

Report of a Colloquium on Larval Fish Mortality Studies and Their Relation to Fishery Research, January 1975

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ABSTRACT

One of the critical problems in fishery research today is the inability to determine how the abundance of adult fishes affect the strength of incoming year classes. The report summarizes the discussions of experts on how studies of larval fish mortality may assist in solving this problem. Included in this report are discussions of the principle causes of larval mortality and their possible relation to stock size. Guidelines and recommendations are made regarding future research on the mortality of larval fish.

INTRODUCTION

One of the critical problems in fishery research today is our inability to determine how the abundance of the adults affects the strength of incoming year classes. Thus, the management strategy that should be adopted to ensure good recruitment is unknown. Relating recruitment to parent stock seldom gives useful answers even when many years' data are available. It was agreed that a precise determination of the stock-recruitment relation earlier in the life history lies in a better understanding of mortality and growth in the larval stage.²

Similarly, the factors which maintain the stock within the observed limits or which cause the occasional and remarkable rises or falls in population (e.g., the collapse of the Pacific sardine populations), as well as many of the critical aspects of competition between species, also appear to have their effect in the first year of life. Neither those changes in growth nor those in natural mortality, which occur after recruitment, are sufficient to be controlling factors. Studies of larval mortality appear to hold the key to determine the factors controlling the fate of fish populations.

On the other hand, it appears unlikely that it will be practical to use the results of larval counts and measurements to provide timely estimates of year-class strength. Several other methods may be available for early estimation of year-class strength, including commercial catches of very small fish, and trawl or acoustic surveys on different sizes of fish. The choice among these will be determined by the costs involved, the general variability of year classes in the stock, and the timeliness and accuracy required. It appears that the high costs and time delays in processing catches of larval fish to provide estimates of year-class strength are reasons for using alternate methods to determine year-class strength. However, for species that have a distribution greater than the range of the fishery, or for those where no commercial fishery exists, the best available method for estimating abundance is the egg and larval survey even with its inherent limitations.

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² All stages between egg and recruitment would be interesting to investigate and may have importance in the stock and recruitment relation. However, this Colloquium has focused primarily on the contribution of studies of the larval stage.

The importance of the stock-recruitment relation and the difficulties in solving it suggest that as long as larval mortality studies offer some reasonable chance of resolving the problem they should be actively pursued. However, no certainty exists that larval mortality studies will, in any reasonable time, resolve the stock and recruitment problem in a fully satisfactory manner. Attention needs to be concentrated on differences in larval mortality rates between high and low adult densities, between years resulting in good and bad year classes, and between areas of better or worse larval survival.

The work required includes the estimation of larval mortality at sea under different conditions of food and stock; construction of models to simulate larval mortality with limits set on food, predation, and stock; and laboratory and field experimentation designed to estimate the parameters needed for the models. Although it is important to treat the problem of stock and recruitment in a holistic fashion, it is unlikely that any new general models can be formulated at the present time. Variables requiring detailed examination are likely to differ from stock to stock. Similarities may exist within systematic groups, for example in codlike fishes or within ecological associations, such as that of Pacific sardine, *Sardinops sagax* (Jenyns), and northern anchovy, *Engraulis mordax* Girard; but even here, differences in seasonal phenomena, such as time of spawning, may require different approaches.

CAUSES OF MORTALITY

It is our opinion that the major causes of larval mortality are starvation and predation, and that these may interact. Larval research has been weighted toward studies on food, feeding, and starvation in fish larvae. Relatively little work has been done on predation. We believe that effort should be directed to studies of the relative importance of starvation and predation and, in some cases, other possible sources of larval mortality, such as disease, parasites, pollutants, turbulence, transport, and mechanical damage.

The number of eggs per female, as well as quality of eggs (biochemical content, size, and genetics) may also be important. In a given species, e.g., the Atlantic herring, *Clupea harengus harengus* Linnaeus, fecundity and egg size are inversely related, hence if a large number of eggs is produced, the average egg size is small and the average time to starvation of larvae will be shorter. Field studies on the

fecundity-egg size relation would appear not to have immediate utility in relation to density dependence.³ On the other hand, the number of eggs spawned per female can be influenced by abiotic factors, such as temperature. Temperature can influence onset of spawning and even the duration of the spawning season; in the 1950's this was true for the Pacific sardine. Temperature may control the number of eggs that could be matured and spawned and therefor influence recruitment.

DENSITY-DEPENDENT MORTALITY

The principal concern of larval fish studies should be to study the density-dependent aspects of starvation and predation because these aspects of mortality, we believe, will provide the understanding of the stock and recruitment relation. To determine density-dependent mortality one must either measure it directly or measure density-independent mortality and subtract it from total mortality. To separate density-independent mortality from density-dependent mortality is probably not possible at present. Nevertheless, some possible density-dependent mechanisms for starvation and for predation are described below.

Mechanisms of Density-Dependent Mortality Caused by Starvation

Three density-dependent mechanisms relating to starvation are 1) intraspecific competition for food, 2) increases in adult population that lead to the expansion of spawning into areas where the probability of concentrations of food suitable for larval survival are very low or nearly non-existent, and 3) interspecific interactions.

Intraspecific Competition for Food.—The spawning behavior of the adults must be understood before considering the intraspecific competition of larvae for food. In demersal spawners, the density of spawn in a patch may be a function of population size and an increase in population size may lead to increased spawning intensity within the optimal habitat rather than an increase in the breadth of the spawning area. On the other hand, in pelagic spawners, a possible result of an increase in size of the spawning population is an increase in the size or number of patches of eggs and larvae rather than a higher density of eggs or larvae within a patch. Thus, population size may not control the outcome of intraspecific competition within the patch of first feeding larvae of pelagic spawners. Intraspecific competition for food that produces a density dependent mechanism could occur after the larvae begin schooling and consequently become aggregated. By this stage, the larvae have a greater food storage capacity, greater body reserves, and increased speed so that their susceptibility to starvation is less than that of younger stages.

Expansion of a spawning population.—The second mechanism considered here is the expansion of a population and consequently its spawning activity into less suitable areas. The tacit assumption in this mechanism is that at lower population levels, the boundaries of the spawning

population become confined to an area where the long-term probability of the larvae finding food is greater. Two density-dependent mechanisms relating to food can be proposed depending on the characteristics of the area to which the species becomes confined under lower population levels. One such area could be relatively large geographically, where survival depends on coincidence of larvae with concentrations of food (patches) that are highly unstable and vary greatly in space, annually, and within a season. The alternate possibility is that within the typical spawning area of a species there exists a limited area that consistently produces suitable concentrations of food throughout the spawning season and from year to year. This area would be a relatively stable food enclave that is consistently used for spawning. One can conceive of many intergradations of these two extremes, but the important point is that each would produce different mechanisms relating to starvation, and the problem of starvation and density dependence should be examined in this context.

Interspecific competition.—Starvation mechanisms must be viewed in the context of possible interspecific interactions. The enclave mechanisms described in the preceding section could lead to more intense interspecific competition between ecologically similar species,⁴ e.g., the anchovy and sardine. If at low population levels, a population spawns principally in a small consistently favorable forage area, it might be expected that the eggs and larvae of ecologically similar species might also be concentrated in that area, and consequently the likelihood of competition for food increases. Population changes may also be mediated through rather subtle interspecific interactions. For example, an infrequent, unbroken series of years disadvantageous to any two species might exceed the longevity of one species but not the other, allowing the latter species to achieve subsequent dominance by reproduction of the survivors.

Knowledge of which mechanisms are important for a species would require measurements of the distribution of patches of eggs, larvae of all species at the same trophic level, their food, and determination of the persistence of these patches within a season and from season to season. The approach used to collect these data would differ depending on the hypotheses to be tested. Intensive field work over a limited area would be required for the enclave work whereas extensive rather than intensive field work would be required for the mechanisms involving large geographic areas.

Mechanisms of Density-Dependent Mortality Caused by Predation

Predation on larval fishes that could produce density-dependent effects include: cannibalism by adults; reproductive response of a predator population to the production of eggs and larvae; attraction of predators as a function of the size or density of patches of eggs or larvae; selection of prey by the predator as a result of experience; and survival of the predator as a function of the abundance of eggs or larvae.

Predators could be planktonic or nektonic. The latter, such as fish, could aggregate in patches of larvae or eggs by kinetic mechanisms such as changes in swimming speed or

³Some members of the Colloquium believed that critical studies on the fecundity-egg size relation need to be done on a population basis.

⁴Researchers should recognize that some species may compete only during the larval stage.

frequency of turning which could be a function of the size or density of patches of larvae or eggs. Planktonic predators may select eggs or larvae as the result of past experience. There also may be a minimum quantity of larvae needed to elicit selective predator response.

To evaluate the reproductive response of a predator to eggs or larvae, the duration of spawning of the prey must be considered. In subarctic areas where the spawning period is short, there may be little time for a predator to specialize on any particular developmental stage of the fish population. On the other hand, in the tropics where spawning often is continuous, a predator could specialize on a particular developmental stage and predators with long generation times could cause density-dependent mortality of larvae. Predators could also produce density-dependent effects through changes in their survival rate. The response of a predator population to an abundance of eggs and larvae could be decreased mortality from starvation. Hence, the predator could have a potentially greater impact at high population levels of eggs and larvae than at lower levels.

GUIDELINES FOR THE STUDY OF STARVATION

Certain laboratory studies are essential for an understanding of starvation as a cause of larval mortality. They are needed to interpret field data and to identify parameters and their range of values. The committee suggests the following kinds of laboratory studies, not necessarily in order of priority:

1. A study of the feeding strategy of larvae to determine patterns of activity, feeding, aggregation mechanisms, search patterns, and prey selectivity.
2. Studies of effects of temperature to determine hatching times and developmental rates and to know when larvae require food.
3. Studies of larval fish energetics that allow one to specify the concentration sizes and nutritional content of food particles required for maintenance and growth.
4. The determination of digestion, assimilation, and food conversion rates.
5. Establishment of anatomical, histological, biochemical, or physical criteria that indicate larval starvation or viability.
6. A study of the development of sensory and motor capabilities of larvae.
7. The study of egg-size distribution within a species and its effect on larval size, early swimming ability, size of potential prey, and resistance to starvation.
8. The study of the relation between a larva's ability to avoid predation and its physical condition and size.

Many of these studies have been done for some of the more frequently studied and cultured marine fishes, e.g., plaice (*Pleuronectes platessa* L.), northern anchovy, and Atlantic herring; but in no species is all this information complete. On the other hand, attempts to relate these laboratory findings to field conditions are rare. We believe, therefore, that the most critical areas in the study of starvation as a cause of mortality are transitional studies

that bridge the gap between laboratory and sea work. Three approaches exist: 1) application of laboratory results to the field situation; 2) development of new experimental techniques that can be used at sea; and 3) development of new mathematical models from existent laboratory and field data.

Development of models to relate laboratory studies to starvation at sea are greatly hindered by the lack of adequate information on the abundance and spatial and temporal distribution of food of the appropriate size for fish larvae. Few studies of this kind exist and there is an urgent need for this information before realistic models can be developed. These models should point out where there are critical gaps in our knowledge and thus provide a guideline for future studies. Where studies exist, data seem to indicate that the average density of food in the sea is often insufficient to provide a larva's daily requirement. When the average density of food is less than a larva's daily requirement, it becomes advantageous to larvae for food to be distributed in patches. Thus, it appears that the patchiness of food may be a factor that reduces larval starvation. For this reason, we shall deal separately with the problem of patchiness of food and then consider transitional field studies.

Patchiness of Food and Larvae

Patchiness of larvae and their food must play a crucial role in survival. Confusion exists in the terminology used to describe patchiness. Patchiness may be examined at various spatial levels which need to be accommodated within existing descriptions. Patches may range from tens of kilometers, large enough to be sampled and studied conveniently, to patches equivalent to the perceptive field of the organism or its cruising range. The latter category could vary with organism size; for example, the patches of larval food could be measured in meters, patches of larvae in tens of meters, and patches of their predators in hundreds of meters.

The factors associated with patchiness of phytoplankton and zooplankton include nutrient distribution and diffusion, light penetration, growth and reproduction, and the presence of strata of food organisms as well as the swimming kinetics of some food organisms. Patches of eggs and larvae could be caused by spawning habits of the parents, selective survival of larvae, kinetic mechanisms of larvae, and schooling or other social behaviors of larger larvae. Kinetic mechanisms that could produce patchiness of larvae are motor patterns that result in larvae finding and remaining in areas where they find food. This mechanism may be significant only on a small scale whereas patchiness produced by selective survival, that is, patterns of larval distribution produced by discontinuous areas of survival and mortality, might be evident only on a much larger scale. Larval schooling could produce patchiness, but in many epipelagic larvae, schooling develops late in larval life and consequently would be of greater significance to juvenile survival.

Variables that could cause dispersion of larvae and their food include: wave-induced turbulence, wind-induced shear, upwelling, tidal currents, and eddies of various time and space scales. Dispersion of patches can best be studied by measuring changes in the distribution of the organisms and not by measuring the continuous characteristics of physical and chemical factors of seawater.

Scale, persistence, and other characteristics of patches of

larvae and their food should be studied. It should be recognized, however, that such work should be considered as a first step in the broader objective of obtaining time series data showing the changes in patchiness from season to season or from year to year. Recent observations indicate that the relation between persistence of patches and abiotic factors, such as wind strength, should be investigated.

Transitional Field Studies

In this section, six types of field studies will be considered that should help relate laboratory to field studies on starvation as a cause of mortality.³ Each is considered separately below.

1. **Assessment of age of larvae in the sea.** A critical problem in larval mortality studies is the assignment of absolute age to larvae collected at sea. The ability to age sea-caught larvae in increments of a day or several days would greatly facilitate estimates of mortality and other life history parameters. It is particularly important to evaluate growth in terms of temperature and food availability. Aging may possibly be done using size and morphological characteristics corrected for temperature in selected species. More general means must be sought for other species. A promising technique is the use of otoliths for measuring daily growth increments. This technique should be explored intensively to ascertain how early a valid age determination can be made. Other age determination techniques also need to be developed.

2. **Bioassay experiments.** In these studies, laboratory spawned larval fish are used in shipboard feeding experiments designed to determine if water from a particular location and depth in the sea is suitable for larval survival. Owing to possible differences between laboratory-reared and wild larvae, these experiments may have to be confined to younger larvae. Work of this kind is already under way at several laboratories (Bergen, Norway; Brookhaven National Laboratory; Southwest Fisheries Center, U.S.A.), and it seems to be a useful method for determining suitable areas and depths of larval food and for estimating patchiness.

3. **Assessment of starvation in the sea using net-caught larvae.** In these studies, criteria are developed in the laboratory to identify starving larvae, using anatomical, biochemical, or other criteria. Net-caught larvae can then be examined using these criteria to determine the incidence of starvation or general health of the larvae. Work of this type is under way in several laboratories (Dunstaffnage, Scotland; Southwest Fisheries Center) and seems promising.

4. **In situ growth and mortality experiments.** In these studies, larval fish are placed or entrapped in an enclosed or partially enclosed volume of water at sea, and mortality and growth measured over a period of days or weeks. A completely enclosed container, like the plastic bag experi-

ments of the past, could be used; or a cylinder could be provided with a bottom that can be pursed. In the latter case, the depth of the cylinder would have to exceed the vertical migrating tendencies of the larvae. To assess density-dependent mortality, different stocking densities of larvae could be used. Predation could possibly be simulated by use of a plankton net. Such experiments with larval fish are untried and the panel was not in general agreement on the value of such an approach.

5. **Following cohorts of larvae at sea.** It is proposed that a cohort of larvae or group of cohorts could be followed to record growth, estimate mortality, and estimate abundance of food and predators. This technique allows multiple pairs of observations of mortality and other parameters to be obtained from each spawning cohort. Plaice larvae in the southern North Sea form clearly recognizable patches that have been followed for 10 to 20 days. The continued identity of plaice patches is ensured by the complete vertical mixing in this area. Elsewhere, shears at different water depths could break up identifiable patches. It might also be possible to choose an area without a patch and to follow the population of larvae through that region; but this approach would be practical only if the initial spawning is limited in area and time.

6. **Coincidence of larvae and their food.** Many plankton surveys in the past have not sampled the microzooplankton which is eaten by fish larvae. It is important that such surveys be made so that the coincidence of larvae and food of the appropriate size can be determined. The scale of sampling is an important consideration of this work, because scale must be considered in terms of larval behavior and the patchiness of the food. Systematic work on the naupliar and copepodid stages must be encouraged as the early stages of many important species cannot be identified. Work on the production of biomass for these stages must also be done.

GUIDELINES FOR THE STUDY OF PREDATION

Predation studies have been so neglected that it is difficult to specify in detail the work that needs to be done. Indeed, the brevity of the following section reflects the paucity of knowledge. We believe that predators need to be identified; their co-occurrence with larvae and eggs, their abundance in time and space, their feeding strategy, and their ability to capture different life stages need to be determined. It is of major importance in any study of predation to examine the possible interactions between starvation and predation. Clearly, if slower growing larvae and larvae weakened by starvation are ingested much more frequently than healthy ones, the controlling mechanisms must be sought in food abundance rather than in predation alone. It is also of major importance that density-dependent mechanisms, such as those described in preceding sections (e.g., cannibalism, reproductive response, and other responses by predators) be evaluated.

Hypotheses on the nature of larval predation should be tested by appropriate analyses of past data and specially designed studies. As a first step, potential predators must be identified by examination of their gut contents. Residence time of eggs and larvae in their intestines should be determined. Predators may be identified by observing

³Professor John Isaacs remains convinced that "the remarkable relationships between the numbers of day-caught and the numbers of night-caught larvae (over the properly sampled size range) of the sardine and anchovy are interpretable in terms of relative growth rate changes and relative mortality of the two larval species. These criteria, derived from the zooplankton net samples of the CalCOFI Cruises, 1951-1957, correlate closely with estimated recruitment."

aggregations of potential predators in areas where spawners, eggs, larvae, or later stages are congregated. Potential predators may also be identified by analysis of the abundance and co-occurrence of possible predators with eggs and larvae from ichthyoplankton survey collections and other survey data. In concert with field studies, laboratory experiments should be done on the effect of larval size, larval condition, predator search patterns, and feeding behavior on the degree of predation. Laboratory studies should also be done on larval avoidance mechanisms, recovery from predator attack, and residence times of identifiable eggs or larvae in guts of predators. Once predators are identified and their predatory potential evaluated, sea studies should be made to determine density and distribution of predators in relation to target species, and field models of predation (e.g., an encounter model) should be developed.

RESEARCH RECOMMENDATIONS

1. We recommend that efforts be made to develop methods to directly age larvae captured at sea on an absolute time scale to confirm age determination based on length frequency. Such studies should first be carried out in the laboratory and then applied to sea-caught larvae.
2. We recommend that studies be initiated in the laboratory and at sea to assess the effect of predation on larval mortality and that interactions between starvation and predation be emphasized.
3. We recommend that work be continued on relating food supply to larval mortality. Of particular importance is the need for transitional studies that link laboratory and field studies, including estimates of the relevant microzooplankton biomass that constitutes the food of larval fishes; studies of the patchiness of food distribution in the sea and its impact on larval survival; and development of methods to determine larval viability from sea-caught specimens.
4. We recommend that simulation models of the recruitment process be developed. These models should have the following characteristics:
 - a. The models must be able to account for mortality rates of the observed order of magnitude.
 - b. They must be able to account for density-dependent mortality if it exists at some stage between egg and recruitment.
 - c. They must be sufficiently generalized to obtain simultaneous estimates of mortality in more than one species to allow the possibility of detecting competition if it exists.
 - d. Realistic variations in the basic input parameters should not generate variations in the resultant recruitment any greater than those observed in the sea.

e. They should be biologically plausible.

5. Finally, we recommend studies of the relations between numbers of larvae alive at various stages and subsequent recruitment, in order to establish the earliest stage at which recruitment is determined. This would reduce the number of life stages needed to be studied to determine the density-dependent effects of larval and juvenile survival on the strength of future year classes.

SELECTED REFERENCES

Listed below are a selection of general references dealing with larval fish research and related fishery problems. General reference books and reports of symposia were chosen because most of the pertinent information on larval fish mortality can be found in them. In a few instances, individual research papers are given because the work was too new or was not included in one of the cited reviews.

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