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DRAFT REPORT

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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 Organisation 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 attendees at the workshop and their affiliations are given in Appendix I. The Agenda for the workshop is given in Appendix II.

The major emphasis of the workshop centered on the descriptions of existing 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 evaluating 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.

Several background documents were provided by the attendees, from which much of the discussion and most of this report will refer.

These documents summarize our understanding of relevant biological and oceanographic properties at the various scales of accurrence 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 often contributes more than half of the total fishable stock.

If recruitment is highly variable as is usually 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 dissapearance twenty years ago. On the other hand, the Japanese sardine fishery suddenly recovered form nearly undetectable levels to a present level supporting a multimillion ton fishery. Perhaps the most 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 goverment and industry are faced with the problems of long-term planning in an uncertain enviroment. There is a demand for a forecasting ability providing at least a six-month lead time

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 (*Tranchurus symmetricus murphi*), 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 spp.*), due to the large amount of scientific and fishery information which has been gained on the genus, especially including the California and Peruvian resources. The biology of Peruvian anchoveta constrains the predictive information which can be gained. 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 month 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 recruitment.

The possibility of a six-month forecasting ability based on enviromental 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 enviromental monitoring are unlikely to provide useful information to the commercial sector in the immediate future. Goverment and industry planners are seldom equipped with a scientific understanding of the nature of uncertainty. 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 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.

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 occuppied 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 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 relation between recruitment and stock depends upon our ability to define the "system state (e.g.

carrying capacity 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 environmentaly induced effects. In a sense this workshop was a response to the void in effort to combine the more realistic environmental variation with modern concepts of feeding limitations as a major obstacle to be overcome if any survival and subsequent recruitment is to be observed, or forecast with any degree of accuracy.

Classical stock and recruitment considerations

The general biological knowledge on the stock and recruitment relationship is poor. However we do know that the mean recruitment level is almost constant in a large intermediate domain of variation of the parental stock (see Figs. 1 to 3) .

For example, in the case of North Sea herring, it follows from Fig. 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} . It is important to note that this low 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 (i.e. growth overfishing) , not of the recruitment. It is only when the rate of fishing is increased beyond a certain level to strong growth overfishing that recruitment is affected (i.e. recruitment overfishing according to Cushing, 1972, 1974) . In case of North Sea herring, such a transition from growth overfishing to 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 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 ,

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

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.

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

where N (t) is the number of survivors or the size of the year class (population) at age t and M the instantaneous rate of mortality . Eq. (1) is the solution of this differential equation if

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

where t_r is the age at recruitment.

In the Ricker type of recruitment,

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

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 $E = 1/R_2$) towards zero as the production of eggs increases. This recruitment decline is explained by cannibalism of the young by adults. These matters are described more fully by Ricker (e.g. 1954). We merely note here that the basic assumptions underlying Eq. (2) are that there is food competition between the young fish and that their mortality rate is constant until the fish have achieved a certain size.

This is about all that is known explicitly about recruitment. Almost all available data on stock and recruitment refers to the medium range of variations in the spawners. It is here that most 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 show relatively small variations about this mean level considering the great reduction in numbers from the egg stage until maturity (Ursin, 1979 b).

The stability of recruitment

Table 1 gives relative recruitment variations for 11 commercial 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 set 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 billions 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.

We could also consider stability in terms of recruitment to the mature stock. During its life time a cod must produce an average of one mature female and one mature male. Only extremely small deviations from this number (2) are 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 lay, say, two millions eggs in its short life time, or whether we are considering an average production of 40 millions 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 fine adjustment of recruitment to maturity.

Note that North Sea haddock and Norway pout show a remarkable instability in recruitment (Table 1). It could be that stabilizing mechanisms 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 recruitment stability among the North Sea species, but rather end by considering the stock and recruitment problem from general points of view.

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 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 ($M_{overall}$) by

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

If we assume a constant fecundity (f) for members of the spawning stock (5), we have

$$E = f\ S$$

We can combine these two equations to give

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

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

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

$$\text{where } (M_1 + M_2 + M_3 + \ldots.) = M_{overall}\ ,$$

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 concentrations of esculent particles, which indicates a higher likelihood of subsequent successful feeding, which may not require as high a density of food at later stages as for larvae which had less available food initially.

Alternatively, the sum of many such probability distributions 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 component 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.

Toward' modelling recruitment

It is difficult to attack the 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 only achieve one new recruitment data point per species each 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 hypotheses, all of which lead to different conclusions but none of which can be rejected on the basis of the data available (Beyer, 1976 a) . The situation is not better with respect to explanations of recruitment stability. 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 before hand unimportant mechanisms of mortality regulation from available data. Apparently we need to build more biological knowledge on the causes of natural mortality in the first year of life into the recruitment models.

Andersen and Ursin (1977) state that the mechanisms which regulate mortality in early life, must meet the requirements:

(1) A high mortality shall be induced at the 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.

And, as a temporary solution, they introduce an instantaneous larval mortality coefficient of the following type for each animal species:

$$M\,3\,(t) = \frac{N\,(t)}{R_o} \cdot \frac{1}{w\,(t)} \left[\frac{dw\,(t)}{dt}\right]_{max} \qquad (3)$$

where N (t) is the number of live fish (with body weight w/t at age t) and $(dw/dt)_{max}$ is the highest possible growth rate at age t. R_o 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 because the second part - the maximum relative growth rate at age t - decreases with increasing size of the fish (cf. $dw/dt = H\,w^{n} - kw^{n}$) 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) .

Since this initial attempt there have been several different approaches taken including those of Vlymen (1977) , Beyer (1976 a and b) , and Beyer and Laurence (1980) to explain the effects of feeding behavior, 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.

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

Density dependent egg cannibalism

The number of hatched eggs effectively introduced into the larval environment (here called effective fecundity) is likely one of the strongest density-dependent elements of the stock-recruitment relationship for the anchoveta. 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 actually hatch to produce 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 ruther constant over a wide range of population sizes. In the latter case, the proportion of spawners increase linearly with stock size, but in warm-water years there is a domed relationship, with the maximum number of spawners occuring 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 (oral presentation). Egg size may vary due to biotic and abiotic factors, and particularly, there may be an inverse relationship between egg size and fecundity (e.g. see Bagenal 1969) . While a relatively small change in egg diameter may not seriously affect egg survival, the associated larger change in egg volume 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 larvae, probably requiring higher densities of prey for sufficient feeding to promote growth. Also predators must also consume more at high temperatures due to their increased activity and metabolic demands.

Mortality due to predation on eggs in conveniently assumed to be independent of, for example, anchovy stock density. However, there may be a correlation of unknown sign: on one hand adults may tend to congregate and spawn in areas of high food supply, and egg predator abundance may also tend to be high; on the other hand, 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 numbers of eggs and larvae in anchovy stomachs have not appeared significant. However, if the number of eggs consumed between spawnings is calculated, a sizeable percentage of virtual fecundity may be lost. Hunter (in press) has calculated that fifty percent of the total mortality rate of E. mordax eggs may be accounted for by cannibalism.

Mac Call (eq.4) has developed a model for anchovy egg cannibalism, which relates effective egg production to measureable variables. This model also provides on analytical basis for Csirke's (1980) stock-cpue-recruitment model for peruvian anchoveta, which includes stock density as so 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 197-) . 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) :

$$E = f\ N\ e^{-mt}\ e^{-pvt\ N/V} \qquad (4)$$

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 natural mortality , although the value of the maximum is not. Assuming a habitat depth of 39 m, and a p of 1.0 , the optimum population density is 3 fish (C 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 (Johanneson and Vilchez, this volume) , and densities greatly exceeding these values have been observed. For example, in 1976, densities of 1500 to 3000 tons/mi^2 were common, and this almost certainly indicates a harvestable excess of fish over optimal spawning densities.

Csirke's (1980) empirical model of the peruvian anchoveta remains the only useable model of anchoveta stock-recruitment which recognizes density effects. For Mac Call's model (this volume) to be a useful management tool, 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.

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.

jgt.

CAUSES OF CHANGES OF POPULATION ABUNDANCE

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 lifes' 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 esculence) 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) .

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 anyones perceptions regarding the behavior of "traditional" stock status estimators. The present evidence indicates that there are 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 southern most population center. 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 was the lowest experienced to the date, leading to a rapidly observed effect which has been hailed as the onset of the demise of the anchoveta stocks.

There were several events prior to the 1972 recruitment failure which suggest that the decline in anchoveta abundance was "determined" 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 can be hypothesized to have provided the final necessary precondition which led to the eventual 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 and 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 was only 40% as compared to 90% in previous years. The fat content of the 1971-72 catch was anomolously high. Although 1971 was judged to be a "normal" oceanographic year, the stimulous to transfer accumplated body fat to gonad products did not occur. Recruitment was poor as a result of this physiological "malfunction".

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 fishery abundance variations without a better understanding of the interactions between the food, fish and exogenous 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) shows that high egg density (abundance) may yeild low recruitment, even with high phytoplankton abundance. On the other hand, in 1975 there appeared to be both low food and low egg densities, which yieled a relatively high recruitment. The interesting "anomaly" in this year was the high concentration of <u>Gymnodinium</u>, over 100 particles per ml were measured in one spawning area. <u>Gymnodinium</u> 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 typical size-weight expectation. This condition was likely due to a low abundance of phytoplankton in the pre-spawning period.

There are several characteristics of the anchovetta eggs and larvae which vary with increased latitude. For example, egg size increases as latitude increases, yeilding larger larvae. As the larvae develop into juveniles even more diversity in available food, and basic behavioral 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 the 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 (oral presentation) 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 yeild a somewhat trendless proportion which varies from 8.0 percent up to 24.4 percent. The warm years range from only 4.1 percent to 10.5 percent at large adult biomass ($>$ 12 K 10^6 mt), and 6.7 to 30.0 percent at lower adult biomasses. Figures 4 and 5 show these data.

These observations indicate that several inter-related changes have occured in response to climatic, oceanographic, and/ or fishery related pressures. The problem is 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. One of the major problems in most fisheries research is the over-emphasis of fishery associated sampling, and lack of appropiate fishery independent biological and environmental information. Fisheries are notoriously biased samplers of resource populations and often yeild misleading results if not carefully evaluated in comparasion with other data sources.

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

In fisheries, the term availability is used conceptually to indicate that a variable portion of any population is susceptible 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 asurred. 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 accoustic surveys, are also by nature selective, and low levels of sampling effort make them higly 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 stock size, recruitment, egg and larval survival, etc. fail so regularly and dramatically. The most basic of these intuitive concepts is that associations should de 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 attemts to by-pass the biological processes and information completely by relating stock size or recruitment to environmental factors alone. It has also led to the conclusion that a management strategy cannot usually be determined by 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 yieled remarkable insights into the changes in behavior and occurence in and among years which cannot be evaluated from fishery 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 availabe regarding population abundance variations.

The responses of populations to subtle oceanographic ambient changes is often not apparent from only 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 these are preferred fishing areas and species, or conditions which promotie high vulnerability through aggregation phenomena (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 poorly sample the resource adding to the uncertainties of stock status in the absence of independent methodologies.

Primary productivity and fishery production

Guillén (oral presentation) has related the overall production from the four major areas in the Peru Current to the total catch taken in the fishery. He has shown a relation between the major upwelling area off Chimbote, with fishery production and the hydroacoustic 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 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 production periods and areas correspond with the changes in spawning peak periods and areas.

The Chimbote area differs from the other upwelling areas in that it has more moderate upwelling rates, over a longer period (i.e. February thru October) than any other area. Adult fish appear to be able to cope with the transport rate induced by both the wind and upwelling, and thereby staying within the system can 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 long 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.

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).

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.

The "ultimate" model would be completely rational, but in nearly all relevant cases our ability to measure adequately all important parameters and analyze their interactions, resulting in a "forecast", would likely take more time and resources than are available, or practical.

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 in 73% of 22 particle profiles and 53% 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 behavior, 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 (83 %) 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 that 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 denisty 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 nutient 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 (Fig. 18) . Small ciliates (20-50 μm) were the most numerous larval fish food item present, showed pronounced patchiness on the sub-meter scale but were not clustered on the 5 cm scale, as indicated by small differences between replicates. Large ciliates (50-100 μ m) were less numerous but covaried 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 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 meters 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.

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. Laevastu and Favorite ( ) have constructed a large book-keeping or 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 much more realistic than the single species approach which has dominated fishery science for several generations. The question becomes whether fishery assessment programs are really ready for integrated efforts to resolve the problems of evaluating the various commercial species' status. Doing less appears to be integrating out most of the important processes, resulting in 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 programs and analyses which would be needed, where today's research programs tend to emphasize the simplistic, desk-top science approach. The resolution of this dichotomous situation will be left in the hands of resource evaluation program 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 programing level.

The apparent failure of most stock assessment programs to evaluate resources, implement their recommendations and provide for effective resource management (Saeterstal, 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 measureable qualities and quantities as habitat stratification, distribution, and variations in time and space. The need for developing multi-disciplinary fishery data collection programs has been long recognized and responded to in many fishing cultures. The generalization of this approach seems warranted.

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Available conceptual models for evaluating environmental effects on fish survival

Parrish, Nelson and Bakkun (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. Mac Call (this volume) has given a supporting underlying model of the density dependent process (cannibalism) under 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 on 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 behavioral 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, multispecies level would appear to be an ideal, but perhaps unachievable objective, if one could fill in 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.

Bakkun 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 as realistic a 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 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, Guillen'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 production is not retained to the same degree, and this alone may account for the differences in fish production between the two systems. Bakkun and Parrish hypothesize that the offshore transport of the phytoplankton and zooplankton (as well as eggs and larvae in some areas) could limit the availability of the egg-larval requirements, but not the adult's, as the adult requirements are far less in proportion to available food than is the larval habitat availability to the larvae.

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The Role of Modeling in Predicting Survival of Fish Larvae in the Ocean Environment

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 be utilized for examining the sensitivity of the overall model to changes in a particular (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 heirarchy 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 biology would have its Newton, then psychology, then economics. But since Newtonian-like description has turned out to be inadequate even for physics, few beliebe this anymore. 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 emphasis of this workshop has been 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 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 measureable parameters or 2) any attempt to describe (model) the mechanisms of complex biological-enviromental-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 limitation 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 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 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".

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 parametrized in the model as a continual addition to the existing stock.

One way to improve the predicability of a model is to reduce the level of parameterization of important processes. One may do this in fishery model 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 funtions which are "guessed" from some poorly related source.

Types of Models

There are three level of sophistication in modeling, which we will call 1) "back-of-the envelope" calculations, 2) over-simplified models and 3) complex "-ecosystem" models. However complex, 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.

Over-simplified models involve more mathematical computations than types I models (i.e. they take more than one "envelope"), but are still too simple to compare directly with field data. An example in the context of predicting spawning success would be a fisheries model which incorporated environmental influence on value of r. 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 may be difficult to sort out the most important processes. 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 I 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 nonlinear, 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 nonlinear 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.

An example of a useful "back of-the-envelope" model which can yield insights into the relation between environmental processes and egg and larval survival is a simple scale analysis.

Scale analysis as a tool for identification of the important processes governing fish larvae survival in the ocean environment.

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 cannot 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 behavior, physiology and predation primarily determine larval survival.

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

$$\frac{dF}{dT} + \nabla\cdot \underset{\sim}{V} F - \nabla\cdot(K\Delta F) = \text{biological processes} \quad (1)$$

Where t is time 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 dept h. The advection terms in equation (1) can be rewritten

$$\nabla\cdot \underset{\sim}{V} F = u\frac{dF}{dx} + v\frac{dF}{dy} + w\frac{dF}{dz}$$

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

$$\nabla\cdot(K\nabla F) = K_h\frac{d^2F}{dx^2} + K_h\frac{d^2F}{dy^2} + K_v\frac{d^2F}{dz^2}$$

One can compare the relative influence of the physical and biological processes in determining the distribution of larvae by scaling all terms in equation (1). Let

$$x = Lx' \qquad u = Uu'$$
$$y = Ly' \qquad v = Uv'$$
$$z = Lz' \qquad w = Uw'$$

Where L and H are characteristic horzontal 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 d, the critical time scale for larvae survival, then scaled time Finally, if $\bar{F}$ is a typical value for F so $F = \bar{F}F'$, equation (1) becomes

$$\frac{dF'}{dt} + \left[\frac{U}{L\alpha}\right]\left[u'\frac{dF'}{dx'} + v'\frac{dF'}{dy'}\right] + \left[\frac{W}{H\alpha}\right]\left[\frac{w'dF'}{dz'}\right] \quad (2)$$

$$-\left[\frac{K_h}{L^2\alpha}\right]\left[\frac{d^2F'}{dx'^2} + \frac{d^2F'}{dy'^2}\right] - \left[\frac{K_v}{H^2\alpha}\right]\left[\frac{d^2F'}{dz'^2}\right] = \text{scaled biological processes}$$

The magnitude of the nondimensional coefficients in equation (2) 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 nondimensional coefficients, clearly for small length scales (meters) the physical processes of advection and turbulent diffusion are very important relative to the biological, processes. If one evaluates the magnitude of these coefficients for upwelling regions where vertical velocities are relatively large, vertical advection can be the same order of magnitude as biological porcesses (Wroblewski, 1977). During strong wind events when mechanical mixing of the water column gives rise to vertical eddy diffusivities of 100 cm^2/sec, the turbulent transport terms can be critical in determining larval survival. (Lasker (1975) observed the dissipation of the chlorophyll maximum and the associated food for larvae during a wind event off Southern California, from which this hypothesis arose).

Scale analysis of equation (1) has shown that for small length and short time scales, physical processes in the water column are at least as important as biological factors in determining larval survival.

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 behavior and physiology of fish larvae during the period when they are most susceptable to starvation. Kullenberg (1977) , Woods (1979) and other physical oceanographers have modeled the physical processes which govern stratification and mixing in the upper layer of the ocean. Stratification of the water column permits plankton 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 modeled 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 continous 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 (1973 and 19[illegible]) and Mendiola and Ochoa (1973) . For 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 rom 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

$$E_{IN,L} = \sum_{i=1}^{N_{\Delta T}} SS(D_i) * cal(D_i) * S_c{}^* \qquad (1)$$

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 level required for feeding C^* .

Depending on the size specific energy requirements for capture, processing and maintainance, 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

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

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[1] SS (D_i) includes the ability to capture food and the willingness to attack i.e SS $(D_i < D_L)$ = SS $(D_i > Du) = 0$.

From equation (1) it is clear that the input energy $E_{IN, L}$ depends only on the product SS (D_i) * 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 $C >$ the critical level C^* and when

$$D_L < D_i < Dw ,$$

the number of attacks in the interval ΔT depends upon the characteristics of the environment in which the larvae is found. In particulars 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, behavioral 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 could vary from 20 to 70 per cent 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 meter but the amount of effort required to adequately describe large areas of the sea by this technique is too great for 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 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 behavior 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 when determine the degree to which patches formed at the thermocline are able to persist in the mixed layer.

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 centimeters to a few kilometers and horizontal length scales from centimeters to 1000's of kilometers. 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 physical processes and models we associate with these scales. The smallest physical scales we shall consider are 1 cm. At centimeter 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 ratio 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 anisostropy still exists with 100 to 1000 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 kilometers.

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 kilometers. 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 boundery current systems, weather patterns and El Niño are features to be described on these scales.

Distribution problems of biological variables in relation to physical oceanography conditions

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 homogenous 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.

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

$$C\,(t) = \frac{M_o}{\sqrt{2\pi}\cdot H_o \cdot L_o \cdot P \cdot t}\; e^{-\frac{\pi^2 \cdot K_z \cdot t}{H^2}}$$

where M_o, H_o, L_o 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

$0.01 \leq P \leq 2.0 \ \mathrm{cm \cdot s^{-1}}$ and

$0.01 \leq K_z \leq 200 \ \mathrm{cm^2 \cdot s^{-1}}$

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.

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)

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

where W_{10} is the wind speed at 10 m, $N^2 = -\frac{g}{\rho}\frac{d\rho}{dz}$ is the stratification parameter with ρ the density and g the acceleration of gravity; $\mathbf{q}$ is the horizontal current vector. The numerical constant = $Rf \cdot \; - \frac{\rho_a}{\rho_c}$ is about 10^{-7} (Rf is the flux Richardson number, 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, ( ) can be estimated over time scales of hours and an expression for the momentum transfer coefficient and the momentum 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

ω = omega
σ = sigma

$$\sigma_y^2 = \left(\frac{dv}{dz}\right)^2 \cdot \frac{K_z \cdot t}{\omega^2}$$

with σ_y^2 being the lateral concentration variance where $\frac{dv}{dz}$ is the shear of the oscillating current component perpendicular to the line source and is the fre - quency 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, assumming 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.

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 meters to tens of kilometers and vertical scales from tens of centimeters 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.

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 $m \cdot s^{-1}$.

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 matter (chlorophyll, passive tracers) can be built up in these transitions or interface layers.

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 the surface layer (euphotic zone) in not too clear water for zenith sun is of the form

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

where E_o 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

$$E = E_o \; e^{-K(90^\circ) \; z/\cos\Theta}$$

where K (90°) 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 disorption properties, and dissolved organic substances.

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

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 one day, then these patches can't 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 Niiler 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 one 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 behavior 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 doesn't 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.

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:

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

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 :

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

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:

$$\frac{h}{u_B^2 u_D} = \frac{2c\rho_B k \varepsilon}{\alpha g Q}$$

In the original paper it was assumed that the right-hand side of the above equation was constant in time and space . A critical value of $\frac{R}{u_B^3}$ was then shown to be associated with the transition between stratificacion 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:

$$\frac{u_B^2 u_D}{Q h} > \frac{\alpha g}{2c\rho_B k \varepsilon}$$

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:

$$\frac{u_B^2 u_D}{h} \doteq \frac{u_B^3}{h} > 13 \quad \text{(cgs units)}$$

(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

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 $d\rho$ = 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

$= 6\pi\eta r w_s$ (Stokes law)

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

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

Now , $r \sim 10^{-2}$ to $10^{-2.5}$ cm.

$d\rho \sim 10^{-4}$ (in mixed layer) cgs

to -10^{-3} (below mixed layer) cgs

$g \sim 10^{3}$ (cgs) , $\eta \sim .01$ (cgs)

w_s is in range 5×10^{-4} to 5×10^{-5} cm/sec
(in mixed layer)

or 5×10^{-3} to 5×10^{-4} cm/sec
(below mixed layer)

(The values of $d\rho$ 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:

a) For a length scale of 3000 cm. (the thickness of the surface mixed layer) the corresponding settling time is greater than one week.

b) Active particle (eg. dinoflagellates) can overcome density effects if their swimming speed is in wxcess of 5×10^{-3} cm/sec.

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 rhickness equal to:

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

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

The above thickness is hence in the range

0.2 cm. to 20 cm. $(K = 10^{-3})$

2×10^{4} cm. to 2×10^{6} cm. $(K = 100)$

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

0.15 to 15 cgs.

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 of fish at present. However, a wind-driven 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, and pelagics like Trachurus, 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 anchovetta 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 persistant 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 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.

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 (T dep)
2. Gut volume (L dep)
3. Digestion/ evacuation times (T dep., food dep)
4. Metabolic rate (T dep)
5. Length/weight relation
6. Age/length (T dep, food history dep)
7. % successful capture (age dep, particle dep)
8. % body weight = ration per day
9. Gross growth efficiency (assumes constant energy expediture)
10. Size specific prey selection
11. Seasonality of spawning - egg deposition
12. Behavioral information

Much of this requires intensive laboratory 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. Appropiate (esculent) food particle distributions
6. Stratification/mixing frequency related to (5)
7. Insolation rate
8. Tidal flux

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 occuring in late winter and maximum temperatures occuring in late summer. The upwelling maxima cycles show considerable differences in the two regions. The upwelling maxima in the Perú 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 occuring near the upwelling maxima and maximum dinoflagellate abundance occuring 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 6 gives the spawning periods of the four important pelagic species in the California and Peru Currents, where known.

The early life history concepts developed at the workshop appear to lend themselves to testing by comparing the spawning cycles and environmental conditions occuring 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 (ala Tsukayama and Alavarez, this volume)
4. Frequency of spawning (ala 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 are readily constructed system models which would be useful in testing the first feeding success leading to 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.

CONCLUSIONS

The trend in the past larval fish 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 it 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 to be dealt with in egg 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 obtains his first meals, he becomes 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".

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 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 (meters) and food distributions would improve our conceptural 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.

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 process 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 method 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 centers, including climate and oceanographic science in this realm , that the uncertainties of population abundance prediction can be reduced by intense, integrated efforts to sample, study and interpret results of research at appropriate scales, namely tens of meters 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.

jgt.

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