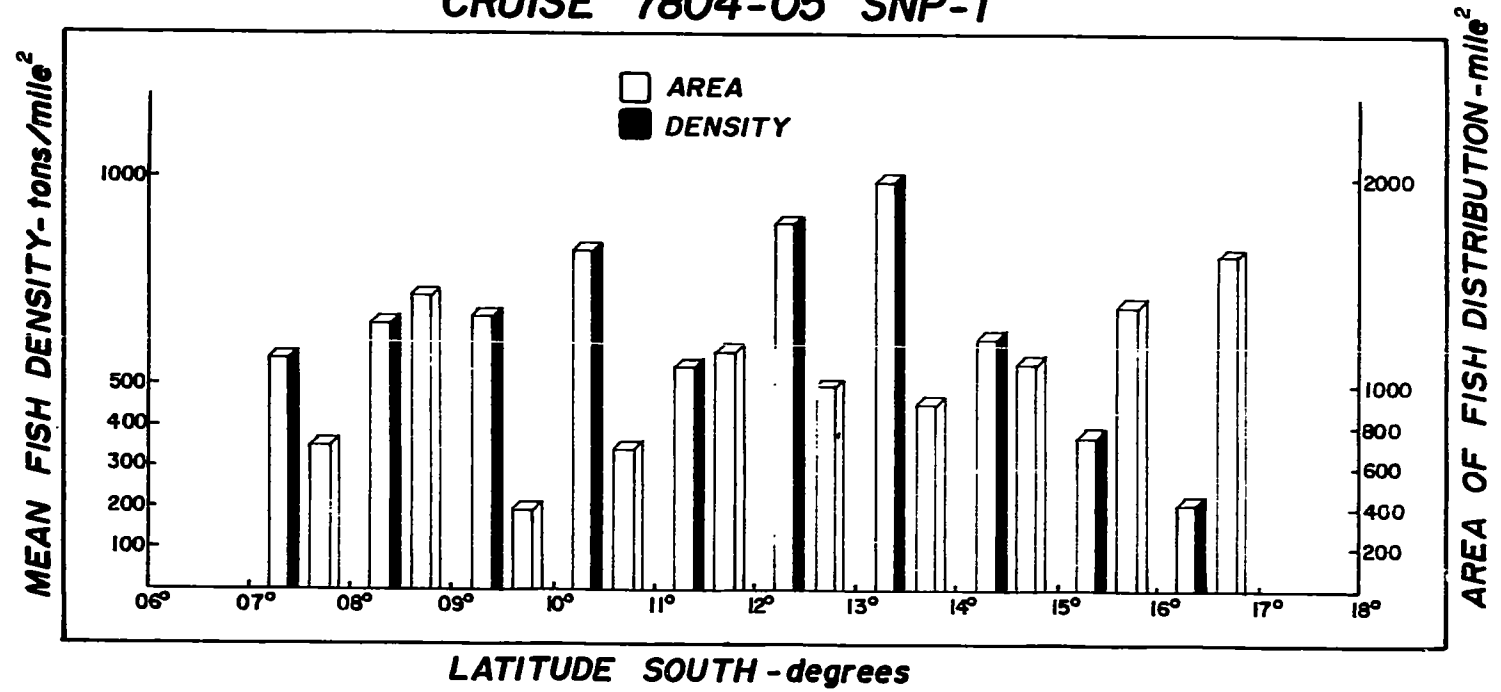


FIG. 20

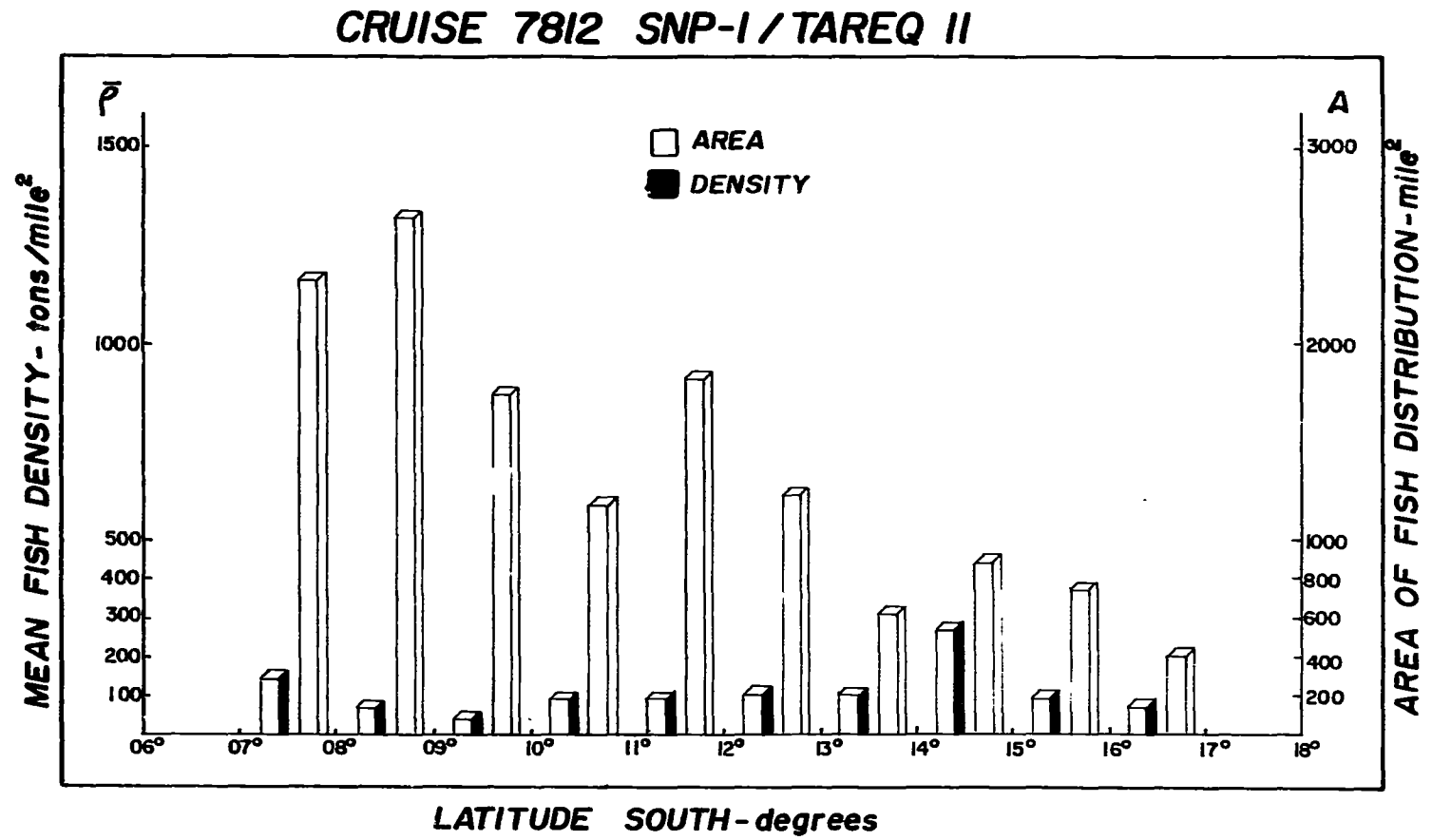


FIG. 21

CRUISE 7903-04 SNP-1

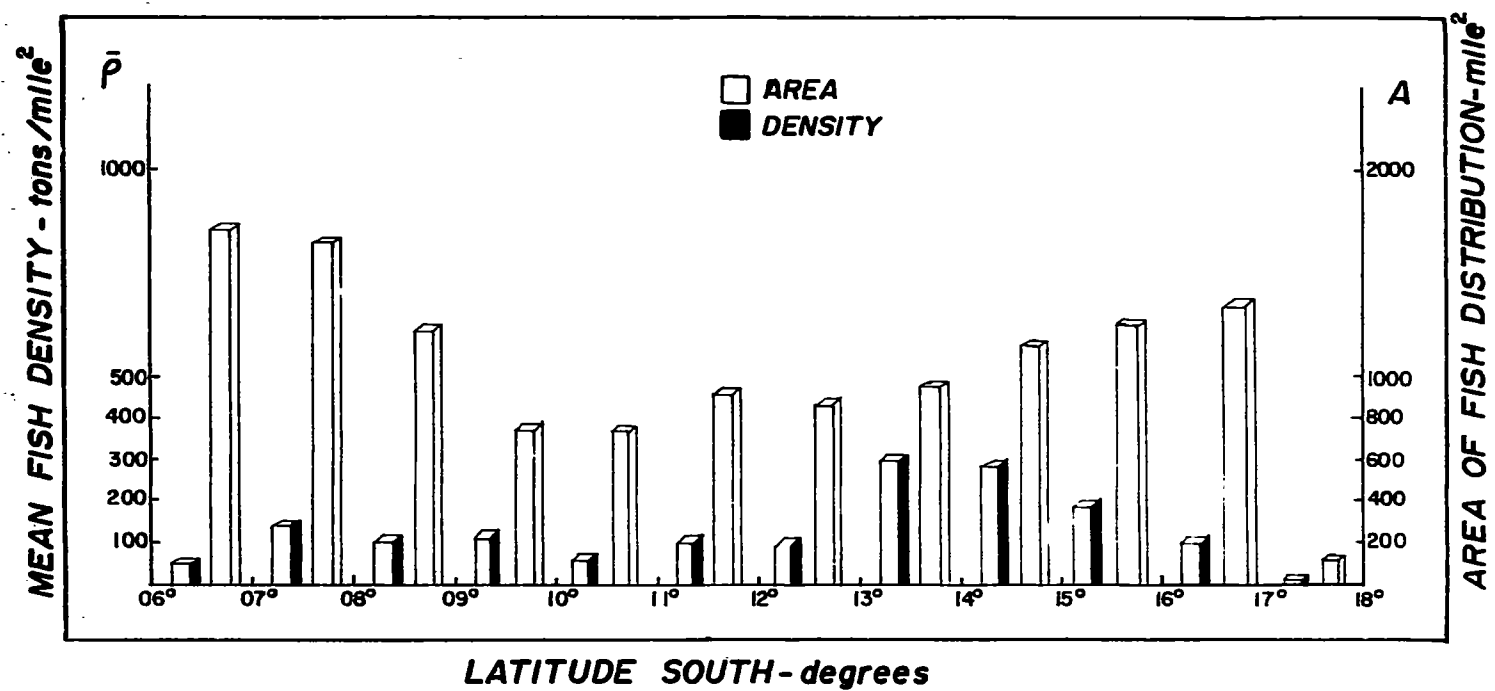


FIG. 22

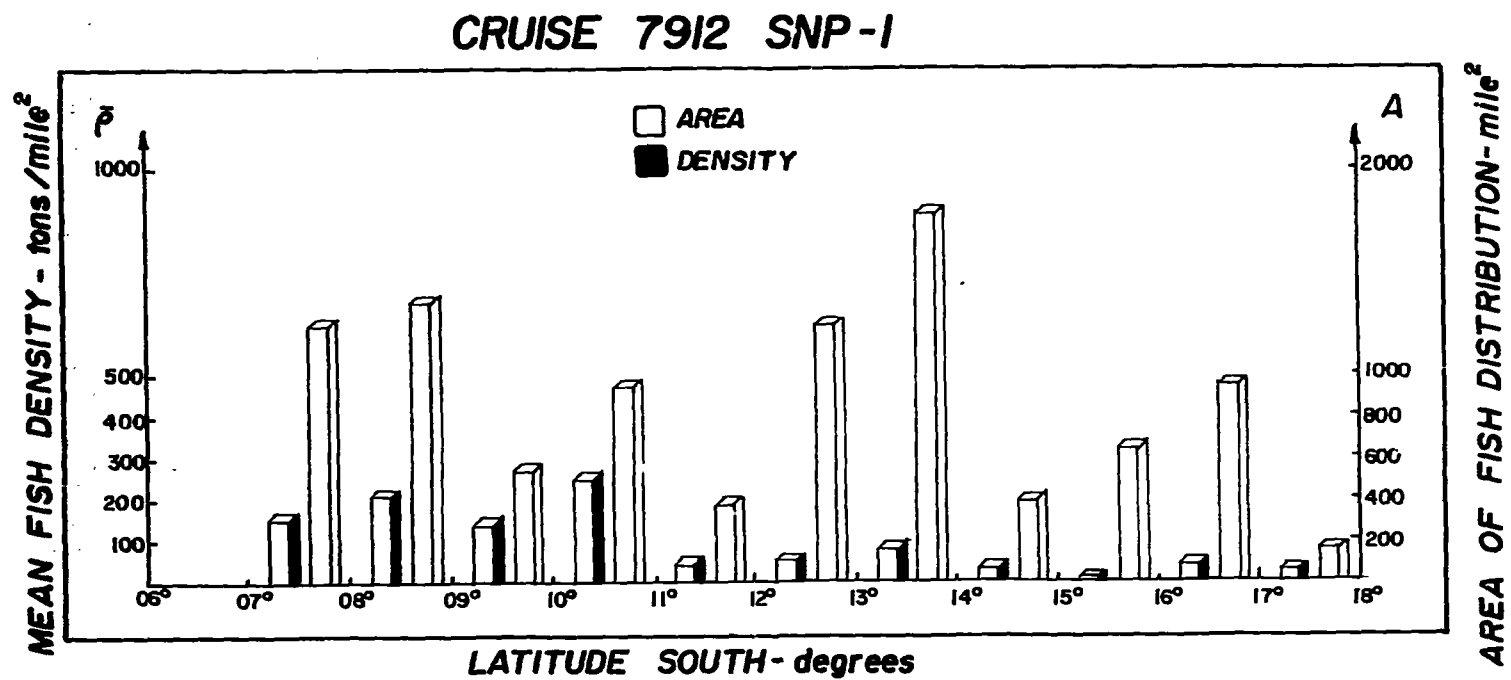


FIG. 23

that the data points for 1973 and 1974 are obtained from Jóhannesson and Robles (1973) and Edwards, 1975, respectively. The 1973 estimate was adjusted in the light of improved calibration techniques.

The density graph shows violent oscillations in mean stock density between years with a minimum of approximately 80 tons/mile² in 1975 and 1977, and a maximum of about 900 tons/mile². Also, very sharp density changes are observed on a seasonal basis, notably from summer to winter 1976, and similarly, though on a varying scale, in 1977, 1978 and 1979. In addition, a drastic within-season increase in density level was measured in winter 1976, a change caused by the massive recruitment in late 1975 and early 1976, which again contributed to what became a temporary recovery of the stock in 1976.

It should be pointed out that the concept of mean stock density with respect to hydro-acoustic estimation procedures should be treated with caution because of nonrandomness in distribution. For better illustration of the point, it can be mentioned that estimates derived from the 7302 cruise data showed that 55 percent of stock biomass was concentrated in only 13 percent of the total area of distribution. Likewise, during the cruise 7603, 36 percent of the biomass fell within only 3.4 percent of the total area.

Comparison of density- and area-graph (Fig. 24) indicates that these variables can either follow the same direction or, to the contrary, an increase in density may coincide with a reduction in the area of distribution. Hence, the graphs do not bear out earlier assumptions that in winter-time the stock will disperse and thus occupy a larger area, while during the summer seasons the stock will generally concentrate near-shore with consequent reduction in area of distribution. On closer scrutiny of the graphs, it seems reasonable to suggest that the violent fluctuations within the anchoveta population (represented in the density graph) are of such a magnitude as to obscure a behavioural pattern considered characteristic of a "normal" situation.

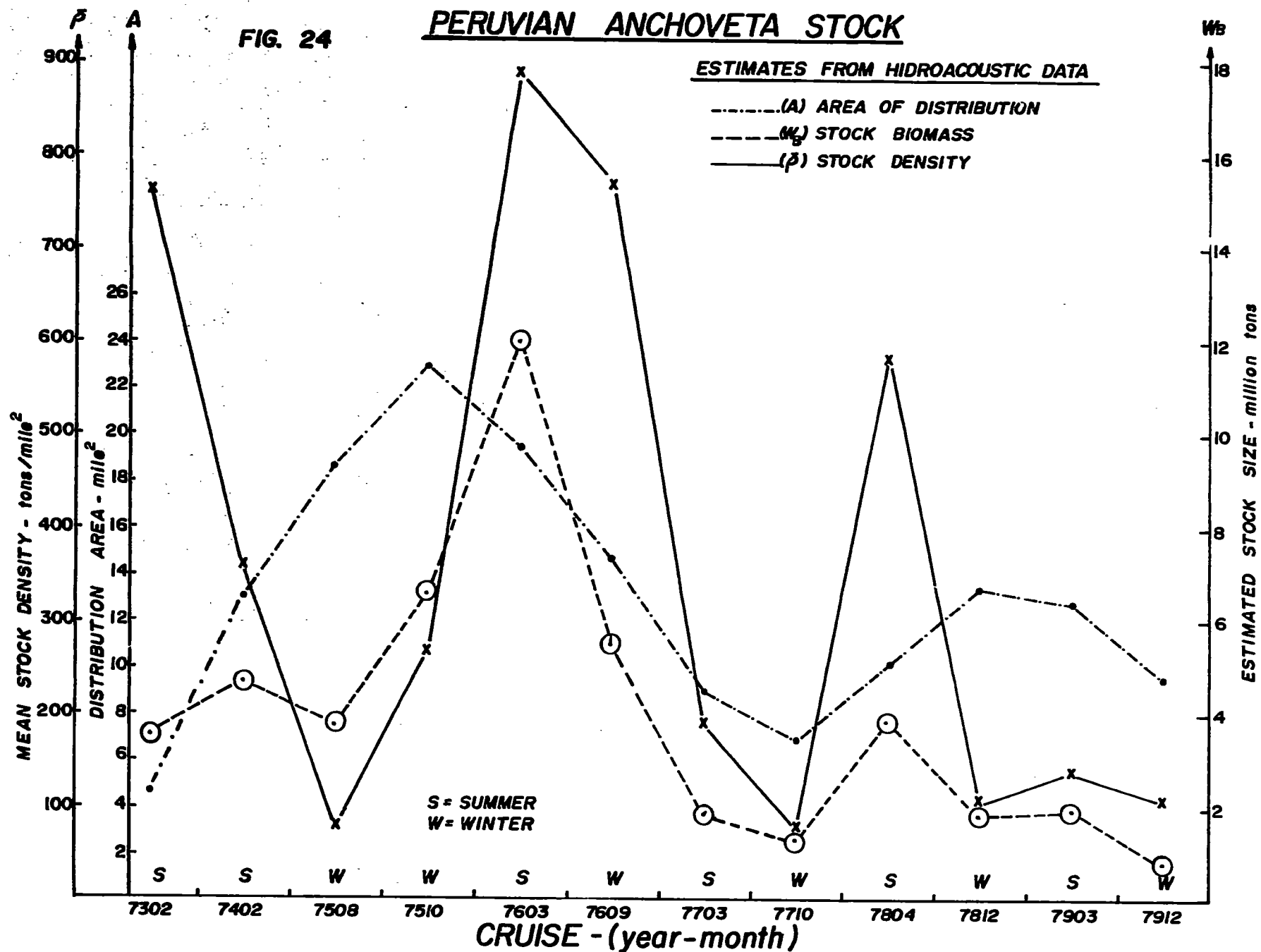
Other pelagic species

For the purpose of this note "other species" are defined as: sardine (pilchard); caballa (Pacific mackerel); jurel (Pacific jack mackerel); and agujilla (saury).

For these species, only a brief and very generalized description can be produced on the basis of the hydroacoustic data available. The role of the acoustic surveys in the study of these particular species has been basically to provide absolute estimates of the total biomass, and to monitor possible variations with special reference to recent exploitation of the resources.

Distribution

Generally, the heaviest concentrations of jurel, caballa and the big sardine are found offshore at a distance of roughly 20-60 nautical miles. The small sardine is usually found closer inshore and mixes with the anchoveta within the area but not so much within schools. Both species exhibit similar schooling pattern and density characteristics, a fact which prohibits hydroacoustic distinction to be made between them. The agujilla is mostly detected in the southern part; occurring typically near the surface, is a highly mobile species, and is found within wide bands or swaths along the coast. It is therefore a relatively poor target for hydroacoustical estimation techniques and probably makes up an insignificant component of estimated biomass for "other" species. A typical chart showing the geographic distribution of "other" species in four density categories is shown in Fig. 25. Data from cruise 7803/04, made in March/April 1978, was used to graph total biomass (including anchoveta and the small sardine) in the form of relative echo-abundance profiles perpendicular to the coast, by degree latitude. The results, presented in Fig. 26, show a fairly well defined bimodal distribution in the area from Callao to Pimentel. In the area south of Callao and down to San Juan, the same tendency to a bimodal distribution is shown, although not so marked as in the north. This bimodal characteristic of the coastwise distribution is better



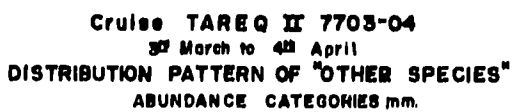


FIG. 25

CRUISE 7803/04 R/V SNP-1
(25 February - 20 April, 1978)

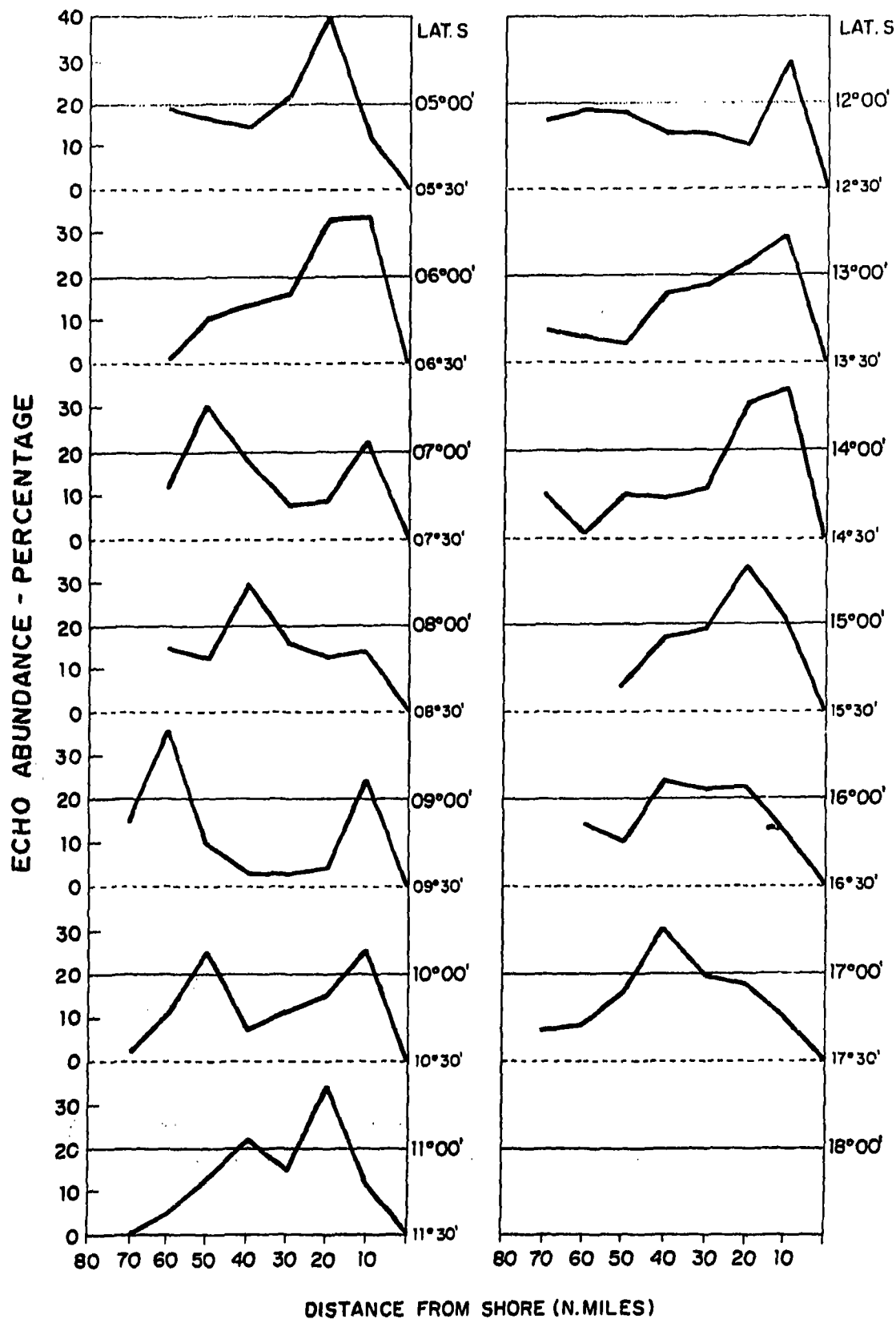


FIG. 26

brought out from an example of three-dimensional plotting (from Jóhannesson and Mathisen, 1980) of data from cruise 7603 in March 1976, shown in Figs. 27 and 28. The figures clearly show the dense near-shore concentrations of anchoveta predominantly, followed by a zone of low fish abundance and then increased biomass on the shelf break by other species, mainly mackerel and jack mackerel. To date, five separate estimates have been made of the magnitude of "other" species; these are presented in Fig. 29-b which is largely self-explanatory. However, it should be noted that the survey cruise corresponding to estimate (d) failed to give a realistic result due to adverse survey conditions and insufficient area coverage. This was confirmed by the subsequent survey which yielded a much higher estimate (e), still thought to be an underestimate of the biomass, mainly caused by considerable offshore migration of jack mackerel beyond the boundaries of the area sampled. A verification of this assumption was provided by results of a recent survey carried out with the Polish research vessel "Professor Siedlecki", which covered an area up to 180 nautical miles offshore. At the time of writing, no official biomass estimate has been worked out from the data, but it seems that the forthcoming assessment will be considerably higher than the approximately five million tons shown as estimate (e) in Fig. 29-b.

In the light of the result obtained from the above surveys, it is reasonable to conclude that they have generated a general picture of the distribution and changes in the abundance of "other species" during the past four-year period. Future research efforts aimed at improving the acoustic information input should include revised survey design, so as to cover the whole sampling area of interest, and also give higher priority to detailed analysis of the data collected.

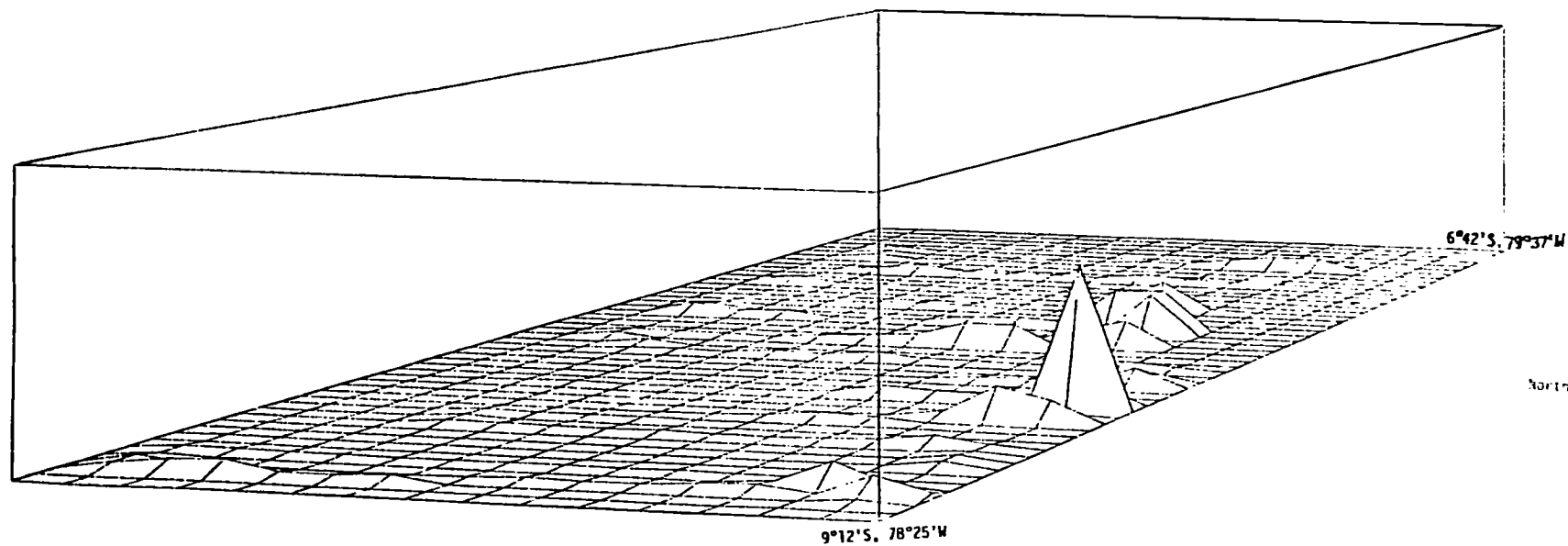
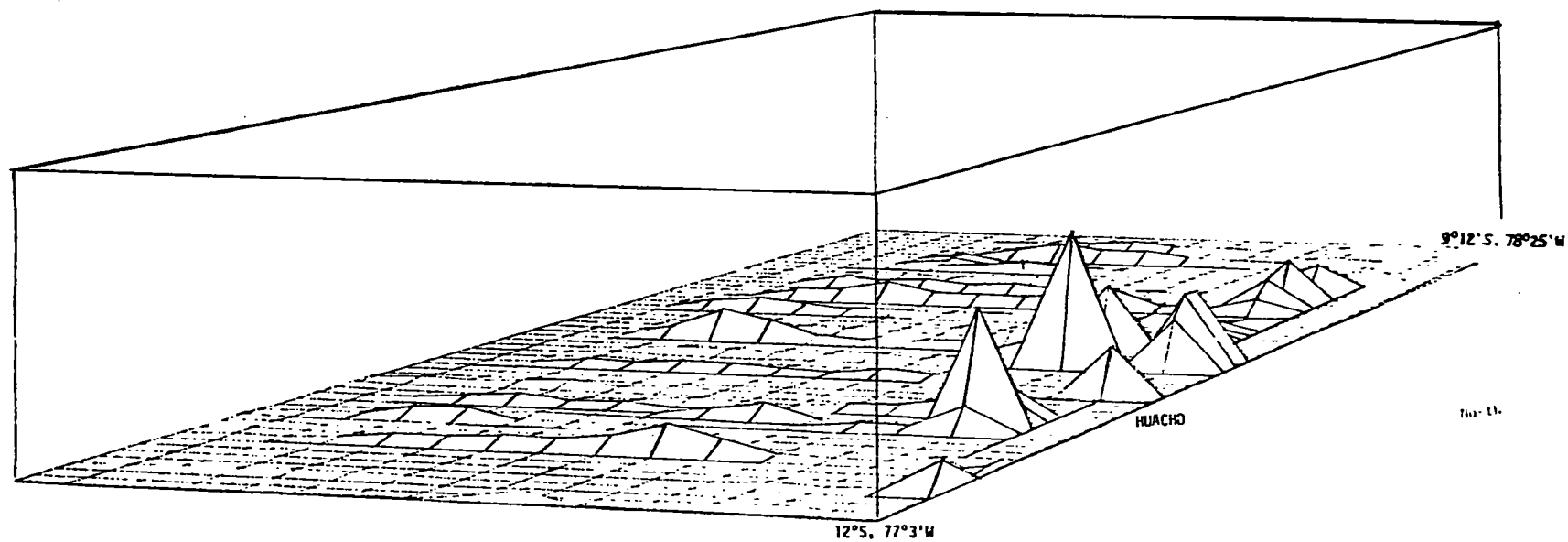


Fig.27. Integrated echo intensities plotted on a real scale.

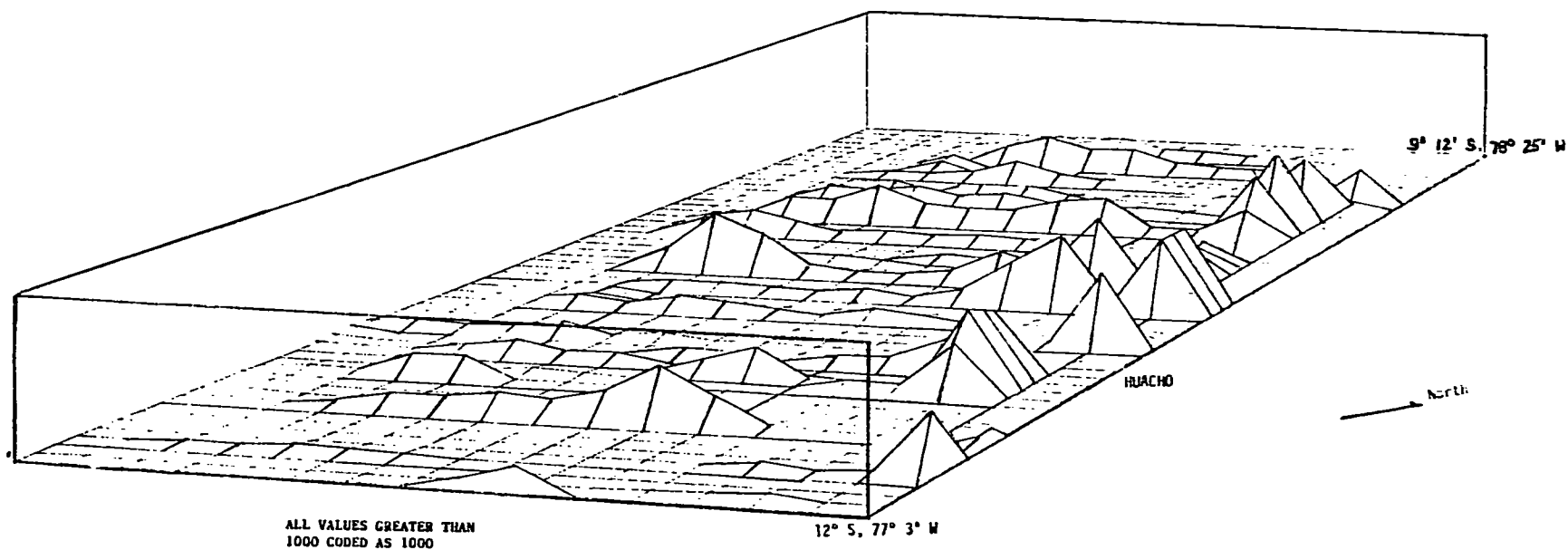
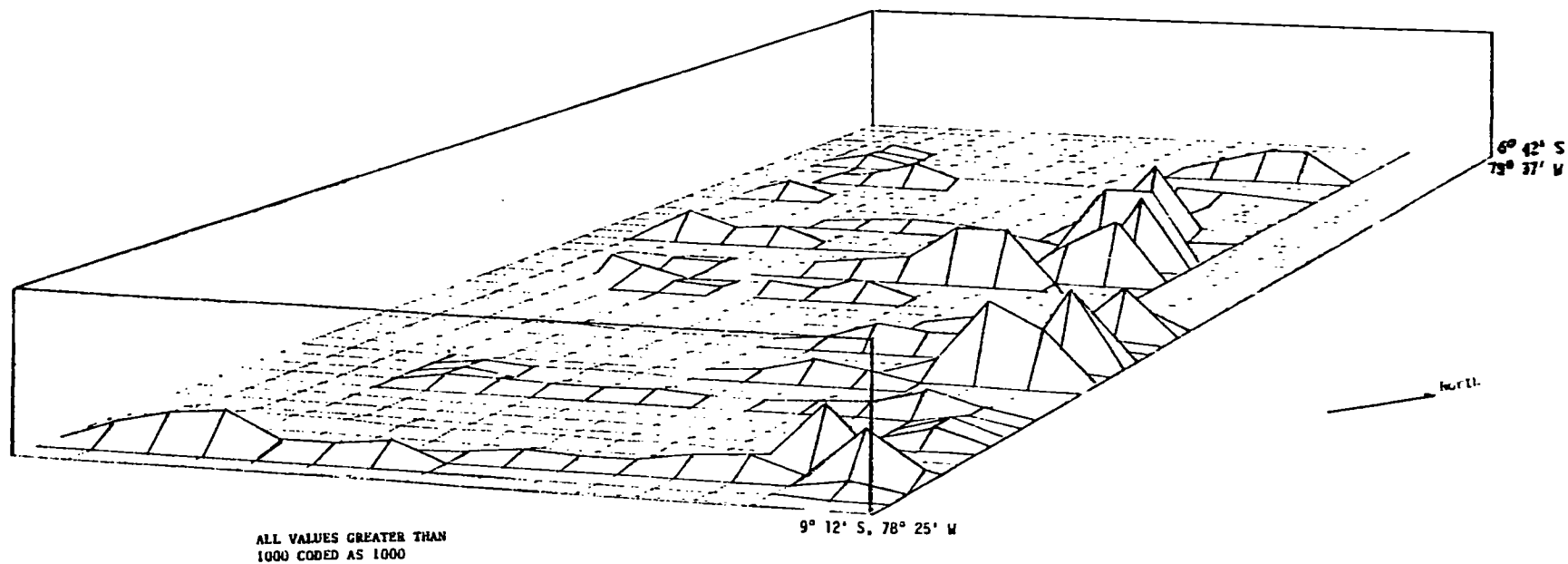
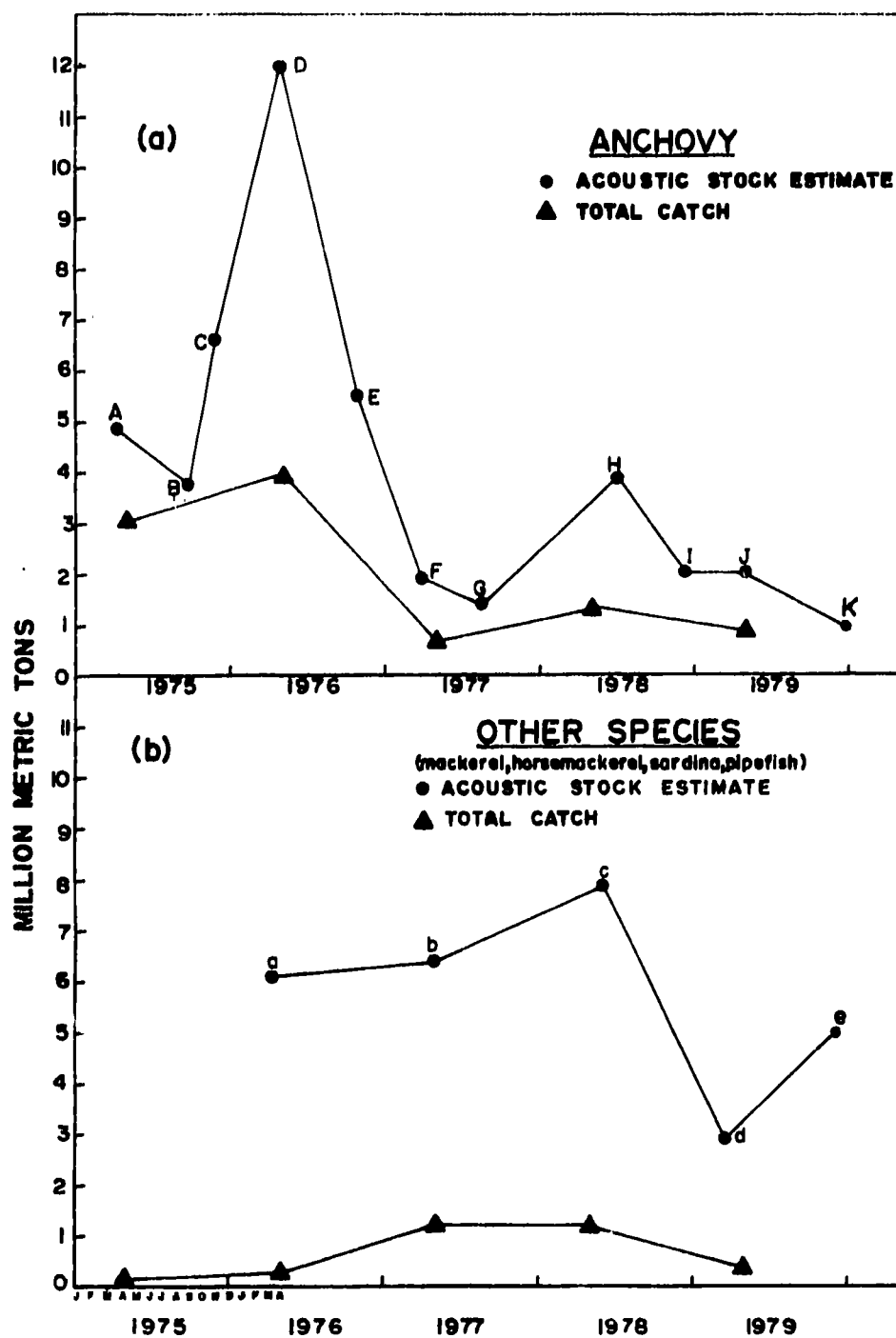


Fig.28• All integrated echo intensities censored above a value of 1000.



REFERENCES

- JOHANNESSON, K.A. and A.N. ROBLES. 1977. Echo surveys of Peruvian anchoveta. Rapp. P.-v. Reün.Cons.Int.Explor.Mer., 170:237-244
- JOHANNESSON, K.A. and R. VILCHEZ. 1979. Application and some results of echo-integration methods in monitoring Peruvian anchovy resources. USA/USSR Meeting on Acoustic, M.I.T., June 1979. M.S. 23 pp.
- JOHANNESSON, K.A. and O.A. MATHISEN. 1980. Monitoring surveys of the Peruvian anchovy (*Engraulis ringens*). Acoustic krill estimation, Working Party-News, Vol.2, No. 3, April 1980.
- MATHISEN, O.A. 1979. Adaptation of the anchoveta (*Engraulis ringens* J.) to the Peruvian upwelling system. USA/USSR Conference on upwelling, October 1979. 36 pp. (mimeo)
- VILLANUEVA, R. 1975. The Peruvian Eureka Programme; Rapid acoustic surveys using fishing vessels. Technical Conference on fish finding, purse seining and aimed trawling. Reykjavik, Iceland, 24-30 May 1975. 12 pp.