The Role of a Stable Ocean in Larval Fish Survival and Subsequent Recruitment

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Pelagic fish populations can and do undergo precipitous and catastrophic recruitment failures. Peru suffered a massive collapse of its fishery for anchoveta, *Engraulis ringens* (Valdivia, 1978), resulting in a reduced catch from 1971 to 1973, i.e., from 12 million to 2 million tons, an economic disaster. Experts called in by the Food and Agriculture Organization of the United Nations and the government of Peru noted that the decline in the population of the Peruvian anchoveta had much in common with similar declines of other clupeoid species, e.g., the Atlanto-Scandian herring, the Pacific sardine, the Hokkaido herring, and the Japanese sardine (Murphy, 1974). They concluded that heavy fishing on a parent stock after the appearance of several poor year classes is sufficient to reduce the stock's reproductive potential to a point where it can no longer produce enough recruits for the fishery.

However, a very small population size did not prevent the recent resurgence in the fishery for the Japanese sardine, *Sardinops melanosticta*. This is a striking example of how a pelagic fish population can undergo a remarkable recruitment success. From 1964 to 1972, the Japanese sardine was virtually absent from local waters around Japan, but within five years (1973–1978) this fish increased steadily in numbers and now appears as a very large population around the home islands, particularly in local waters east of Honshu. The catch increased from a negligible one of a few thousand tons in 1972 to almost 1.64 million tons in 1978 (Fig. 1). Kondo (1980) attributed this increased catch to a single large year class which appeared *de novo* in 1972 and whose subsequent spawning successes from 1974 through 1977 provided the large tonnage of sardines to the fishery. Kondo believes that the breakdown of a long-established cold water cell adjacent to the coast permitted the Kuroshio Current to approach close to the home islands of Japan, that this led to an increase in the quantity of food available for larval fish (chiefly copepod nauplii), and resulted in enhanced larval survival with a subsequent increase in the sardine population.

The causes of natural large population changes cannot consistently be shown to be density dependent. The Japanese sardine is a good example of this. Its resurgence from extremely low population levels to one supporting a two-million-ton fishery in just a few years highlights anew the questions asked by fishery scientists: "To what extent can a pelagic stock be fished before subsequent year classes resulting from that stock are affected?" "At what

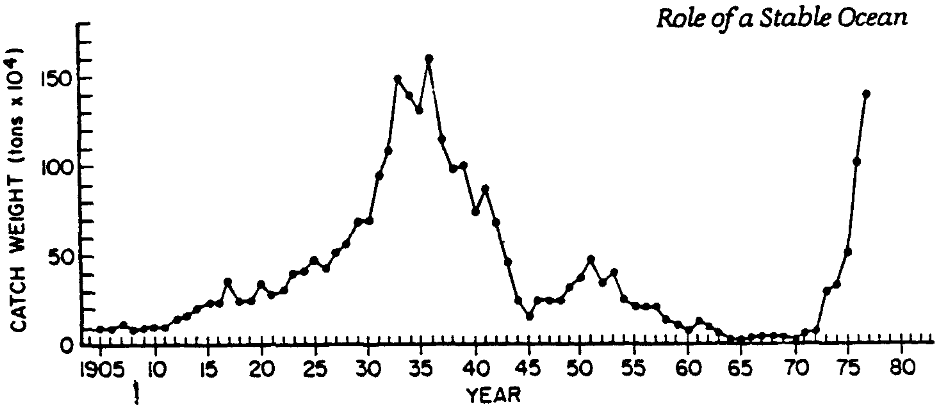

Figure 1. Fluctuation of the sardine catch around Japan (after Kondo, 1980).

population size of a fish can recruitment, the successful survival of fish from hatching to a size exploitable by a fishery, be shown to be density dependent, if at all?" Answers to these questions would help greatly in elucidating the relationship between stock and recruitment and ultimately the management of highly volatile pelagic stocks.

Over the past three decades, scientists have tried to find correlative physical, chemical, and biological ocean parameters which could be used to predict migration patterns, recruitment, and large fluctuations in population biomass—but with very limited success. The management of fish populations has marched apace, with decisions usually based on historical precedents but rarely on scientific principles. Yet the collapses of recruitment-limited fish populations have had enormous economic and social effects on fishing nations. These might have been avoided had there been reasonable predictions on the fate of the fish populations due to fishing and the environment.

The vastness of the ocean and the difficulty of sampling spatially and temporally present major problems to fisheries scientists. Fisheries managers would like useful "real time" information, but it is not uncommon to have to wait a year or longer to obtain data, process them, and reduce them to an interpretable form. Long delays in assessing the strength of incoming year classes introduce great uncertainties about future recruitment. Furthermore, most clupeoids recruit into the fishery from one to two years after they are born, accounting for a built-in delay. Statistics on cohorts, age, growth, and relative mortality must wait at least for the fish to grow up and be caught by the fishery. Predictions based on catch statistics are frequently too late to be useful, and the mechanisms determining the amount of future recruitment are not elucidated at all by a study of the catch.

Johan Hjort's Hypothesis of the Larval Fish Critical Period

While there have been a number of suggestions for investigating the stock and recruitment problem, in recent years scientists have tended toward the belief that vulnerable early life stages of pelagic fish hold some important clues to understanding large variations in recruitment. This idea is not new. In 1914 the eminent Norwegian fishery biologist, Johan Hjort, suggested that year classes of the Atlanto-Scandian herring, *Clupea harengus*, fluctuate in magnitude according to the availability of food to its very earliest larval stages. He hypothesized that resultant year classes are small when food is scarce and large when food is abundant. Although Hjort had no direct measurements to support his idea, scientists find it attractive even today, although supporting evidence is still mostly inferential and speculative. After a 60-year hiatus, Hjort's idea has been resurrected and elaborated upon, and evidence has been and is being accumulated from the ocean and the laboratory to test its basic tenets.

Does a Good Year Class Depend on a Stable Ocean and Good Food?

In California at the National Marine Fisheries Service, Southwest Fisheries Center (SWFC), La Jolla, Lasker and his coworkers have developed an extension of the Hjort hypothesis which accepts the initial premise that food for first-feeding larvae may be limited but suggests that there are times and places in the sea where food aggregation occurs and that survival of larvae depends on these. Lasker (1975) describes the use of laboratory-produced first-feeding anchovy larvae to detect good feeding areas in the sea and to establish the threshold concentrations for feeding by the larva. The importance of a stable environment for feeding was demonstrated in these experiments, and at the time of this study the nearshore less-turbulent environment was shown to be better for larval anchovy feeding than offshore in the mainstream of the California Current. Cruises in late 1974 and 1975 (Lasker, 1978) revealed a 300-kilometer-long by 4-kilometer-wide patch of the thecate dinoflagellate, *Gonyaulax polyedra*, along the southern California coast in December and its extension to 40 kilometers wide in January. While present in concentrations above the threshold for feeding during these two months, *G. polyedra* also was demonstrated to be a poor food for anchovy larvae (Scura and Jerde, 1977). A massive upwelling along the coast in February 1975 wiped out the patch and reduced particle concentrations far below threshold-for-feeding by first-feeding anchovy larvae.

In addition to food density, survival of fish larvae also depends on particle size and species composition of food organisms (Lasker et al., 1970; Scura and Jerde, 1977). For instance, in March–April 1974 the naked dinoflagellate *Gymnodinium splendens* was the dominant food particle in the larva's environment and was known to be nutritious and desirable (Lasker et al., 1970). Thus species succession, particularly after upwelling periods, may result in the replacement of desirable food organisms (e.g., some species of dinoflagellates) with undesirable ones (e.g., diatoms), once again resulting in poor larval feeding conditions despite the fact that primary production may be high.

The 1975 spawning season of the northern anchovy can be summed up as follows: (1) *Gonyaulax polyedra*, a thecate dinoflagellate but a very poor food, dominated the first-feeding larva's environment; (2) an upwelling occurred late in the spawning season which swept out this poor food, but no suitable food appeared in its place; (3) 1975 produced one of the worst northern anchovy year classes on record.

To test these ideas further, Lasker and Zweifel (1978) produced a simulation model, based on laboratory and field data, of survival and growth of first-day-of-feeding anchovy larvae, *Engraulis mordax*, on different prey sizes and concentrations. They showed that at nominal capture efficiencies of 20–30 percent, there is a threshold of 30–50 small particles (45–55 μm diameter) per milliliter needed for substantial survival and growth. Large particles, e.g., copepod nauplii (95–105 μm diameter), can enhance survival when they are in concentrations of between 10 and 100 per liter, but the same environment must contain above-threshold numbers of small particles. This simulation showed an important distinction between survival and average growth; i.e., larvae may survive in significant numbers in feeding regimes in which the *average* growth for the population is negative. The concept relating larval fish food aggregation to stability of the water column and its relation to oceanographic and meteorological conditions needs to be tested in a variety of habitats.

Vlymen (1977) showed the importance of the geometry of prey distribution in his study of the larval anchovy in physical relation to its food. In particular, his simulation model indicated that extremely different larval anchovy growth rates in the sea are the most likely functions of prey contagion, with the highest growth rates not necessarily occurring at the highest level of prey contagion. Owen (in press) sampled within chlorophyll maximum layers on a vertical scale only 20 cm apart and found significant differences in numbers of potential larval fish food organisms, often between adjacent 20 cm water samples. This seems to confirm Vlymen's contention that the centimeter scale of aggregation must exist in the sea and that it occurs for every food type yet identified as needed for larval anchovy growth and survival.

Larval fish drift and the conditions which cause it are further elaborations of the Hjort hypothesis. Some scientists believe that upwelling events, if strong enough, can carry fish larvae out of good feeding areas into poor ones. At the California coast, when upwelling is weak, the stable environment inshore results in good feeding for young fish and enhanced survival. Working with fishery statistics on Pacific mackerel (*Scomber japonicus*) year-class strength, an upwelling index (Bakun, 1973), and a wind curl index (Bakun and Nelson, 1977), Parrish (1976) and Parrish and MacCall (1978) have shown good correlations of upwelling, surface transport patterns, and year-class strength of Pacific mackerel off California.

On the east coast of the United States, Nelson et al. (1977) showed that menhaden larvae, which depend on estuaries for food, are carried into estuaries during downwelling periods. In this case, upwelling acts to the detriment of larval survival by keeping larvae offshore, a mechanism different from the disruption of food aggregations shown to be important for northern anchovy larvae.

Storms also were found to disrupt larval food aggregations, and it has been inferred that this probably results in heavy larval mortality during the anchovy spawning season (Lasker, 1975). A regional cube-of-the-wind-speed index for the anchovy spawning grounds off California has been developed by Andrew Bakun at the Pacific Environmental Group (SWFC) of the National Marine Fisheries Service and used by Lasker (in press) to correlate with good and poor anchovy year classes.

While the data are still sparse, indications are that an index of this kind, which reflects the amount of mechanical energy available for stirring the upper layers of the ocean (Niiler and Krause, 1977), may be a valuable predictor of poor feeding conditions of larvae and hence the degree of recruitment. For example, a violent mid-December 1977 storm in southern California destroyed layers of potential larval anchovy food; stability was not restored to the upper layers of the inshore anchovy spawning region until March. Lasker, at the 1978 CalCOFI Conference, suggested that unusual storm conditions during winter 1977–78 would adversely affect the 1978 anchovy year class. Results of otolith birthdate analysis of recruits from the 1978 year class by Methot (quoted in Lasker, in press) bear this out; recruits were born mainly in March and April 1978, despite extensive spawning in December 1977 through February 1978.

Walsh et al. (1980) also provide evidence from Peru that confirms the idea that strong winds and turbulent seas can be detrimental to the survival of the Peruvian anchovy. On the other hand, Ware et al. (in press) suggest that aggregations of food for Peruvian anchovy larvae may be a *result* of strong winds by the production of Langmuir cells and consequent accumulation of likely food items in "windrows." The space and time scales of the events being considered differ greatly, and reconciliation of these ideas requires additional research into the effects of wind-mixing and the distribution of larval fish food particles.

The findings that anchovy larvae cannot feed on filamentous diatoms (Lasker, 1975, 1978), that only certain food organisms of the right size for feeding are nutritious (Lasker et al., 1970; Scura and Jerde, 1977), and that there is a low probability of the larva encountering copepod nauplii at first feeding (Lasker and Zweifel, 1978) have provided the biological framework with which to predict the quality of the ocean environment for survival of early anchovy larvae. Similar data are needed for other pelagic fish larvae, and studies have begun on a number of commercially important species to test the ideas suggested here (Ellertsen et al., in press).

Predation on Larval Fishes: An Unknown Factor

Predators on marine fish larvae usually are not discussed very much in relation to recruitment, despite the possibility that they may have great effects on larval survival and year class formation. Studies in the laboratory and in the sea have been more qualitative than quantitative. Exceptions to this rule are the recent studies of Hunter and Kimbrell (1980), who demonstrated that anchovy adults can be voracious predators on their own eggs and larvae, and the work of Lillelund and Lasker (1971), who pointed to the possibility that many pelagic copepods co-existing with fish larvae can bite and lethally damage them. Theilacker and Lasker (1974) also implicated euphausiids as potential predators of larval anchovies. Some fish larvae, such as those of the Pacific mackerel, are piscivorous and, in the laboratory at least, are known to eat their siblings (Hunter, this volume). Alvariño (1980), in an interesting investigation of the distribution of larvae, interpreted the inverse relation of patches of potential predators to patches of anchovy eggs and larvae as an evolutionary development in spawning behavior favoring survival of larvae.

Most of the information concerning predation on larval fishes is too sparse and unquantifiable. A great deal of work needs to be done in this area of study and requires a combination of laboratory and field observations before we will be able to assess the role of predation in recruitment processes.

Conclusion

While the bulk of the recruitment research described here has been on clupeoid fishes, the concepts advanced may be applicable to a wide variety of fishes having planktonic larvae. Minimum concentrations of food must be present in the larva's environment with associated stable ocean conditions to insure that threshold-for-feeding concentrations are maintained. Cube-of-the-wind-speed, upwelling, and wind curl indexes are new tools which can be used by fishery scientists to correlate with larval mortality, larval food distributions, and subsequent year-class strength. Biological information on larval fishes obtained in the laboratory now has even greater meaning since it can be used to erect useful predictive models of recruitment and, with specific data on the ocean environment, provides a hope for meaningful fishery prediction. If managers want to respond before there are sudden collapses or substantial increases in fish populations, it seems clear that they must take into consideration the increasing evidence that environmental factors have major effects on the survival of larval fish and that density-independent factors may be more important than previously believed.

References

Alvariño, A. (1980). The relation between the distribution of zooplankton predators and anchovy larvae. Calif. Coop. Oceanic Fish. Invest. Rep. 21:150–160.

Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946–1971. U.S. Dept. Comm., NOAA Tech. Rept. NMFS SSRF-671, 103 pp.

Bakun, A., and C.S. Nelson. 1977. Climatology of upwelling related processes off Baja California. Calif. Coop. Oceanic Fish. Invest. Rep. 19:107–127.

Ellertsen, B., P. Solemdal, S. Sundby, S. Tilseth, T. Westgard, and V. Øiestad. In press. Feeding and vertical distribution of cod larvae in relation to availability of prey organisms. ICES Symp. on the Early Life History of Fish, Woods Hole, Mass., April 1979. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-v. Réun. Cons. Perm. int. Explor. Mer 20:1–228.

Hunter, J.R., and C. Kimbrell. 1980. Egg cannibalism in the northern anchovy, *Engraulis mordax*. U.S. Fish. Bull. 78:811–816.

Kondo, Keiichi. The recovery of the Japanese Sardine—the biological basis of stock-size fluctuations. Rapp. p.-v. Réun. Cons. int. Explor. Mer. 177:322-354.

Lasker, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. U.S. Fish. Bull. 73:453–462.

——. 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp. P.-v. Réun. Cons. int. Explor. Mer 173:212–230.

———. In press. Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California Current: contrasting years, 1975 through 1978. ICES Symp. on the Early Life History of Fish, Woods Hole, Mass., April 1979. Rapp. P.-v. Réun Cons. int. Explor. Mer, 178.

Lasker, R., H.M. Feder, G.H. Theilacker, and R.C. May. 1970. Feeding, growth and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. 5:345–353.

Lasker, R., and J.R. Zweifel. 1978. Growth and survival of first-feeding northern anchovy (*Engraulis mordax*) in patches containing different proportions of large and small prey, p. 329–354. *In* Spatial Pattern in Plankton Communities, (ed. J. H. Steele), Plenum, New York, 470 pp.

Lillelund, K., and R. Lasker. 1971. Laboratory studies on predation by marine copepods on fish larvae. U.S. Fish. Bull. 69:655–667.

Murphy, G.T. (chairman). 1974. Report of the fourth session of the panel of experts on stock assessment on Peruvian anchoveta. Instituto del Mar del Peru (Callao), Boletin 2:605–719.

Nelson, W.R., M.C. Ingham, and W.E. Schaaf. 1977. Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrranus*. U.S. Fish. Bull. 75:23–41.

Niiler, P.P., and E.B. Krause. 1977. One-dimensional models of the upper ocean. *In* Modeling and Prediction of the Upper Layers of the Ocean (ed. E.B. Krause), Pergamon, New York, 323 pp.

Owen, R.W. In press. Microscale plankton patchiness in the larval anchovy environment. ICES Symp. on the Early Life History of Fish, Woods Hole, Mass., April 1979. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178.

Parrish, R. 1976. Environmental-dependent recruitment models and exploitation simulations of the California Current stock of Pacific mackerel (*Scomber japonicus*). Ph.D. thesis, Oregon State Univ., Corvallis, Oregon, 101 pp.

Parrish, R.H., and A.D. MacCall. 1978. Climatic variation and exploitation in the Pacific mackerel fishery. Calif. Dept. Fish and Game, Fish. Bull. 167, 110 pp.

Scura, E.D., and C.W. Jerde. 1977. Various species of phytoplankton as food for larval northern anchovy, *Engraulis mordax*, and relative nutritional value of the dinoflagellate *Gymnodinium splendens* and *Gonyaulax polyedra*. U.S. Fish. Bull. 75:577–583.

Theilacker, G.H., and R. Lasker. 1974. Laboratory studies of predation by euphausiid shrimps on fish larvae, *In* The Early Life History of Fish. (ed. J.H.S. Blaxter), pp. 287–299. Springer-Verlag, Berlin.

Valdivia, G., J.E. 1978. The anchoveta and El Niño. Rapp. P.-v. Réun. Cons. int. Explor. Mer 173:196–202.

Vlymen, W.J. 1977. A mathematical model of the relationship between larval anchovy (*Engraulis mordax*) growth, prey microdistribution and larval behavior. Env. Biol. Fish. 2:211–233.

Walsh, J.J., T.E. Whitledge, W.E. Esaias, R.L. Smith, S.A. Huntsman, H. Santander, and B.R. deMendiola. 1980. The spawning habitat of the Peruvian anchovy, *Engraulis ringens*. Deep-Sea Res. 27:1–28.

Ware, D.M., B.R. deMendiola and D.S. Newhouse. In press. Behavior of first-feeding Peruvian anchoveta larvae, *Engraulis ringens* J. ICES Symp. on the Early Life History of Fish, Woods Hole, Mass., April 1979. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178.