Fisheries on
Coastal Pelagic Schooling Fish

Paul E. Smith

Fisheries on Coastal Pelagic Schooling Fish

Fishery science is undergoing a transition from the management of "stocks" of fish to the management of the entire fish component of an "ecosystem." The major barriers in this transition in the pelagic biosphere are not the construction of theoretical models but are likely to be the logistical problems of assembling verification of theory from field observations.

The nature of the transition from fish stock management to management of the fishery elements in an ecosystem is in part apparent from the broadly-based studies of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). Following the 1947 collapse of the northern "stock" of the Pacific sardine, then the largest fishery of the United States, the CalCOFI program was instigated and funded by the fishermen and organized by Dr. Frances Clark, director of marine research for the California Dept. of Fish and Game, Dr. O. Elton Sette of the U.S. Bureau of Commercial Fisheries, and Prof. Harold U. Sverdrup, director of the University of California Scripps Institution of Oceanography. Their broad mandate was to determine the causes of the major fluctuations of production of fish stocks in the California current region.

From the CalCOFI research program it is apparent that multispecies fishery management in the context of an ecosystem will require several intermediate steps from our current skills at stock management. To emphasize the massive scope of such a transition, the survival of a year-class of fish like anchovy or sardine off California may depend on food strata less than a meter thick; at the same time these fish may be preyed upon appreciably (Smith, 1978a) by young albacore spawned 10,000 kilometers away in the western tropical Pacific or by northern fur seal females born 10,000 kilometers away in the Bering Sea.

Definitions

(1) Stock—that portion of a fish subpopulation available to a fishery. This could be the entire subpopulation.

(2) Subpopulation—that portion of a population which is likely to be interbreeding.

2

(3) Population—that portion of a species which is alive at a particular time.

(4) Species—a group of organisms continuous in time which was likely to be capable of interbreeding.

(5) Guild—a group of populations dependent on the same set of populations for food.

(6) Ecological community—a group of populations likely to be found together.

(7) Ecosystem—a community of organisms and their environment.

The most critical stage of the transition from stock management to ecosystem management from a fisheries standpoint is the guild. In the California Current system and several other productive areas of temperate and tropical seas, the guild of schooling pelagic organisms is an obvious repetitive feature. The major populations of schooling pelagic organisms in the California Current are the northern anchovy, *Engraulis mordax*; the Pacific sardine (or pilchard), *Sardinops sagax*; the jack (or horse) mackerel, *Trachurus symmetricus*; the Pacific mackerel, *Scomber japonicus*; the Pacific saury, *Colalabis saira*; the Pacific hake (or whiting), *Merluccius productus*; and the market squid, *Loligo opalescens*. The guild depends to varying degrees on large phytoplankton, zooplankton, and small fish. Most of the same genera occur together off Europe, South Africa, Australia, Japan, and the west and east coasts of South America, and major fisheries concentrate on the schooling pelagic guild. As repetitive as the group of genera is the tendency for the major stocks to collapse under fishery pressure.

The importance of the guild of coastal pelagic schooling organisms is that it is a human protein source perpetually capable of providing several kilograms of fish per year per capita of the world population. These fish are close to land, and their tendency to be schooled and for the schools to be aggregated makes their capture very efficient by concentrated purse seine fleets. This capture efficiency is also a major hazard to the perpetuity of the yield, and recurrent collapses of members of the pelagic schooling guild are the topics of much applied research in each region of the world where these fisheries occur. The inevitable fluctuations in the available stocks may be smoothed at the market place because canned and fish meal products can be stored for extended periods.

Schooling pelagic fish occupy a hydrographic province whose geopraphic extent can double or triple in a few years and return to the original as rapidly. Also, a pelagic schooling fish occupies a very small portion of its available environment at any instant, but it occupies it very intensely. For instance, we have data which suggest that under each square meter of sea surface there may be 15 kilograms of fish within a fish school (Hewitt et al., 1976). The fish schools occupy only 0.5 percent of the area which is physio-

3

logically defined for them. The early nomenclature, particularly density-dependent and density-independent, is generally inadequate for describing survival in schooling fish. Where the habitat is geographically circumscribed, stock size dependence and density dependence may be identical, but in an area of flexible hydrographic boundaries, density dependence operates on a local scale, such as on the kilometer scale, and stock size dependence operates on a scale of hundreds of kilometers. This distinction is very important for monitoring a fishery because the fishery normally operates not over the ecological range or the entire hydrographic province on which the fish depend, but only over a small part of the habitat where fish concentrate from time to time and are likely to be encountered by fishing boats.

The Pacific Sardine

What really did happen to the Pacific sardine? Our perception of the situation is necessarily simple, because we lack data necessary to erect a complex hypothesis. However, our perception of what happened to the Pacific sardine was important for determining the research attack taken at the Southwest Fisheries Center and for explaining why we are spending so much time in the area of larval and juvenile studies.

The Pacific sardine once occupied an area from the tropics to Vancouver Island. The virgin population was made up of about ten spawning year classes in addition to the year classes about to recruit, and the older ones of these migrated along the entire west coast of America. There were three stocks. One stock we call the northern subpopulation of the Pacific sardine and it is this one that spawned in the spring, roughly from the upwelling area off Punta Eugenia, Baja California, to San Francisco. Another subpopulation occurred south of Punta Eugenia, and one still occurs in the Gulf of California. The limit to spawning was the 13°C isotherm; Pacific sardine eggs do not survive in water colder than 13°C. Following spawning, it appears that the older fish migrated to the north, somewhat in proportion to their size—the largest fish traveling the furthest—and separated out along the coast to feed in the extremely rich area which terminates the west wind drift of the Northern Pacific Ocean. It is, as well, the primary site of an eastern boundary current upwelling system. There they gained weight for the season and moved back to southern California the following spring to spawn.

The time course of the Pacific sardine fisheries has been assembled by Ahlstrom and Radovich (1970). The Pacific Northwest landed up to 100,000 tons and became the first area to notice the changing migration patterns of the Pacific sardine. The fishery there virtually stopped in 1945 and has not yet recovered. Central California was the primary site for phytoplankton production and the place of the largest fishery, half a million tons. The sardine fishery there had collapsed by the end of 1955, after two population failures. Southern California, the residence of the younger sardines, had a sustained fishery that lasted into the 1960s and then it too was abruptly terminated in

4

1964. The Baja California fishery caught both the southern and northern stocks; it now catches anchovy while it continues at a low level of sardine fishing. That fleet shifts seasonally into the Gulf of California, where the primary sardine fishery is now conducted.

Murphy (1966) described what happened to the Pacific sardine. The Pacific sardine had ten spawning year classes in the virgin stock. Since short-term anomalies in the environmental conditions are more common than long-term anomalies, the sardine, which has ten spawning year classes, is not very prone to periodic recruitment failures. However, when the sardine population was reduced to a population having only two spawning year classes: two recruitment failures in a row virtually destroyed the stock. Murphy believes that this is the direct effect of fishing because fishing changes the age composition of the stock. This final age composition was then more vulnerable to shorter and shorter term environment anomalies, which eventually destroyed the stock.

I have made a slight addition to the Murphy hypothesis regarding reducing the number of year classes to two. I believe it is also true that anomalies which cover small areas are more common than environmental anomalies which cause year-class failure over a large area. The sardine stock collapsed from north to south. This probably also implies that the sardine occupied a smaller and smaller area of the pelagic environment and, having occupied these smaller areas, was then more subject to anomalies over a small area. The changing year-class structure is the basis of Murphy's main hypothesis on why the Pacific sardine collapsed. Added to this is the probability that a smaller distribution area is more subject to destructive anomalies.

The Sardine Investigation and CalCOFI

CalCOFI is the California Cooperative Oceanic Fisheries Investigations. It was begun by state, federal, and university scientists at the request of the fishermen and processors who were put out of business by the drastic sardine population collapse. The industry wanted to know if population variations could be predicted and if fishery regulations would shield it from these variations.

To find out, they taxed themselves from 1947 to 1978 a dollar a ton on all of the "wetfish" catch to support research on pelagic California commercial fish. The fishermen themselves were interested enough to find the causes for these drastic declines in population. They took a large fraction of their catch dollar and put it toward specific research to study these variations. Even though the actual dollar amount was never very large in terms of a major fishery research program, the program guided and coordinated the research of three major organizations for more than thirty years. So the less than half a million dollars put in by the fishermen out of their own pockets guided the use of four or five times that much research money over this period.

5

The primary reason the processors and fishermen withdrew their financial support in 1979 was not that they were unhappy with the progress, but that the federal Fishery Conservation Management Act (FCMA) 200-mile-limit legislation had taken the responsibility for the management of these fish, and it was concluded at this time that private industry could now retire from its funding of these activities. Today the primary research components of CalCOFI—the Southwest Fisheries Center of the National Marine Fisheries Service, the California Department of Fish and Game, and the Marine Life Research program of the Scripps Institution of Oceanography—continue their research in the same coordinated fashion but with broader objectives.

Field Studies

The primary activity of CalCOFI has been the field population study. A large proportion of ship time was planned around studying pelagic schooling populations in the field. This was not done at the expense of monitoring the catch in the age, weight, condition, sex ratio—those programs continued. Two additional surveys were mounted. One was a sea survey of juveniles and adults conducted by the California Dept. of Fish and Game. They began by attracting fish to night lights and catching them with lift nets or dynamite. Their techniques for studying sardines had to be modified so that they could also study anchovy, jack mackerel, and Pacific mackerel.

The second major field population survey was conducted on eggs and larvae. In 1949, when high seas oceanographic work started, there was no capability to capture adults on a routine basis over their entire range. One solution was to monitor spawning behavior, stock size, and spawning. Particularly important to the interpretation of field data has been the laboratory study phase which began in the mid-50s.

What do we expect from a larval survey? At the beginning, larval surveys to determine distribution and abundance of eggs and early larvae were supposed to give us an index of the spawning biomass; the later larvae were to be used to project how many survivors there would be from each year's spawn. The precision of larval surveys is greater with small stock sizes than it is with large stock sizes. The catch-per-unit-of-effort monitoring, done when a fishery is operating, is accurate with a large stock size and becomes less dependable with small stocks. The larval survey therefore augments the normal fishery monitoring in a useful way. The spawning surveys also monitor changes in spawning biomass. One obvious shortcoming has been that the best estimates of the abundance of surviving large larvae will not predict in a correlative sense the size of the recruitment.

Ahlstrom (1965) examined the CalCOFI larval surveys, the recruitment of fish into the fishery, and the oceanographic conditions on the spawning grounds. He reasoned that variations in "general productivity" could not have
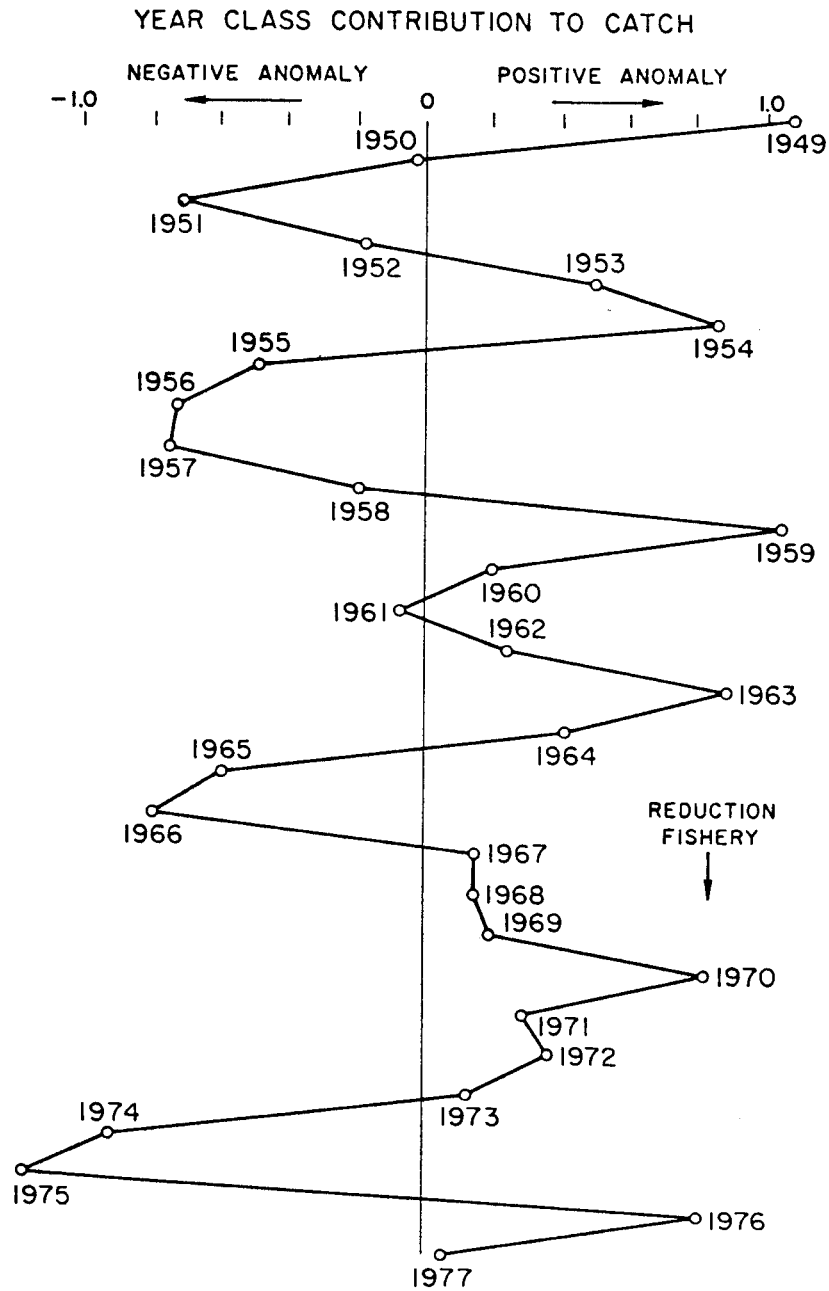
YEAR CLASS CONTRIBUTION TO CATCH

Figure 1. The central population of northern anchovy year-class contribution to catch. The numerical contribution on each year's catch by each year-class is calculated from the sum of the proportionate contribution for the first through fourth years. The sum was normalized for the purpose of constructing a bilaterally symmetric time series with a mean of zero, and the anomalies are expressed in the number of standard deviations. The fisheries before 1966, from which these data were derived, were small and local. The reduction fishery, which began in 1966, has been sampled by the California Dept. of Fish and Game in the Los Angeles area (after Smith et al., in press).
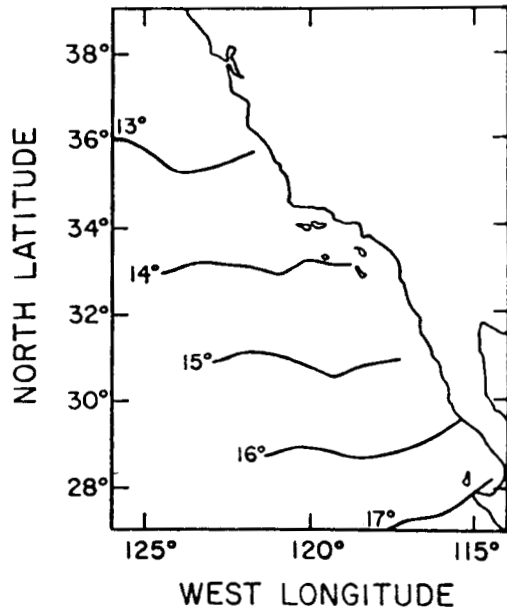
Figure 2. The arithmetic mean temperature at 30 meters depth for January from 1950 to 1968 is derived from a regional summary of CalCOFI standard depths. The 14°C isotherm is oriented zonally at 33°N latitude.
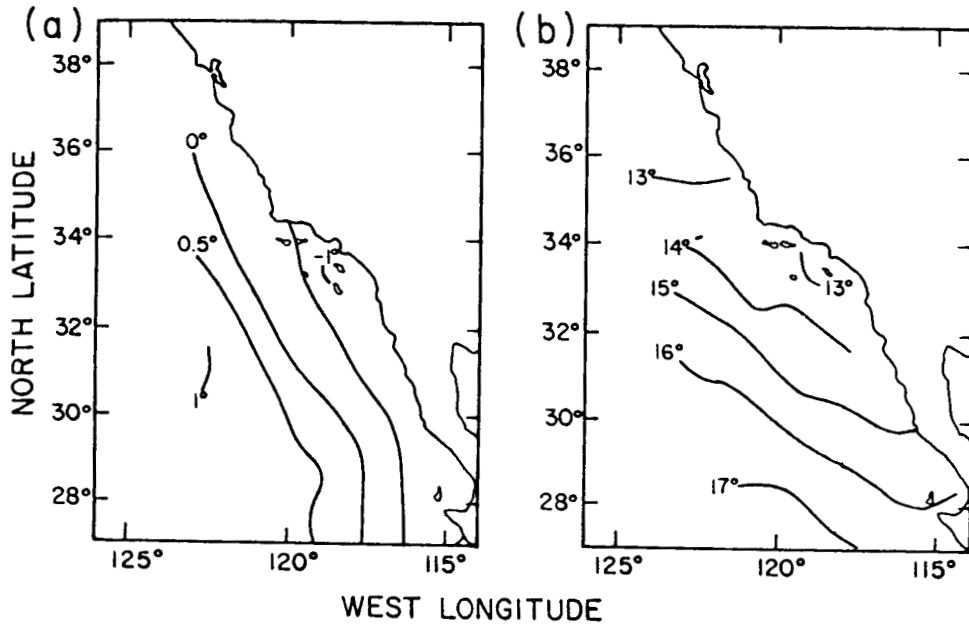

Figure 3. The 30-meter temperature anomaly (a) and temperature (b) at the first of four negative anomalies in the contribution to catch (Fig. 1), January 1951. The 14°C isotherm is oriented diagonally and the 13°C isotherm is in the Southern California Bight. The anomalies are oriented meridionally; and regional anomalies are negative within 100 n.mi. of the coast: part of the Southern California Bight has more than 1°C negative anomaly.

(a)

38°

36°

34° -0.5°

32 -1°

30°

28° -1.5° -2.5°
-2.5°

125° 120° 115°

NORTH LATITUDE

(b)

38°

36°

34° 13°

32

30° 14°

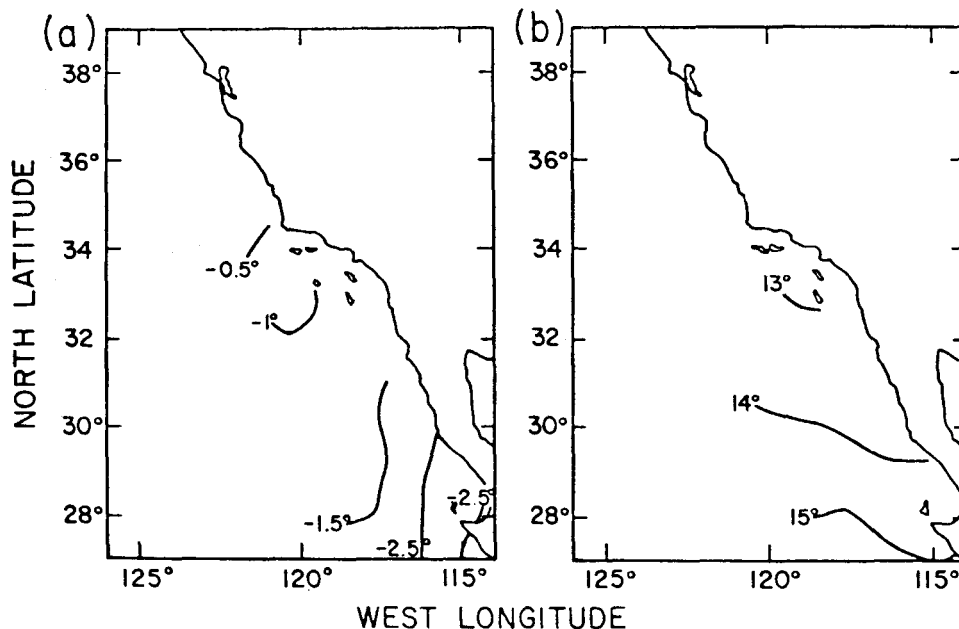28° 15°

125° 120° 115°

WEST LONGITUDE

Figure 4. The 30-meter temperature anomaly (a) and temperature (b) at the second of four negative anomalies in the contribution to catch (Fig. 1), January 1956. The 14°C isotherm is at 30°N latitude, 180 miles south of the mean position. The 13°C isotherm encompasses the Southern California Bight, and the anomalies of from 0.5°C to 2°C colder than normal over the entire distribution of the central subpopulation of the northern anchovy.

been a major control on these fish stocks because a general decline should have been observable in all species, but the good years for anchovy, sardine, and Pacific mackerel did not coincide. In fact, he stated, some of the "poorest years for larval survival have been years of high productivity," as measured by high standing crops of sardines. Even with these changes in the success of year classes, he found no significant variation in relative numbers of large larvae and concluded "this consistency pulls the rug out from under any attempts to relate variation in larval survival to environmental conditions." At the time of his study, only eight annual surveys (1951–58) had been analyzed.

Twenty-nine years of age composition data have been assembled from the bait, cannery, and reduction fisheries on the central subpopulation of the northern anchovy (Fig. 1). Large-scale features of the California Current were examined for some of the maxima and minima in anchovy year-class "contribution to catch," a measure of spawning success (Smith and Haight, 1980). One constant feature, a large-scale cold anomaly in the Southern California Bight (Smith et al., in press), coincided with the four episodes (1951, 1955–56–57, 1965–66, and 1974–75) of anomalously low contribution to catch. Moderate and high contribution to catch resulted indiscriminantly from average and warm conditions.

The diagnostic sign of these years of poor contribution of a year-class to catch may be seen from comparing the average January temperature at 30

meters over the distribution of the northern anchovy central subpopulation (Fig. 2) with the same temperatures in January of 1951, 1956, and 1975 (Figs. 3, 4, and 5) and their resultant anomalies. The average plot has the 14°C isotherm parallel to and overlying 33°N latitude. In the "cold" years the 14°C isotherm is no longer parallel to or overlying 33°N latitude. The nearshore end is replaced by 13°C water. An estimate of abundance of the larger larvae (15 mm) similarly shows some concordance with the "poor" recruitment years (Fig. 6).

Not only the abundance but the timing of the peak abundance of large larvae appears important. In the failing years—1951, 1956, 1965, 1966, and 1975—the spring and summer abundances were low. None of the regional average temperatures shown is near the lethal limit for anchovy (Ahlstrom, 1965), so one must conclude that the temperature is an indicator rather than the cause of adverse conditions for survival. Some of the possible causative factors (such as low vertical stability and mixing) will be discussed in the following section.
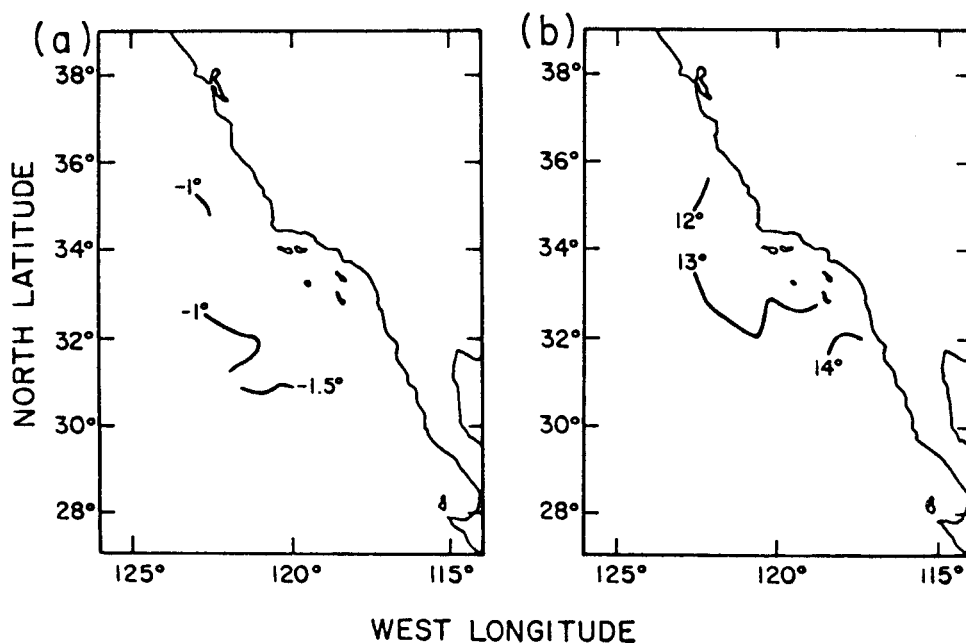

Figure 5. The 30-meter temperature anomaly (a) and temperature (b) at the fourth of four negative anomalies in the contribution to catch (Fig. 1), January 1975. The 14°C isotherm has been replaced by the 13°C isotherm, and the temperature anomaly is from 1°C to 1.5°C below average over the whole distribution of the northern anchovy.
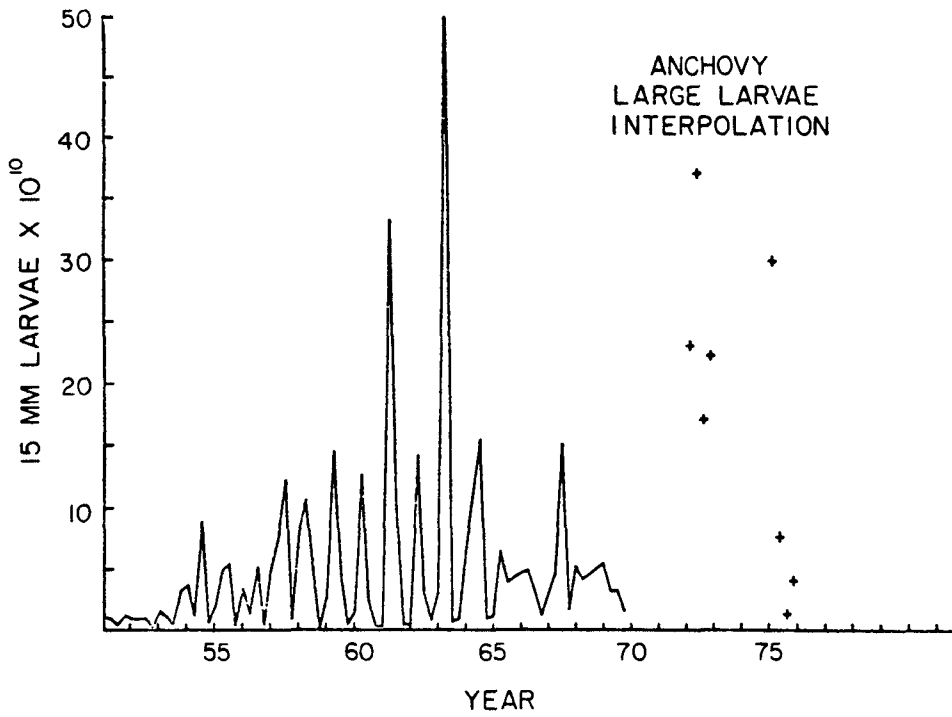
Figure 6. Estimated abundance of 15 mm standard length anchovy larvae, 1951 to 1975. Low relative contribution to catch occurred in four sets—1951, 1955–56, 1965–66, and 1974–75. Moderate and high contribution to catch cannot be distinguished at the 15 mm stage. Values are quarterly estimates which result from single cruises in 1961–65; in other years the quarterly values result from more than one cruise in winter, spring, and summer and usually a single cruise in autumn.

Sampling to Determine Anchovy Larval Mortality in the Sea

It is impossible to make unbiased estimates of the number of fish larvae in the sea, and precise estimates require many carefully taken and sorted samples. The major biases are caused by extrusion through the meshes of nets used to captur.: embryos and early larvae and evasion of the approaching net by older larvae. The major source of imprecision is the tendency of larvae of all sizes to be aggregated, or "patchy." Larval mortality may be determined from a sufficiently large set of imprecise samples by monitoring the sources of bias. We may begin to specify small-scale sampling requirements for describing larval mortality by examining the mass effects of mortality on a very large set of samples (> 30,000) over the CalCOFI grid area (200,000 sq.n.mi.) for the 24-year period, 1951–1975.

It would be foolhardy to specify sampling requirements in detail without some information on a hypothesis to be tested. For example, a space-extensive survey might be required to test the null hypothesis about larval transport—"no important effects on mortality are due to the area in which they are spawned." A time-intensive survey would be required to test the null hypothesis about critical period—"no discernible differences in mortality occur over short periods." Thus for a widely distributed species like the northern anchovy, a test of the "larval transport" hypothesis would require a different sampling emphasis from a test of the "critical period" hypothesis.

For the purpose of this chapter, then, I will discuss some significant sources of bias and how a sampling program would be established to test several hypotheses relating to larval anchovy survival in the sea. Knowledge of the distribution of mortality in the life cycle, variations in mortality, and models of cause and effect should provide background for rational management of a fishery on this stock by direct monitoring and prediction of recruitment and population size.

Anchovy mortality is extremely high, and each successive life stage represents an improving chance for survival (the "Type IV" survival curve of Slobodkin, 1962). I have arbitrarily divided the life cycle into six stages: embryonic, early larval, late larval, juvenile, prerecruit, and adult. In Table 1, I have listed these stages with nominal durations, estimated daily mortality rates, and the abundance of a hypothetical cohort spawned in a week and evaluated at each of the stage margins. The model has been constructed so that crude estimates of fecundity (Hunter and Goldberg, 1980) allow the population model to represent a stationary population (Fig. 7). The model is

Table 1. Example of negative binomial weighted model solution for 14 size groups of anchovy larvae (Bissell, 1972; Zweifel and Smith, 1980).

Group	Preserved size (mm)	Recorded preserved size (mm)	Average* live size (mm)	Age from spawn (days)	Days in interval	Predicted LCL	Predicted UCL (No. 10m^{-2})	Predicted Mean
1	3.25	2.5	3.23	1.98	1.95	3.1×10^2	4.8×10^2	3.9×10^2
2	3.25–4.25	3.75	4.49	6.45	4.69	1.8×10^2	2.5×10^2	2.1×10^2
3	4.25–5.25	4.75	5.57	9.32	2.67	1.1×10^2	1.5×10^2	1.3×10^2
4	5.25–6.25	5.75	6.62	11.84	2.40*	6.8×10^1	9.0×10^1	7.8×10^1
5	6.25–7.25	6.75	7.66	14.14	2.21	4.2×10^1	5.5×10^1	4.8×10^1
6	7.25–8.25	7.75	8.68	16.27	2.07	2.6×10^1	3.4×10^1	3.0×10^1
7	8.25–9.25	8.75	9.68	18.29	1.97	1.6×10^1	2.1×10^1	1.8×10^1
8	9.25–10.25	9.75	10.69	20.22	1.90	1.0×10^1	1.3×10^1	1.2×10^1
9	10.25–11.25	10.75	11.69	22.09	1.85	6.2×10^0	8.3×10^1	7.2×10^0
10	11.25–12.25	11.75	12.68	23.92	1.81	3.8×10^0	5.3×10^1	4.5×10^0
11	12.25–13.25	12.75	13.68	25.71	1.78	2.3×10^0	3.4×10^1	2.8×10^0
12	13.25–14.25	13.75	14.68	27.48	1.76	1.4×10^0	2.2×10^1	1.8×10^0
13	14.25–15.25	14.75	15.67	29.24	1.76	6.7×10^{-1}	1.1×10^1	8.6×10^{-1}
14	15.25–16.25	15.75	16.66	30.97	1.71	5.2×10^{-1}	9.0×10^1	6.9×10^{-1}

* Corrected for abrasion and shrinkage (Theilacker, 1980).
LCL = lower confidence limit.
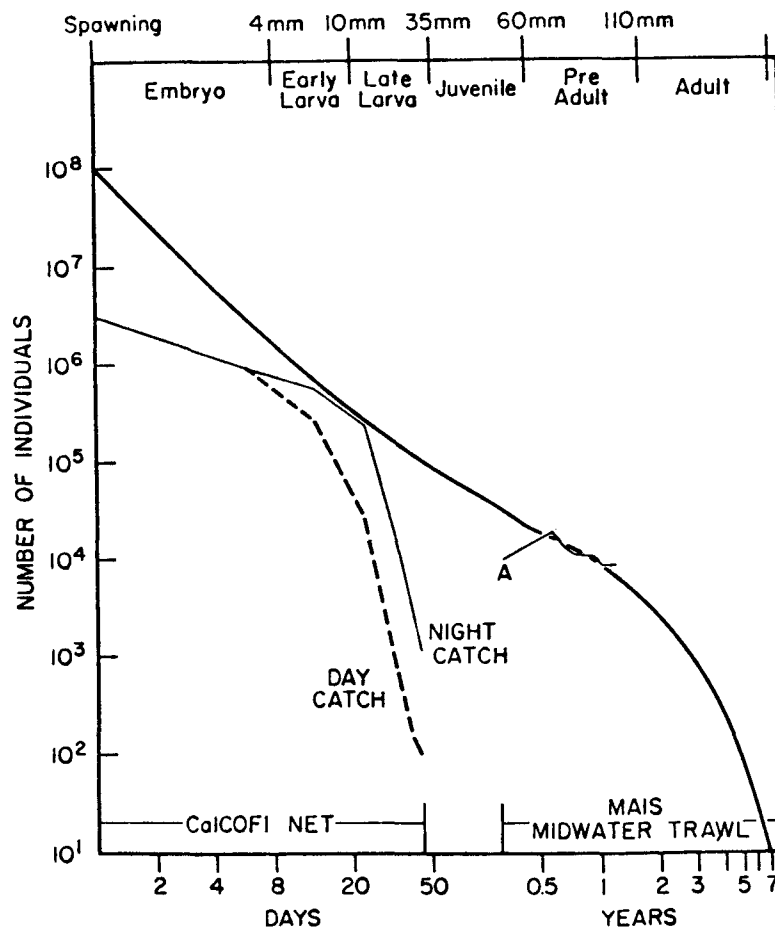UCL = upper confidence limit.

Figure 7. A comparison of a total life history model of the northern anchovy central subpopulation and sample data from the CalCOFI standard silk net (Kramer et al., 1972) and the California Dept. of Fish and Game midwater trawl (Mais, 1974). The main bias at the embyro stage is extrusion through the mesh of the net. The main bias of the early larval stage is daytime evasion of the net, and the main bias of the late larval stage is day and night evasion of the net. Further evidence of nighttime evasion of nets by fish larvae contained in a plankton purse seine compared with a towed plankton net is given by Murphy and Clutter (1972). The point "A" represents occasional juvenile anchovy captured in the midwater trawl liner. These juveniles may be underestimated by behavioral, geographic, and bathymetric differences from the adults.

artificial because absolute mortality rate estimates are available only for the early larvae (Zweifel and Smith, in press) and for the adults (MacCall, 1974). These rates are joined only to satisfy the condition of stationarity. The reader is cautioned that the population of anchovy probably does not exhibit stationarity and that all estimated rates have been assembled from multiyear samples over wide ocean areas.

14

Biases

Four biases have been evaluated: escapement, extrusion from nets, evasion from nets, and stage duration. The first three are negative biases, but deviation in stage duration can contribute either a positive or a negative bias. The nature of these biases is discussed here in preparation for the next section on sampling procedures and program (tactics and strategy) for the analysis of population change through studies of mortality at sea. Another bias may result from statistical transformation of abundance data.

Escapement

Escapement is defined here as the passage of the sampled organism through the mesh apertures of a net. A major consideration, then, is the size of the mesh aperture. As a first approximation it may be assumed that escapement will occur when the minimum dimension of the anchovy larva is less than the diagonal of the mesh aperture. The selection of an appropriate mesh aperture is important because larger apertures yield variable retention when, for example, filamentous algae impart retention characteristics of smaller nominal mesh apertures. Smaller than necessary net apertures retain more plankton from which the larvae will have to be sorted; costs of sorting anchovy larvae from other plankton are high, so this too is an important consideration.

Extrusion

Extrusion in this context is the forcing of the larvae through the meshes of the net. This can result either from improper design of the net or from towing the net at too high a speed. Towing speed may be acceptable on the average, but an increase in speed near the end of the tow can extrude larvae retained for most of the tow duration. Extrusion may also be increasingly probable with the lengthening of towing time or with vertical towing in rough seas. As a first approximation, extrusion and escapement should be evaluated at tow speeds of 70 cm/sec with increments of 20 cm/sec (Smith and Richardson, 1977, Table 3.2.3).

Evasion

Evasion is the swimming of larvae out of the volume to be filtered by the net. Evasion is demonstrable from day/night (Fig. 8) differences in catch of anchovy larvae and sardine larvae as small as 5 mm preserved length. The existence of a day/night difference also demonstrates night avoidance (Smith and Richardson, 1978). For a first approximation the evasion bias can be regarded as total when the length of the anchovy larva is 3 percent of the radius of the net when the net is being towed at 5 larval body lengths per second. For bridle-free nets (which are recommended), larvae will be sampled somewhat better. Evasion will likely be reduced by improved filtration efficiency and nets with low visual contrast.
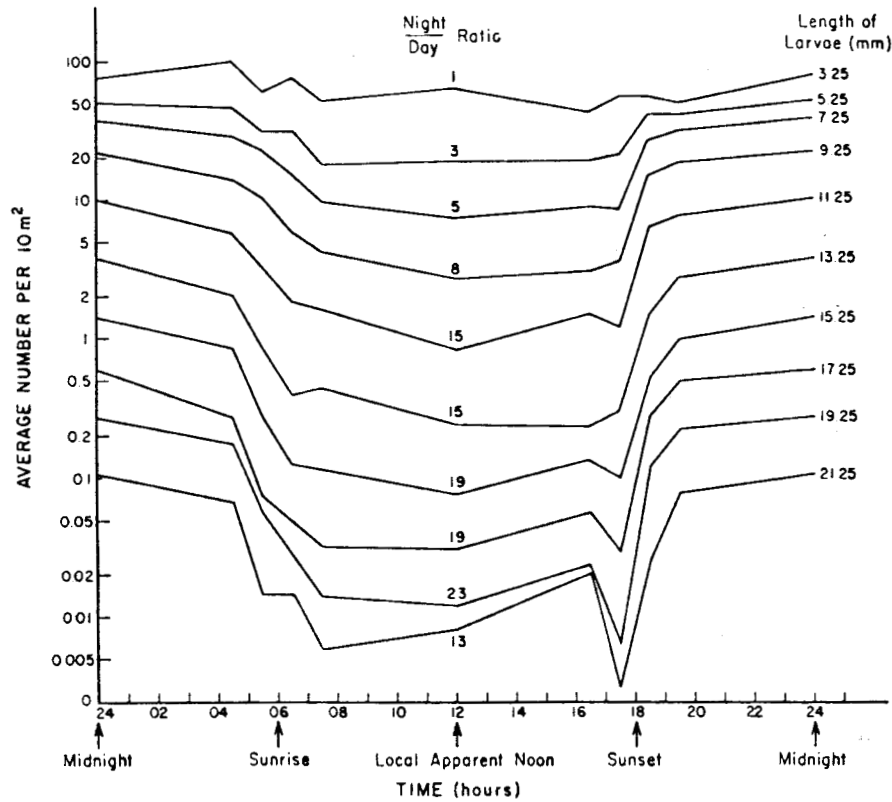
Figure 8. Larval anchovy capture by time of day and size, total California Current Area, 1951–1969. Marked asymmetry at dusk may be attributed to the tendency of larvae 10 mm standard length to approach the surface to ingest a bubble to fill the gas bladder (Hunter and Sanchez, 1977). The night to day ratio of catches is likely due to enhanced ability to react effectively to the slow approach (70 cm/sec) of the CalCOFI net in daytime.

Stage Duration

The duration of fixed arbitrary developmental stages of fish larvae controls the estimation of mortality. If all adjacent stages of fish larvae are of identical duration, a precise and accurate estimate of mortality rate is possible from relative estimates of abundance of the adjacent stages. For example, if one stage is twice as long as the following stage, the interstage mortality rate will be overestimated owing to the relative overestimate of the first stage. Of course, mortality "inversions" can occur when the second stage is so long as to appear more abundant than the first. Unbiased mortality rate estimates may be possible if stage duration is known.

1. Temperature

Temperature can influence mortality estimates over time or area by delaying larval development in colder time periods or areas leading to a longer duration at a stage and an overestimate of relative abundance. Temperature

16

and natural variation may be the exclusive controls on development rate and stage duration in the embryonic period (before feeding) of the larvae. In anchovy the embryonic development period may be doubled by a change from 18°C to 13°C, leading to a twofold overestimate of abundance at that stage.

2. Food

Following total utilization of the yolk, the rate of feeding and energy expended searching for food may markedly influence the duration of predefined stages. No studies of the effect of feeding on duration of predefined stages have been completed. It may be assumed that variability by a factor of 2 in duration may occur in the early larval stages, and a factor of 7 seems possible for the later larvae. However, this high level of variability does not appear to be supported by the age distributions of larvae caught at sea (Methot and Kramer, 1979).

Statistical Tranformation

It seems possible to confuse the graphic (Bagenal, 1955; Aitchison and Brown, 1966) and analytical properties of the exponential decline in abundance with the statistical properties of log transformation. It is, of course, permissible as a first approximation to plot the logs of abundance versus time to obtain a linear form of the exponential mortality and to interpolate on this basis. A problem arises if, instead of plotting the log values of the stage sample means, one plots the means of the logs of the sample values. This is the geometric mean, and the use of adjacent values of the stage geometric means will lead to a bias in the estimate of mortality slope. This bias originates from either or both of two sources related to the dispersal or aggregation of the larvae—changing sample variance and changing sample coverage.

1. Sample variance

The geometric sample mean is a function of the arithmetic mean and the sample variance. Thus changes in the geometric mean have imbedded in them changes in both sample mean and variance. The general trend of mortality in larvae is also accompanied by dispersal of patches in the embryonic and early larval stages and the appearance of reaggregation in the later larval stages. The effect is that the geometric mean is a large underestimate of abundance in the more patchy embryonic stage and a smaller underestimate of abundance in the more dispersed early larval stage; a mortality rate calculated from geometric means will thus be an underestimate of the population mortality rate. Such a comparison of geometric means may even result in changing the sign of the mortality rate. Less serious perhaps in the late larvae would be the tendency for the bias of the geometric mean to be greater in a late stage, and this would mathematically induce an overestimate of mortality brought on by the reaggregation of the population into patches.

2. Log transformation

Two approaches to log transformation arise in the treatment of zero samples: (1) if one adds a constant to all sample values before transformation and (2) if we analyze positive samples only. When analyzing mortality of fish larvae, addition of a constant induces a gradual decrease in the slope owing to the larger proportionate contribution to the total of the constant. Secondly, the dispersal of the embryonic stages entails expanding coverage of the habitat, possibly reducing the number of "zero" samples for a time and changing the proportionate contribution of the added constant. Analysis of only positive samples under these same conditions results in an overestimate of the mortality rate. For different species of larvae, I consider it prudent to examine these effects before proceeding with analysis of mortality. Alternately, methods not employing logarithms could be used.

3. Weighted negative binomial

The weighted negative binomial model (Bissell, 1972; Zweifel and Smith, in press) can be used to obtain unbiased sample means and maximum likelihood estimates of the upper and lower confidence limits. The advantage of this model has no biological basis but is related to the explicit treatment of "zero observations," the use of the arithmetic mean as one parameter, and the ability to accommodate all scales and intensity of contagion from Poisson distribution to log-normal.

Sampling Strategy

Limited resources for collection of larvae at sea, sorting, identifying and measuring on land, and analysis of the data lead one to consider questions of sample strategy. From examination of CalCOFI data used for biomass assessment, one may gain some insight into sampling requirements for more specific hypotheses regarding larval mortality. Some preliminary considerations of the extent of sampling and the temporal and spatial intensity of sampling may be deduced from existing survey data. The CalCOFI surveys usually covered tens to hundreds of thousands of square nautical miles, with one station for each 800–1600 square nautical miles. Surveys were at monthly or quarterly intervals, and annual estimates of species abundance were formed from 1500–2000 samples. This data set has limitations at the smaller scale for determining sampling strategy, but the scale of patches is probably from 0.2 to 1 nautical square mile (the size and movement of a spawning school) and the period of vulnerability of larvae to a plankton net is of the order of three weeks. For this purpose we will consider six hypothetical larval mortality situations: larval transport, critical period, predation (including cannibalism), starvation, preschooling distribution, and spawning condition.

Larval Transport

The null hypothesis is "changes in geographic distribution of the larvae

relative to the geographic distribution of spawning have no important influence on the numbers of fish which survive to become mature." To test this, one needs an estimate of the number of survivors from the cohort of interest and a set of larval samples. This set of samples must be spatially intensive to provide an estimate of mean position at several stages of larvae in the embryonic, early, and late larvae stages. The sample set for northern anchovy would also need to be temporally and spatially extensive because of the long duration and wide area of spawning from which the survivors eventually emerge. Space-time units for anchovy could be several hundred square miles at biweekly or monthly intervals from December to July. Within each space-time unit there would be sufficient precision for a useful mortality estimate from fewer than 100 samples.

Critical Period

The null hypothesis is "larval mortality is constant for all stages of embryonic larvae and early larvae, or there is a gradual improvement in survival as the larvae differentiate sensory and locomotor structure." The term "critical period" is an aquarist's phrase for the transition from rearing yolked larva stages to those requiring the provision of the proper kind and amount of food. It is reasonable to assume that first-feeding is also important in nature. The demonstration of this phenomenon at sea should probably begin with temporally intensive sampling over a small area near the maximum concentration of larvae. Because the embryonic stages and the early larval stages which ensue are still highly aggregated following the schooled spawning, adequate precision of estimates of the mean and standard error of the mean will require 500–1000 samples taken with sufficent precaution to eliminate escapement or extrusion through the meshes at the time of hatching. Mesh size should be 0.333 mm for northern anchovy, and the total volume filtered should be kept low to minimize variance.

Predation

The null hypothesis is "species 'A,' which coincides in space and time with the anchovy eggs or larvae, does not prey on the anchovy to such an extent that the anchovy egg or larva mortality rate is appreciably changed." In the test of this hypothesis, one requires spatially intensive samples which are adequate to sample both predator and prey. For example, in the special incidence of "cannibalism" it was found necessary to deploy plankton nets with 0.333 mm mesh and in the same area to deploy commercial-scale trawls to capture the adults. Other predators could require intermediate net sizes or could be obtained from the same samples as required to determine the larval mortality rate. To assemble a model of changes in larval mortality rate as a function of changes in the coincident populations of predators, the quantitative deployment of several scales of samples is required. It does not seem likely that population models for predators will be necessary on this time scale.

19

Starvation

The null hypothesis is "in nature the larval mortality rate is not affected by the amount, kind, spatial distribution, and production of food organisms." To gather evidence for this hypothesis, one would need the usual spatial and temporal intensity of sampling required to define larval mortality and the ability to sample with high spatial definition the food of the anchovy larvae. This would require the coupled deployment of sampling equipment with sufficient retention capacity to retain the food of the larval anchovy. The food samples would need only to cover the spectrum of sizes below the sampler used for the larval samples. The smallest size of interest is determined by the acuity of the larval eyes, and the largest size of interest is determined by the gape of the larval mouth. Since the larval mortality rate needs to be monitored for several months, one needs population models of the prey organisms to estimate food production. Another aid in resolving the horizontal and vertical dimensions of spatial intensity would be a series of models concerning the formation and destruction of food aggregations. Also, the changes in larval growth under various conditions of starvation will be required to adjust the size-specific mortality rate and the time-specific mortality rate estimates.

Preschooling Distribution

The null hypothesis is "in nature there are no important regional or temporal changes in dispersal rate which would materially influence the rate of formation of schools by juvenile anchovy." The tests of this hypothesis would require verification of the size and number of juvenile fish schools as a function of the distribution and number of fish larvae from which the schools were formed. Like the "predation" hypothesis, this would require a wide range of sampling apparatus. The deployment would be different in that the predation test requires simultaneous samples while the "preschooling distribution" hypothesis requires a sequential arrangement of samples of various sizes. For example, plankton nets or pumps would be deployed for the larval mortality rate, 60 days later micronekton net samples of juveniles would be needed, and later still, commercial size samples of prerecruits and adults would have to be taken. Sample repetition and the resultant sample variance would be used to evaluate the intensity of aggregations. Determining the scale of aggregation would require high spatial intensity and continuity for resolution.

Spawning Condition

The null hypothesis is "within the observed range of physiological condition of spawning adults, there will be no important changes in the subsequent survival rate of larvae." This test would require samples of the adult anchovy for six months prior to the spawning season and temporally intense samples of the egg production and larval survival.

Conclusions

While many plausible hypotheses exist to explain the variation in survival rate of larvae and the rate of addition of young fish to the commercial stock, there have been few tests. The scarcity of tests of hypotheses is caused by the lack of identification of the spatial and temporal intensity needed for samples required for the tests of single hypotheses. The evaluation and comparison of two or more mechanisms is far more difficult, and multiple tests are likely to be necessary. This may be stated as a null hypothesis, "the fundamental cause of variation in the survival of anchovy from spawning to recruitment is the same from year to year."

Larval Anchovy Patchiness

In the previous section I pointed out how larval anchovies have been used to assess biomass. Underlying this technique is the recognition that the larvae occur in patches and that a knowledge of the causes of patchiness is central to applying this technique. An investigation of larval survival must take into consideration patchy distribution of larvae as well. Anchovy larval patchiness has many origins, among them schooling of spawning adults (Smith, 1978b), diurnal periodicity in spawning behavior, local sites of high larval mortality, dynamic oceanic events like convergence zones, and larval aggregation behavior. Unfortunately, it has not been possible to study these contributing causes to patchiness in sufficient detail to detect the importance, scale, and consistency of the causes of patchiness (Fasham, 1978).

Schooling of Adults

The adult northern anchovy is found in schools, but it is not known whether schooling is a necessary condition for survival. Mais (1974) reported several years of surveys with a sonar using the "sonar mapping" technique (Smith, 1970), which yields an estimate of the number of schools per unit area and an estimate of the distribution of school sizes. Table 2 is a summary of measured targets from all seasons in the California Dept. of Fish and Game Surveys (Mais, 1974). From this table it is seen that about 94 percent of all fish schools are less than 80 meters in diameter, but if school tonnage is proportional to school cross-sectional area, the 6 percent of schools larger than 80 meters in diameter contain more than half the anchovy biomass.

Seasonal data from Mais (1974), summarized in Table 3, show that the number and size of anchovy schools increase rapidly in summer and fall. There is reason to believe that the additional schools may contain radically less biomass ($\frac{1}{3}$ to $\frac{1}{2}$) per unit surface area (Hewitt et al., 1976, Fig. 4b; Vent et al., 1976, Figs. 7d and 7e). These may not be spawning schools. Instead, they may be the large schools of loosely compacted juveniles spawned in the preceding fall, winter, and spring.

Anchovy schools are probably more compact in the daytime (when we have measured the schools with sonar) than they are at night when they are spawning. For example, the average daytime compactness of 15,000 grams of anchovy per square meter of school horizontal area (Hewitt et al., 1976) could have 7500 grams of female anchovy of which one-sixth (1250) are spawning; 380 eggs per gram of female would yield 475,000 eggs per square meter per night (Hunter and Goldberg, 1980). Our largest samples of eggs

22

are about one-twentieth of this value, or 23,750 eggs per square meter. This value will have been influenced not only by the spawning school becoming less compact at night, but also by gross motion of the school during several (6–8) hours of spawning and by turbulent dispersion of the eggs following spawning and fertilization.

Spawning and schooling behavior in the Pacific sardine is probably analogous to that of the northern anchovy. A localized analysis of 183 plankton samples (from Smith and Richardson, 1977, p. 84) is shown in Table 4. The major features of the development of larval patchiness following spawning are shown. One characteristic is that there are 85 percent positive samples of first-feeding larvae (5 mm SL) and only 66 percent positive samples of first-day eggs. Owing to dispersion, more area appears to be covered by larvae than by eggs. In about three weeks, there have been increases in unit sample areas covered by 2, 8, 32, 128, and 512 sardines per 10 m² and decreases in areas with 0, 8, 192, and 32,768 sardines per 10 m². By the time the larvae are 10 mm long, there are no sample counts of 128 and above, and only 20 percent of the unit sample areas contain larvae.

Last, it should be noted that a condition of random distribution where the variance equals the mean is not attained in the set of data in Table 4. The variance:mean ratio is 11,840 to 1 for first-day eggs and is still 15 to 1 for 10 mm larvae. Unfortunately, we have insufficient observations to determine how much of the patchiness persists from the nocturnal spawning behavior of the adults and, alternately, how much of the larval distribution is the result of pattern-forming activities such as localized areas of high mortality, aggregation behavior of the larvae, and dynamic ocean events like convergence.

Statistical Consequences of Larval Patchiness

The primary statistical consequence of larval patchiness is the requirement for large numbers of samples to allow an estimate of absolute abundance with useful levels of precision. The number of samples required for a constant precision of ±10% of the mean for the 3 days and sardine larvae to 10 mm length are shown at the bottom of Table 4. The range is from 6,759 samples of first-day eggs to 1,093 samples of 5 mm larvae. The rapid increase in samples with no larvae in the 8, 9, and 10 mm classes imposes additional sampling requirements.

Although the trends in sampling requirements by stage of development look reasonable, one should be cautious about the actual values, because the parameter estimates are sample estimates from only 183 samples. The actual number of samples required is a function of the population mean and the population variance, not the sample mean and variance. Current estimates of sample mean and variance are also likely to include sources of variance other than larval patchiness (English, 1964) such as temporal and spatial gradients

Table 2. Anchovy school diameter frequency distribution by school and biomass.

School diameter (m)	School biomass (metric tons)	Frequency	Sample proportions	Cumulative sample proportions	Class biomass (metric tons)	Biomass proportions	Cumulative biomass proportions
10	1.2	9,906	0.4338	0.4338	11,670	0.0274	0.0274
30	10.6	9,002	0.3942	0.8281	95,447	0.2245	0.2519
50	29.45	1,822	0.0798	0.9079	53,662	0.1262	0.3782
70	58	706	0.0309	0.9388	40,755	0.0959	0.4740
90	95	824	0.0361	0.9749	78,631	0.1849	0.6590
110	143	178	0.0078	0.9827	25,374	0.0597	0.7187
130	199	217	0.0095	0.9922	43,204	0.1016	0.8203
150	265	50	0.0022	0.9944	13,254	0.0312	0.8515
170	340	40	0.0018	0.9961	13,619	0.0320	0.8835
190	425	51	0.0022	0.9983	21,690	0.0510	0.9345
210	520	19	0.0008	0.9992	9,871	0.0232	0.9577
230	623	7	0.0003	0.9995	4,362	0.0103	0.9680
250	736	3	0.0001	0.9996	2,209	0.0052	0.9732
270	859	1	0.0000	0.9996	859	0.0020	0.9752
290	991	2	0.0001	0.9997	1,982	0.0047	0.9799
310	1,132	1	0.0000	0.9998	1,132	0.0027	0.9825
330	1,283	3	0.0001	0.9999	3,849	0.0091	0.9916
350	1,443	0	0.0000	0.9999	0	0.0000	0.9916
370	1,613	0	0.0000	0.9999	0	0.0000	0.9916
390	1,792	2	0.0001	1.0000	3,584	0.0084	1.0000

Table 3. Selected parameters of northern anchovy schools in California coastal waters (calculated from Mais, 1974).

Season	Anchovy schools (no/km^2)	Anchovy school size (m^2/school)	Coverage m^2 of anchovy school / m^2 surveyed
Winter	0.79	1151	0.0009
Spring	0.73	772	0.0006
Summer	1.22	1327	0.0016
Fall	1.98	1683	0.0033

(Colebrook, 1969) and regional and seasonal differences in abundance and survival. All data analyzed so far (Smith, 1972; Parker, 1980) indicate that the schooling pattern of the adults is the major source of variance.

Because schools are the major source of variance, any regional or seasonal correlative studies or analyses of variance must expend a high level of sampling effort to ascertain cause and effect of survival and environmental conditions. Log-transformation does not materially aid these comparisons. For example, in Table 4, the geometric mean provided by log-transformation increased from 23 stage "A" eggs to 40 5-mm larvae, while the arithmetic mean decreased from 673 stage "A" eggs to 161 5-mm larvae. It is mathematically possible to estimate the arithmetic mean from the mean and variance of log-transformed data, but there are insufficient studies to date to establish the efficacy of estimating two parameters, mean and variance of the log-transformed sample values, to further estimate another population parameter, the arithmetic mean. This statistical phenomenon should be explicitly solved by simulation before cause and effect studies are planned and conducted at sea.

It is apparent that the variance of numbers of eggs and larvae in samples is a result of the interaction of the size of the sample and the size of the patch. For example, patchiness on the scale of centimeters would not be measurable with a 1-meter net towed several meters. One obvious solution to sample variance would be to lengthen the tow until the proper proportion of larval patch to low-density areas between patches is obtained in a single sample. For this tactic to succeed there should be one scale of patch constant from place to place and from time to time.

It is not yet possible to test the consistency of patch scales; it is known that patchiness occurs on several broadly differing scales at sea. Smith (1970) reported a school group, believed to be northern anchovy, about 10 km in diameter. Fiedler (1978) reported the analysis of several school groups detected by California Dept. of Fish and Game Sea Surveys. The mode of school group radii detected was 8 miles (13 km) and the distribution ranged from 2 to 64 miles (3-100 km), with a log normal distribution with parameters $\overline{\ln x}$ = 2.319 and variance 0.676. Within school groups, the number of schools per

Table 4. Sample frequency distribution of Pacific sardine eggs and larvae and number of samples required to obtain a standard error of the mean of 10% (modified from Table 3.17, Smith and Richardson, 1977).

ln(X+1)	X	EGGS (Days post-spawning)			LARVAE (Standard length, mm)						
		A	B	C	3	5	6	7	8	9	10
0	0	65	44	76	29	27	38	57	91	124	146
1.1	2	7	14	5	13	5	12	23	21	32	23
2.2	8	14	14	16	36	20	32	51	52	19	12
3.5	32	20	27	31	50	46	68	45	18	8	2
4.9	128	36	33	17	29	49	30	7	1		
6.2	512	22	25	26	23	34	3				
7.6	2048	12	21	12	3	2					
9.0	8192	6	5								
10.4	32768	1									
	$\bar{X}$	673	557	225	129	161	43	15	6	3	1
	S_x	2,823	1,433	515	298	272	75	26	13	7	4
	S^2_x	7,968,421	2,054,393	264,757	88,524	73,756	5,574	668	170	46	15

Required samples to obtain standard error of mean = $\dfrac{\bar{X}/1.96}{10}$

	A	B	C	3	5	6	7	8	9	10
	6,759	2,544	2,009	2,004	1,093	1,158	1,141	1,814	1,963	5,762

Percent positive

	A	B	C	3	5	6	7	8	9	10
	66	76	58	84	85	79	69	50	32	20

square mile exhibits a mode at 67 (20/km²) and the distribution ranges from 9 schools to 221 schools per square mile (3–64/km²). The log normal parameters are $\overline{\ln x} = 3.910$ and variance 0.510. School sizes exhibit a mode at 10 meters and a range of distribution of from 0 to 400 meters (Mais, 1974, Table 1). Also, the compaction of fish within the schools (Hewitt et al., 1976) varies from 0.25 to 64 kg/m2, with a mode of 4 kg/m² and a log-normal distribution with parameters $\overline{\ln x} = 1.952$ and variance 1.916. Graves (1977) photographed within fish schools at sea and detected a range of 50–366 fish per square cubic meter (Fig. 9). The underlying importance of the intensities and scales of contagion is that it is unlikely that a sample tow of any particular fixed length will diminish sample variance materially.

Biological Consequences of Larval Pattern

For fish schooled as adults, larval pattern may represent only a brief dispersed interlude in the life cycle. Some of the advantages of schooling as an adult could be conferred on the larval aggregations. Shaw (1978) lists the advantages of schooling as follows: conservation of energy while swimming through hydrodynamic interaction; enhanced reproductive opportunity; improved learning; greater tolerance of toxic substances; and protection from predators. Probably only improved learning and protection from predators would apply to the larval stage.

Protection from predators (Brock and Riffenburg, 1960; Hobson, 1978) through aggregation is implemented by decreased probability of contact and this is most advantageous when the size of the aggregation is adequate to satiate the predator. This latter consequence may operate at the larval stage or the maintenance of aggregations in the larval stage may only facilitate the formation of schools of "viable" size following metamorphosis into schooling juveniles.

Hewitt (1981) has considered the adaptiveness of larval pattern and described the life-cycle pattern through the larval stage for two fishes, the clupeiform anchovy (Engraulidae, *Engraulis mordax*), and the perciform jack mackerel (Carangidae, *Trachurus symmetricus*). He finds that the spawning pattern is less intense for the perciform. An index of patchiness indicates that the pattern becomes identical for anchovy and jack mackerel after two weeks of age.

Our interest in patchiness and particularly the changes in patchiness from one life stage to another stems from the conviction that since mean abundance of older larvae so far does not allow the distinction to be made between highly successful and moderately successful year classes, it may be that the intensity of pattern rather than mean abundance controls the success of survival in the later stages. With this rationale, the maintenance of patches in the larval state secures the advantages of schooling far sooner for the juveniles.

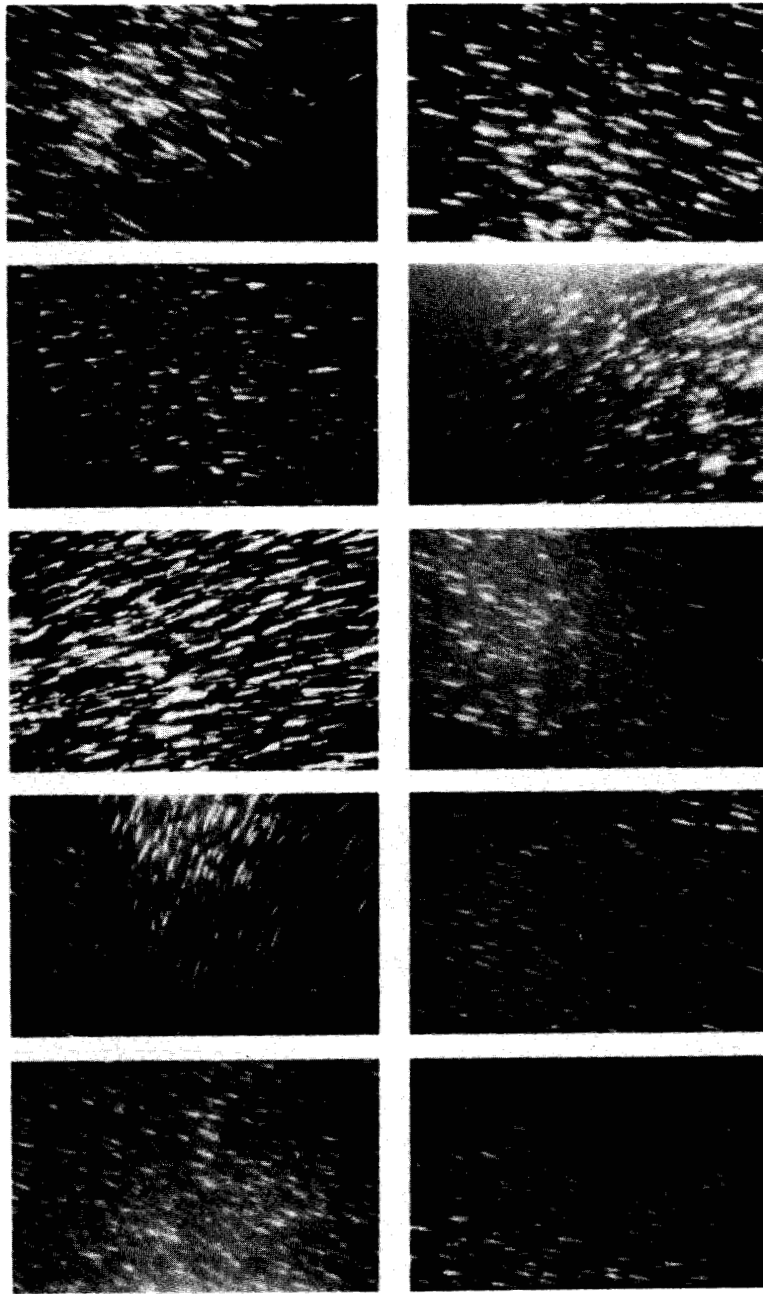Lastly, patchiness may be a requirement for survival. Vlymen (1977)

Figure 9. Portions of anchovy schools photographed at sea (Graves, 1977) with the Isaacs-Brown free vehicle drop camera. The mean of ten schools was estimated to be 115 fish per cubic meter (standard deviation 99, range 50–366, median 69).

demonstrated with a simulation model that larval growth requires patchiness in its food given the quantity of food in the sea. Thus a major oceanographic feature may be the stability to foster and maintain patches of food and permit the larvae to remain in favorable patches (Hunter, 1976; Lasker et al., 1970; Smith and Lasker, 1978; Lasker and Zweifel, 1978; Hewitt, 1981). Possibly one of the more enduring effects of the CalCOFI program has been the transition from regarding patchiness as a statistical nuisance to the appreciation of pattern as a necessity in the pelagic ecosystem.

References

Ahlstrom, E.H. 1954. Distribution and abundance of egg and larval populations of the Pacific sardine. U.S. Fish. Bull. 56:82-140.

———. 1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish. Bull. 60:106–146.

———. 1965. A review of the effects of the environment of the Pacific sardine. Interntl. Comm. for No. Atlantic Fish., Spec. Publ. No. 6, pp. 53–74.

Ahlstrom, E.H. and J. Radovich. 1970. Management of the Pacific sardine. In A Century of Fisheries in North America (ed. N.G. Benson), p. 183. Spec. Publ. No. 7, Amer. Fish. Soc., Washington, D.C.

Aitchison, J., and J.A.C. Brown. 1966. The Lognormal Distribution. Cambridge Univ. Press.

Bagenal, M. 1955. A note on the relations of certain parameters following a logarithmic transformation. J. Mar. Biol. Ass. U.K. 34:289–296.

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

Bissell, A.F. 1972. A negative binomial model with varying element sizes. Biometrika 59:435–441.

Brock, V.E., and R.H. Riffenburgh. 1960. Fish schooling: a possible factor in reducing predation. J. Cons. int. Explor. Mer 25:307–317.

Colebrook, J.M. 1969. Variability in the plankton. Progr. Oceanogr. 5:115–125.

English, T. Saunders. 1964. A theoretical model for estimating the abundance of planktonic fish eggs. Rapp. P.-v. Réun. Cons. int. Explor. Mer 155:174–182.

Fasham, M.J.R. 1978. The statistical and mathematical analysis of plankton patchiness. In Oceanography and Marine Biology—An Annual Review, Vol. 16. Aberdeen Univ. Press.

Fiedler, P.C. 1978. The precision of simulated transect surveys of northern anchovy, *Engraulis mordax*, school groups. U.S. Fish. Bull. 76:679–685.

Graves, J. 1977. Photographic method for measuring spacing and density within pelagic fish schools at sea. U.S. Fish. Bull. 75:230–234.

Hayashi, S. 1961. Fishery biology of the Japanese anchovy, *Engraulis japonica* (Houttuyn). Bull. Tokai Reg. Fish. Res. Lab., 31:145–268.

Hewitt, R.P. 1981. The value of pattern in the distribution of young fish. ICES Symp. on Early Life History of Fish, Woods Hole, Mass., April 1979. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:229–236.

Hewitt, R.P., P.E. Smith, and J. Brown. 1976. Development and use of sonar mapping for pelagic stock assessment in the California Current area. U.S. Fish. Bull. 74:281–300.

Hobson, E.S. 1978. Aggregating as a defense against predators in aquatic and terrestrial environments. In Contrasts in Behavior (ed. E.S. Reese and F.J. Ligher), Wiley & Sons, New York.

Hunter, J.R. 1976. Culture and growth of northern anchovy *Engraulis mordax* larvae. U.S. Fish. Bull. 74:81–88.

Hunter, J.R., and C.K. Sanchez. 1977. Diel changes in swimbladder inflation of the larvae of the northern anchovy *Engraulis mordax*. U.S. Fish. Bull. 74:847–855.

Hunter, J.R., and S. Goldberg. 1980. Incidence of spawning at sea and fecundity in the multiple spawning fish *Engraulis mordax*. U.S. Fish. Bull. 77:641–652.

Kramer, D., M. Kalin, E. Stevens, J. Thrailkill, and J. Zweifel. 1972. Collecting and processing data on fish eggs and larvae in the California Current region, NOAA Tech. Rep. NMFS CIRC-370.

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

Lasker, R., and J.R. Zweifel. 1978. Growth and survival of first-feeding northern anchovy larvae *(Engraulis mordax)* in patches containing different proportions of large and small prey. *In* Spatial Pattern in Plankton Communities(ed. J.H. Steele), pp. 329–353, Plenum, New York.

Lenarz, W.H. 1971. Modeling the resource base. *In* Symposium on the Development of the San Pedro Wetfish Fishery—a Systems Approach (ed. A.R. Longhurst). Calif. Coop. Oceanic Fish. Invest. Rep. 15:28–32.

————. 1972. Mesh retention of larvae of *Sardinops caerulea* and *Engraulis mordax* by plankton nets. U.S. Fish. Bull. 70:839–848.

Lloyd, M. 1967. Mean crowding. J. Anim. Ecol. 36:1–30.MacCall, A.D. 1974. The mortality rate of *Engraulis mordax* in southern California. Calif. Coop. Oceanic Fish. Invest. Rep. 17:131–135.

Mais, K.F. 1974. Pelagic fish surveys in the California Current. Calif. Dept. Fish and Game, Fish Bull. 162, 79 pp.

Methot, R.D. Jr., and D. Kramer. 1979. Growth of northern anchovy, *Engraulis mordax*, larvae in the sea. U.S. Fish. Bull. 77:413–423.

Murphy, G.I. 1966. Population biology of the Pacific sardine *(Sardinops caerulea)*. Proc. Calif. Acad. Sci. 4th Series, 34:1–84.

Murphy, G.I., and R.I. Clutter. 1972. Sampling anchovy larvae with a plankton purse seine. U.S. Fish. Bull. 70:789–798.

Parker, K. 1980. Direct estimation of spawning frequency and spawning biomass in a multi-spawning pelagic species. U.S. Fish. Bull. 78:541–544.

Shaw, E. 1978. Schooling fishes. Amer. Sci. 66:166–175.

Slobodkin, 1962. Growth and Regulation of Animal Population. Holt, Rinehart and Winston, pp. 168.

Smith, P.E. 1970. The horizontal dimensions and abundance of fish schools in the upper mixed layer as measured by sonar, p. 563. *In* Proc. of an Int. Symp. on Biol. Sound Scattering in the Ocean (ed. G.B. Farquahar). MC Rep. 805, Dept. of Navy.

————. 1972. The increase in spawning biomass of the northern anchovy, Engraulis mordax. U.S. Fish. Bull. 70:849–874.

————. 1973. The mortality and dispersal of sardine eggs and larvae. Rapp. P.-v. Réun. Cons. Perm. int. Explor. Mer 164:282–292.

————. 1978a. Biological effects of ocean variability: time and space scales of biological response. Rapp. P.-v. Réun. Cons. int. Explor. Mer 173:117–127.

————. 1978b. Precision of sonar mapping for pelagic fish assessment in the California Current. J. Cons. int. Explor. Mer 38:31–38.

Smith, P.E., and S.L. Richardson. 1977. Standard techniques for pelagic fish egg and larva surveys. FAO Fish. Tech. Paper No. 175, Rome.

Smith, P.E., and R. Lasker. 1978. Position of larval fish in an ecosystem. Rapp. P.-v. Réun. Cons. int. Explor. Mer 173:77–84.

Smith, P.E., L.E. Eber, and J.R. Zweifel. In press. Large-scale environment events associated with changes in the mortality rate of the larval northern anchovy. ICES Symp. on Early Life History of Fish, Woods Hole, Mass., April 1979. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178.

Smith, P.E., and C.A. Haight. 1980. A time series of age composition and apparent abundance of the northern anchovy, *Engraulis mordax*, with inferences about the strength of recruitment. SWFC Admin. Rep. LJ-80-07.

Theilacker, G.H. 1980. Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservation. U.S. Fish. Bull 78:685–692.

Vent, R.J., I.E. Davies, R.W. Townsen and J.C. Brown. 1976. Fish school target strength and doppler measurements. Naval Undersea Center, San Diego, Ca., NUC Tech. Paper No. 521, 32 pp.

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

Zweifel, J.R., and P.E. Smith. In press. Estimates of abundance and mortality of larval anchovies (1951–1975): application of a new method. ICES Symp. on Early Life History of Fish, Woods Hole, Mass., April 1979. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178.