

What Limits Clupeoid Production?¹

Reuben Lasker

Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, A 92038, USA

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This review paper explores a number of hypotheses on the control of clupeoid populations. The following are discussed: the effect of fishing; egg mortality (predation); larval mortality (the critical period) with a consideration of starvation and predation and the biotic and abiotic factors that may be involved; larval transport and the oceanographic features that cause it; variable egg production; interspecific competition; and the effect of localized (e.g. storms and upwellings) and widespread (El Niño) oceanographic events. A review of the paleosedimentary record is also given showing the magnitude of natural fluctuations when no fishing occurred. Recent resurgences in clupeoid populations are reviewed and suggested causes are analyzed.

Le document aborde un certain nombre d'hypothèses concernant le contrôle des populations de clupéidés. Il y est question entre autres des conséquences de la pêche, du taux de mortalité parmi les oeufs (activité des prédateurs), de la mortalité des larves (période critique) de sous-alimentation, des prédateurs, des facteurs biotiques et abiotiques qui peuvent entrer en ligne de compte, du transport des larves et des facteurs océanographiques connexes, des variations au niveau de la production des oeufs, de la lutte entre les espèces, de même que des conséquences de certains faits océanographiques localisés (tempêtes, remontées d'eau, etc) et plus étendus (courant El Niño). L'auteur traite également des facteurs paléosédimentaires, illustrant l'amplitude des fluctuations normales en l'absence d'exploitation commerciale. Le document étudie enfin les réapparitions récentes de populations de clupéidés et analyse les causes qui expliqueraient pareils phénomènes.

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Research devoted to the subject of recruitment mechanisms has been growing in the last few years. The fluctuations in populations of clupeoids in particular have given impetus to these investigations because of the great economic and food value of these fishes. For example, anchovy and menhaden fish meal are used as a protein source in poultry and cattle feed, and sardines, herring, anchovy, and a variety of other clupeoids are used directly for human food. In all, clupeoids make up about 30% of the 70 million metric ton (t) world fish catch alone. The importance to individual nations is exemplified by the fishery for the Peruvian anchoveta, *Engraulis ringens*, which at its height accounted for over 12 million t/yr or 15% of the world fish catch. The rise and fall of this great fishery and the economic changes that occurred in the fishmeal and soybean markets when fishmeal became scarce and a protein substitute was needed are shown in Fig. 1a. A number of other examples of the rise and fall (Murphy 1977) and sometimes rise again of specific clupeoid fisheries are available, e.g. the sardine fishery in Japan (Kondo 1980), the herring fishery in the North Sea (Hempel 1978), the Peruvian-Chilean sardine (Lasker and MacCall 1983) and anchoveta (Barber et al. 1980), and the Pacific sardine off California (Marr 1960). My

paper reviews a number of hypotheses on the control of clupeoid populations.

The Paleosedimentary Record

There is little question today that there are natural fluctuations of great magnitude in fish populations which are attributable to causes other than fishing. The best evidence for naturally occurring increases and declines is from the sedimentary record of anaerobic basins. For example, Soutar and Isaacs (1969) reconstructed the population fluctuations of some of the common fishes occurring off California by identifying and counting fish scales in cores taken from anaerobic sediments of the Santa Barbara Basin. The Pacific sardine, *Sardinops sagax* (also *S. caerulea*), was greatly abundant about 1000 yr ago, much more so than in the recent history of the fishery when peak biomass was estimated to be only about 2 million t. Similarly, the northern anchovy, *Engraulis mordax*, while always abundant, also declined in biomass from 1600 yr ago to the present. Of greater interest, perhaps, is the 19th and 20th century history of anchovy and sardine fluctuations which was presented in a later paper by Soutar and Isaacs (1974). They showed that the modern decline of the Pacific sardine started about 1890, 30 yr before the inception of a fishery off the west coast of the United States. Exceptional year classes could be seen as having occurred in 1855 and 1865, yet these were not sufficient to prevent "a precipitous and natural decline" in the 1870s. In considering the paleosedimentary record, Lasker and MacCall

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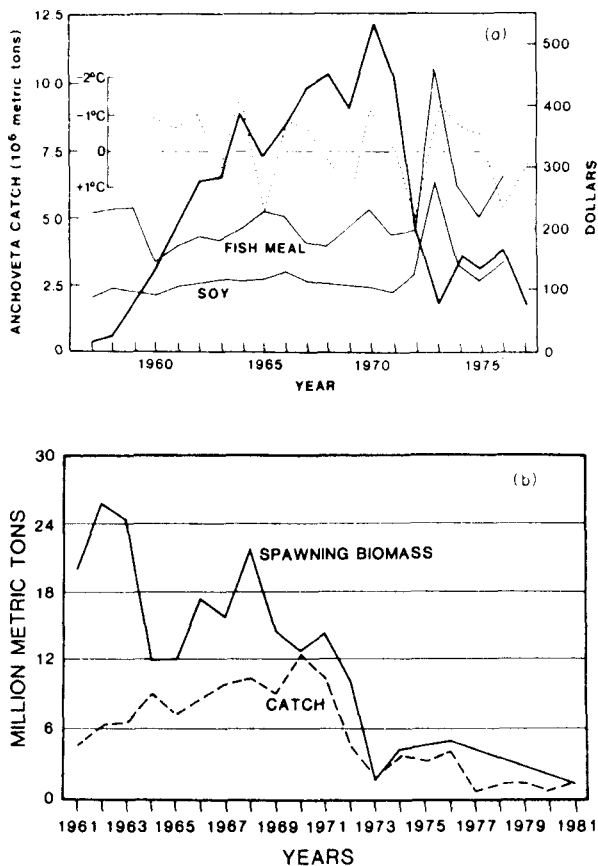


FIG. 1 (a) Peruvian anchoveta catch from 1957 to 1977. The temperature anomaly around a 19-yr mean of 23.8°C is shown with a dotted line. The El Niño of 1972 corresponds with a sharp decrease in catch. This is discussed in the text. Fish meal and soybean prices are plotted to indicate the possible effect of the diminished Peruvian anchoveta catch on the world protein market (after Barber et al. 1980). (b) Peruvian anchoveta catch from 1961 through 1981 compared with the spawning biomass (after Csirke 1980; Tsukayama 1982).

(1983) concluded that the Soutar and Isaacs (1969, 1974) data were probably too insensitive to detect below 500 000 to 1 million t sardine biomasses. The most recent (1983) biomass figures put the Pacific sardine in California waters at less than 20 000 t (Klingbeil 1983). Thus, the decline of the sardine in the 1870s and 1890s was not the same phenomenon as that which occurred off California in the 1940s. The latter was undoubtedly much more drastic and obviously had a component of heavy exploitation which appeared to force the population below its minimum spawning stock size.

Following the recent sardine population decline, there was an increase in the anchovy population off California (Huppert et al. 1980), but the anchovy was also at much higher population levels in the late 19th and early 20th centuries. In comparison, off Peru, DeVries and Percy (1982), using the techniques of Soutar and Isaacs, showed that the clupeoid biomass off Peru has also fluctuated greatly; the stocks of anchoveta and sardine were not as abundant in the late Pleistocene (11 000 yr ago) as they have been in recent times.

The Effect of Fishing on Clupeoid Production

For many years there have been two schools of thought on the effect of fishing on clupeoid year class survival and its ultimate effect on the fishery. In their joint paper, Clark and Marr (1955) held diametrically opposing views on the merits of density dependency versus independency, but there were a few points upon which they did agree. First, they believed that there must be some minimum spawning stock size below which year class size is a function of stock size, and second, that the magnitude of additions to a population is not determined by the number of eggs spawned but rather the degree of mortality between the time of spawning and when the juveniles or adult fish enter the fishery.

The history of clupeoid fisheries is long enough now to suggest that man has fished near the critical minimum stock size many times. A clupeoid collapse can be due to heavy fishing mortality, which reduces the mean age of the population and forces the very young fish to sustain the reproductive load of the population. If the environment intervenes in some way to cause excessive mortality of the eggs, larvae, or even small juveniles, then at the most, only two successively poor year classes with continued fishing on the adult stock will reduce the population below the critical minimum stock size. This appears to have happened to the Pacific sardine population in 1949 and 1950 (Murphy 1974) and to the Peruvian anchoveta (Fig. 1b). Thus, part of the solution to the "stock-recruitment problem" is to determine for a species the population level below which it will no longer sustain a future fishery should there be some subsequent poor year classes. More important is the need to discover what environmental conditions cause a year class to succeed or fail.

It might also be argued that there is no definable minimum stock size as judged from the observation that clupeoid recoveries are common, albeit unpredictable. An excellent example is the resurgence of the Japanese sardine, *Sardinops melanosticta*, a small, unfishable population (Kondo 1980). In 1972 this residual population gave rise to a formidable year class which has led 11 yr later, to a 3 million t fishery. This is double the tonnage taken at the previous peak of the fishery in 1936 (Fig. 2). Similar year class successes arising from small to virtually nonexistent populations occur from time to time and are not limited to clupeoids, although some other clupeoid species provide similarly spectacular examples, e.g. the Peruvian-Chilean sardine, *S. sagax*. Therefore, barring the unlikely event of the complete extinction of any clupeoid species, there may always be enough fertilized eggs produced, no matter how small the population, to produce a good year class if conditions are right. Just what the "right conditions" may have to be will be examined below.

Hjort's Hypothesis

Johann Hjort, the famous Norwegian fishery biologist, is remembered best for the idea of the "critical period," which he proposed in his 1913 review of the Norwegian herring and cod fisheries (Hjort 1913). He believed that year classes were most probably established in the early post yolk-sac stage of fish larvae when feeding was just beginning (see May 1974 for a discussion of the critical period concept). Hjort felt that spring-spawned herring larvae could not find enough food at the early post yolk-sac stage, and for the most part the larvae were

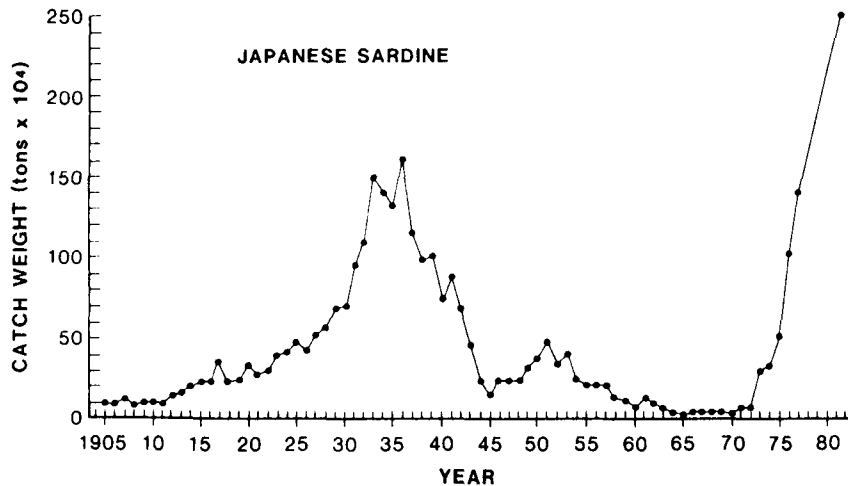


FIG. 2. Catch of the Japanese sardine *Sardinops melanosticta* (after Kondo 1980; Tanaka 1983).

doomed to starve. He reiterated this idea in a provocative paper in 1926 (Hjort 1926). In the latter the suggestion also was made that larval drift could be a mechanism for carrying eggs and larvae out of good food areas.

It has been only in the last three decades that fishery biologists have amassed enough information to begin to tell us whether Hjort was on the right track or not (see review by Blaxter and Hunter 1982). Despite the accumulation of data on the feeding behavior and physiology of the larval herring, sardine, and anchovy, the ultimate experiment, a test of the "critical period" hypothesis, is yet to be done for the herring or any clupeoid. The reason for this is clear: very large data sets on egg production, larval mortality, the larva's environment, and the resulting juvenile survivors are needed over long time periods (probably decades) to obtain the statistical reliability needed with which to test the Hjort critical period hypothesis. However, enough information has accrued in recent years to provide us with the protocol for these studies, and fishery scientists are now in the best position they have ever been to carry them out.

In recent years a number of other ideas have been published on possible year class determinants including interspecific interaction (Lasker and MacCall 1983), cannibalism (MacCall 1980), elaborations of the larval drift idea (Parrish et al. 1981; Nelson et al. 1977), variation in egg survival (Lo 1984), changes in fish fecundity (Picquelle and Hewitt 1983), and the effect of localized oceanographic events (Lasker 1975, 1978) such as stormy periods and upwellings or widespread events such as the unusual warming of the ocean (El Niño) (Valdivia 1978). Some of these depend on the concept of the critical period, i.e. starvation of first-feeding larvae, as the ultimate determinant of the year class, while others emphasize the role of larval survival in density-dependent population regulation.

Food and Feeding of the Clupeoid Larva

There are some generalizations by which the clupeoid larva can be characterized. As hatching it is weak, blind, and depends on endowed yolk to survive. There is evidence that mortality of yolk sac larvae is very great (Picquelle and Hewitt 1983), presumably from predation. At first feeding, a day or so after yolk sac absorption, the larva instinctively snaps at and tries to

capture bite-size food particles. However, if it is unsuccessful it will give up trying (Blaxter and Hempel 1963), i.e. there is a "point of no return" behaviorally, and physiologically in a few days if no food (or too little food) is obtained (Blaxter and Hempel 1963; Blaxter and Ehrlich 1974; Lasker et al. 1970; O'Connell and Raymond 1970). What then must the ocean provide to insure larval survival and a good year class? Obviously, nutritious food of the right size must be present in sufficient quantity during the initial feeding of a larva. This is a necessary condition for the larva to pass its first hurdle. Subsequently, predation and transport may increase in importance, but first-feeding larvae clearly face the immediate danger of starvation.

If we accept this premise, recognizing that the quantitative and qualitative details may differ from species to species, a discussion of recent experiments is useful to see if it is possible to derive some predictive principles of recruitment from our knowledge of what a clupeoid larva needs to eat to survive.

The Stability Hypothesis

In a study of anchovy larvae off California (Lasker 1975, 1978, 1981a) I tried to apply laboratory- and field-derived information to the prediction of the relative strength of an anchovy year class. My approach was to determine the threshold number of food particles needed for successful first feeding (Lasker 1975), and then to sample the ocean to find where food concentrations were at, or higher than, the concentrations needed. Off southern California the waters along the coast were usually rich enough to feed anchovy larvae, particularly where there were strong chlorophyll maximum layers. This changed depending on oceanographic conditions, sometimes resulting in the expansion of the geographical area suitable for larval feeding, but at other times limiting successful feeding to the water immediately adjacent to the coast. Occasionally, within the anchovy's spawning season a variety of conditions prevailed such that only a portion of the season could insure a supply of food particles for first-feeding larvae to insure their survival (Lasker 1981a). In another paper (Lasker 1981b) I pointed out that a stable environment is usually needed to allow aggregations of food organisms to form and be

maintained, and that it is these dense concentrations that must be exploited by anchovy larvae to survive. These investigations led me to suggest that with a knowledge of threshold numbers of food organisms needed for first feeding, and with information on what effect the environment has on preserving or destroying concentrations of food during the anchovy spawning season, the basic principles for prediction of recruitment are available and could be used to test the critical period hypothesis.

Another point of view has been expressed by Houde (1978) who observed in laboratory experiments with the subtropical bay anchovy, *Anchoa mitchilli*, that there are always survivors and some growth of individuals at extremely low food concentrations, and that food concentrations needed to produce 10% survival are generally available in the fish's normal habitat, Biscayne Bay, Florida. However, at low food concentrations larvae lost weight the first few days of feeding and most died soon after (Houde and Schekter 1981).

Recently, Methot (1983) devised an experiment to test the critical period and stability hypothesis simultaneously. He was able to determine very precisely the birthdates of juvenile anchovies by counting the number of daily rings on their otoliths (Brothers et al. 1976; Methot and Kramer 1979) and estimated seasonal changes in larval survival by comparing the monthly age composition of juveniles with earlier larval production and the changes in the physical environment encountered by the larvae. This was analyzed for the 1978 and 1979 year classes. Because the northern anchovy has a protracted spawning season (December through May), changes in the environment over the time of spawning should be reflected in the birthdates of the surviving juveniles. Methot found that survival of larvae from December 1977 to March 1978 was less than survival of larvae from April to May 1978, yet larval production was greater in the first part of the season (Fig. 3a). In 1979 this was reversed with survival coinciding with the heaviest larval production in the latter part of the season (Fig. 3b). Because of the violent storms that occurred in the winter of 1977-78, I predicted that there should be poor survival in the first half of the spawning season for that year with comparatively better survival as a reflection of calm conditions which prevailed from mid-March 1978 to the end of the spawning season in May.

The violent ocean conditions caused by the early 1978 storms kept the ocean sufficiently mixed and too dilute with respect to larval fish food organisms until March when aggregations of potential food organisms appeared (Lasker 1981b). Methot (1983) pointed out, however, that recruitment of the 1979 year class was poorer than in 1978, especially during the latter portion of the spawning season. This pattern seems better explained to him by indices of offshore transport than by indices of food availability for larvae, but the seasonal pattern of survival in 1978 could not be explained by transport. He suggested that both conditions may account for the differences found.

Mechanisms of Larval Transport

Parrish et al. (1981) investigated the reproductive strategies of the most successful fish stocks off California and how these relate to a variety of oceanographic conditions. They concluded that successful fish in the California coastal region minimize their offshore loss of reproductive products by choosing to spawn in areas and at times when upwelling and offshore transport are at a minimum. Thus, they hypothesized that

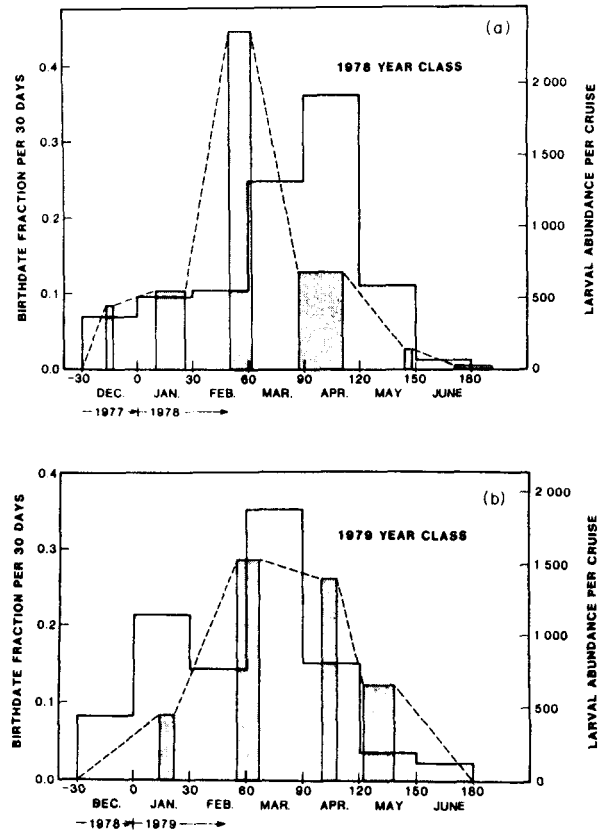


FIG. 3. Comparison of the seasonal distribution of birthdates of juvenile anchovy (open histogram) to the seasonal distribution of larval abundance (stippled bars; the width of these bars indicates individual survey duration). Note that survivorship did not coincide with major larval production in 1978 (a) but did so in 1979 (b). However, total survivorship was better in 1978 than 1979, causing a twofold greater recruitment in the earlier year relative to the latter (after Methot 1983).

deviations from "normal" transport conditions could have profound detrimental effects on a year class by carrying eggs and larvae to areas where there is not enough food to survive. A variant of this idea is the report by Shelton and Hutchings (1982) that the eggs and larvae of the South African anchovy, *Engraulis capensis*, are carried from an area of poor productivity to one of high productivity by a surface frontal jet. When transport slackens, high mortality is the rule.

One of the more interesting studies of larval transport was published by Nelson et al. (1977). They presented convincing evidence that good year classes of menhaden, *Brevoortia tyrannus*, depend on environmental conditions that favor the drift of eggs into estuaries of the east coast of the United States where the larvae presumably find good feeding conditions. They produced a multiple regression model relating recruitment to the following environmental variables: (1) Ekman transport rates from three areas where menhaden abound, (2) the minimum mean sea surface temperature at the mouth of Delaware Bay in the year class year, and (3) the sum of monthly average discharge rates from three rivers in July-September of the year preceding the year class year. These authors used a data

set covering the years 1955–70 with remarkable correlations. However, in recent years the model has not been successful in predicting year class success (W. E. Schaaf, pers. comm.).

Another variation of the hypothesis that suggests that larval transport may regulate populations was described by Iles and Sinclair (1982). In this study they presented the interesting idea that the magnitude of herring subpopulations may depend on the size of oceanographically isolated but stable larval retention areas.

In summary, larval transport may be an effective way of sweeping relatively helpless clupeoid larvae into unfavorable areas or conversely of moving them to areas where they can find optimal survival conditions. Either way the basis for survival is the coincidence of larvae with food for them to survive, as suggested in the Hjort hypothesis of the critical period.

Predation or Starvation? Evidence from Mortality Curves

The literature on clupeoids has blossomed with information on their predators and in some cases how much is eaten. The review by Blaxter and Hunter (1982) provides an excellent summary on predation of eggs and larvae by invertebrates and fishes, including a discussion of the incidence of cannibalism. Undoubtedly, predation at all stages of the life of any planktonic organism must rank high among those factors that regulate its population size. The difficulty has been and continues to be the quantification of predation. Population dynamicists have usually resorted to indirect measures considering the fraction of mortality not accounted for by other means as being due to predation. Hunter (1982) in a recent review article concluded from a series of mortality curves obtained for the northern anchovy that the smooth monotonic exponential decrease in numbers of eggs and larvae "lays to rest the Hjort hypothesis of a high larval mortality resulting from starvation beginning at yolk absorption" at least for the Northern anchovy. His thesis is that egg and larval mortality is most probably a density-dependent result of predation, particularly if the predators are invertebrates that appear in blooms (e.g. the jellyfish *Aurelia*, Möller 1982), or due to filter-feeding fishes, as anchovy adults eating their own eggs and larvae (cannibalism, Hunter and Kimbrell 1980). However, mortality rates are too imprecise to afford us a definite conclusion on this point, and I believe it is premature to discard the "critical period" idea. The mortality curve shown in Fig. 4 is typical of those obtained for the northern anchovy. It is derived from the number of eggs and larvae obtained over a 40-d period in the midst of the anchovy spawning season and from an area over thousands of square kilometres. Corrections are made for a variety of factors, such as extrusion of a proportion of the eggs and larvae through the meshes of the plankton net used to collect them, avoidance of the collecting net as the larvae grow older, adjustment for the individual larval growth rates, and the application of two models, one age-independent instantaneous mortality rate for eggs and an age-dependent mortality rate for larvae (Lo 1984). Since the most precise mortality curves show no apparent critical period, it either does not exist as a distinct portion of the mortality curve or it is essentially not provable by current field methods. Blooms of predators, such as jellyfish in Kiel Bight (Möller 1982), should in themselves provide a break in the mortality curve that we would normally ascribe to a critical period, particularly if predators are size-selective in their feeding and the spawning season is a protracted one. However, none has been detected thus far.

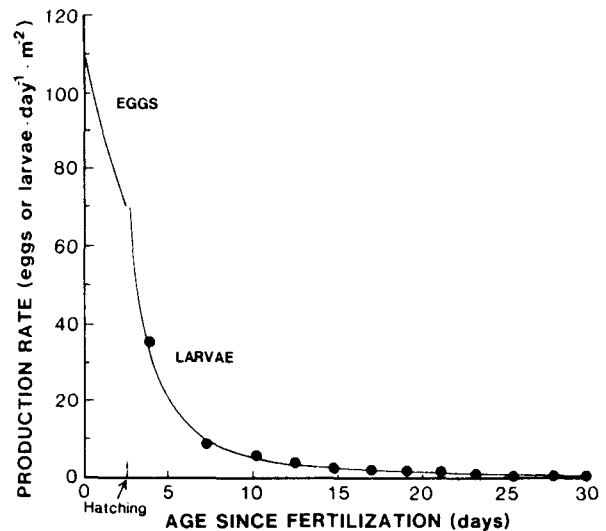


FIG. 4. Mortality curve for eggs and larvae of *Engraulis mordax*, 1983 (after Picquelle and Hewitt 1983). See text for explanation.

Oceanographic Events

It is impossible to consider the fate of pelagic fish without an examination of the effect of the environment on mortality. Parrish et al. (1983) examined a number of environmental processes in relation to anchovy and sardine reproduction in Eastern Boundary currents. They concluded that, in general, upwelling centres seem to be avoided by spawning clupeoids. Yet they also pointed out that the large Peruvian anchoveta population is an exception, since it spawns in an area of strong upwelling. However, upwelling is much stronger off Peru in the summer when spawning is weak as compared with the winter spawning season. In other words the anchoveta lives in an upwelling area known to be extremely rich in forage but minimizes the detrimental effects of upwelling, e.g. offshore transport, by choosing the least oceanographically energetic time to deposit its eggs. These authors showed that spawning tends not to occur in regions where wind conditions would cause turbulent mixing of the upper water column, and this is characteristic of the Peruvian upwelling area. The conclusion from their study is that there has been a strong natural selection acting on clupeoid populations to produce a massive number of eggs over a long spawning season during times and in latitudes where the eggs and larvae are at least risk.

Variable Egg Production and Differential Mortality

Since 1980, scientists at the Southwest Fisheries Center have been perfecting a technique for biomass assessment of the northern anchovy, the egg production method first described by Parker (1980) and now used routinely on an annual basis (Picquelle and Hewitt 1983). Table 1, derived from four years of egg and larva sampling in the California Current, encompassing the entire spawning range of the central population of the northern anchovy, shows the results of differential spawning and mortality of eggs and larvae from year to year. For example, a comparison between 1980 and 1982 shows markedly different egg production between the two years, with 1982 total egg

TABLE 1. Average daily production ($\times 10^{12}/d$) of eggs and larvae by the northern anchovy population off California during the major portion of each spawning season (1980–83) (R. Hewitt, pers. comm.).

Production	1980	1981	1982	1983
Eggs	26.34	20.96	13.51	17.25
Yolk-sac larvae	7.18	14.34	8.53	10.78
10-d-old larvae	0.74	1.59	1.04	0.69
30-d-old larvae	0.10	0.24	0.16	0.07

production being about half that of 1980. Because of very heavy egg mortality in 1980, as compared with 1982, both years had about the same daily production of hatching eggs (yolk-sac larvae). Despite the similar production of yolk-sac larvae an increased rate of larval mortality in 1980 resulted in fewer 30-d-old larvae per day than in 1982. In other words, the number of larvae remaining to metamorphose from any spawn is the result of several mortality rates, each of which may be different from year to year and all are probably the result of both biotic (predation) and abiotic (oceanographic) factors. This is dramatically illustrated in Fig. 5, which shows to what degree the average daily egg production over the entire area of northern anchovy spawning can change from year to year. Lo's (1984) analysis of 30 yr of anchovy egg production off the west coast of the United States and Mexico shows that there have been occasional bumper crops of anchovy eggs but not necessarily concomitant good year classes. For example, 1975 was an enormously successful year for egg production (Fig. 5) and primary production (Smith and Eppley 1982), but the end result was a disastrous year class (Lasker 1981a), the worst of 16 consecutive year classes analyzed. Lasker (1981a) believes that the root cause of this poor year class could be attributed to the presence of a dominant but nutritionally poor larval food source, the dinoflagellate *Gonyaulax polyedra*, which was above the threshold-for-feeding concentrations during the first half of the spawning season, and to the untimely onset of strong upwelling thereafter, which resulted in high production of inedible diatoms.

El Niño Events

The waters off Ecuador, Peru, and Chile historically have had exceptionally large clupeoid fisheries. Upwelling of nutrient-rich water has been the trophic underpinning of these fisheries by supporting an extremely rich phytoplankton fauna fed upon directly by filter-feeding anchoveta and sardines. From time to time, invasions of unusually warm nutrient-depleted water occur, an El Niño, which have, on some occasions, coincided with the collapse of the coastal clupeoid stocks off these nations (Fig. 1a). As Valdivia (1978) pointed out, there is a behavioral modification of anchovy movement and subsequent distribution during an El Niño. Off Peru, the anchoveta drastically reduced the area it occupied during the 1972 El Niño, so that in March, April, and May 1972, large concentrations of fish schooled close to the coast and became unusually available to the coastal fishery. Anomalous spawning of the anchoveta also occurred from September 1971 through May 1972, with a markedly reduced production of eggs. The combination of extremely heavy fishing, which undoubtedly pushed the anchoveta population below its minimum stock size, and the obvious failure of one or more of the following year classes caused the collapse of

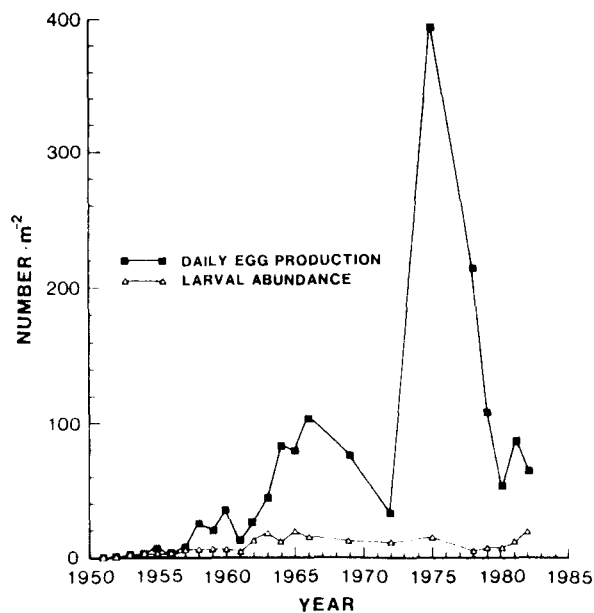


FIG. 5. Daily egg and larval production of *Engraulis mordax* in the California Current over a 30-yr period. The year 1975 was characterized by an enormous spawning but poor larval survival (after Lo 1984).

the fishery with its attendant disastrous economic consequences (Murphy 1974).

While there has been a gradual but persistent return of the sardine to Peruvian and Chilean waters in recent years, there have also been several El Niño events. The severe El Niño of 1983, which began in September–October 1982, was characterized by disruption of anchoveta and sardine schools. In some instances, sardines accumulated “in some small areas” according to Jordan (1983), which made it appear that sardines were abundant, but these were rapidly fished out.

Whether El Niño events affect the survival of fish eggs and larvae is currently undocumented and remains to be investigated. In California the El Niño of 1983 was manifested by a much wider distribution of spawning anchovies than occurred in previous years contrary to the contraction found in Peru. Per capita egg production seemed to be relatively unaffected in California. The amount and extent of surface warming with which the fish had to contend was much different between Peru and California, the habitat in Peru always exhibiting a greater temperature differential and more drastic effects on the behavior of the fish (Fig. 1a).

Competition

Do coexisting species of pelagic fish that inhabit thousands of square miles of ocean compete for food resources and space? This intriguing question has never been answered satisfactorily. Lasker and MacCall (1983) investigated this question indirectly by inferring the relative mean sardine and anchovy size from frequency distributions of sardine and anchovy scales found in anaerobic sediments. The average anchovy size from periods of high sardine abundance was found to be significantly smaller than in periods when sardine populations were low. The authors pointed out that this result is consistent with a competition hypothesis but that there are other possible explanations, e.g.

offshore distribution of small anchovies. An occasional response of an ecosystem when sardines are low in abundance (e.g. off California) is an increase in the population of anchovies, and alternatively, some ecosystems where anchovies are reduced (e.g. Peru-Chile), sardines have increased in number remarkably. Whether competition on a large geographic scale is the causal mechanism has yet to be decided.

Conclusion

The answer to the question, "what limits clupeoids?," seems to be "almost everything." More realistically, the question should be phrased "what limits clupeoids mostly?" Other questions follow this one: When, in the life cycle, does this occur? What are the interrelationships between limiting factors and between species? What can be learned from species life histories and fishery oceanography that will allow us to predict recruitment?

A review of the literature shows that we are on the threshold of significant investigations that may provide the answers to these questions. Studies, such as those conducted by Methot (1983), seem to be the most promising for isolating the factors affecting the recruitment of a year class. The Methot experiment allows us to look back at the environment to see which factors were present or absent when there was good or poor survival within a spawning season when a year class was produced. With a time series of such studies on the same species it seems likely that the factors that are responsible for formation of a year class can eventually be identified.

In the international sphere this approach has been suggested for IREP, the International Recruitment Program, by Working Group 67 of SCOR (Scientific Committee on Ocean Research), intending that several nations work simultaneously on the same fish species group so that data bases could be amassed and compared throughout the world. The essential data can be collected through the use of the newest technological tools available in fisheries research, which include determination of birthdates, growth rates, and ages of fish larvae and recruits using counts of daily rings of the otoliths, the egg production method to obtain total population fecundity, sampling of the biotic environment by sophisticated nets, pumps, and high frequency sonar, and the monitoring of oceanic parameters with the variety of ocean measuring devices perfected by physical oceanographers in recent years.

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