New Ideas on the Fluctuations of the Clupeoid Stocks off California

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Fisheries scientists have been intrigued with the boom and bust phenomenon that characterizes many fisheries but is particularly exemplified by the clupeoid fisheries, i.e. sardine, anchovy, menhaden, herring. Some of the clupeoids achieve huge populations with biomasses in the millions of tons. Exploitation by coastal nations is for human and animal food, the latter by a reduction of fish to meal which is usually included in diets of poultry and cattle to provide essential amino acids for protein metabolism and growth. Many nations have suffered the economic and social distress of industrial failure due to the collapse of a mainstay clupeoid fishery. Today the clupeoids make up about one-third of the world's fish catch. However, between 1968 and 1971 the catch of the Peruvian anchoveta averaged 10 million t per year and alone contributed 15% of the world fish catch. Figure 1 illustrates the precipitous decline of the Peruvian anchoveta (*Engraulis ringens*) catch and some of its related consequences, for example the rise in the cost of fish meal on the world's markets and the substitution of soybean (another protein source) for fish meal.

California coastal fisheries in the late 1930s and through the 1940s rode the economic boom of a thriving sardine (*Sardinops sagax*) fishery. Catches of this species for all California ports totalled as much as 658 000 t in the 1936-37 season but the usual annual catch through the mid-1940s was 400 000–500 000 t (Marr 1960). By 1952, the sardine catch had fallen disastrously and, except for a small resurgence in 1958, the sardine has

"disappeared" from California waters (Fig. 2). That this collapse was unremarkable and more or less typical of
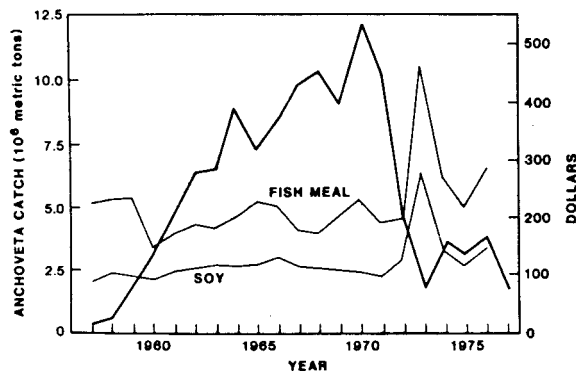

FIG. 1. The Peruvian anchoveta catch from 1957 to 1977 is shown with concomitant dollar prices for fish meal and soy on the world market (after Barber et al. 1980).
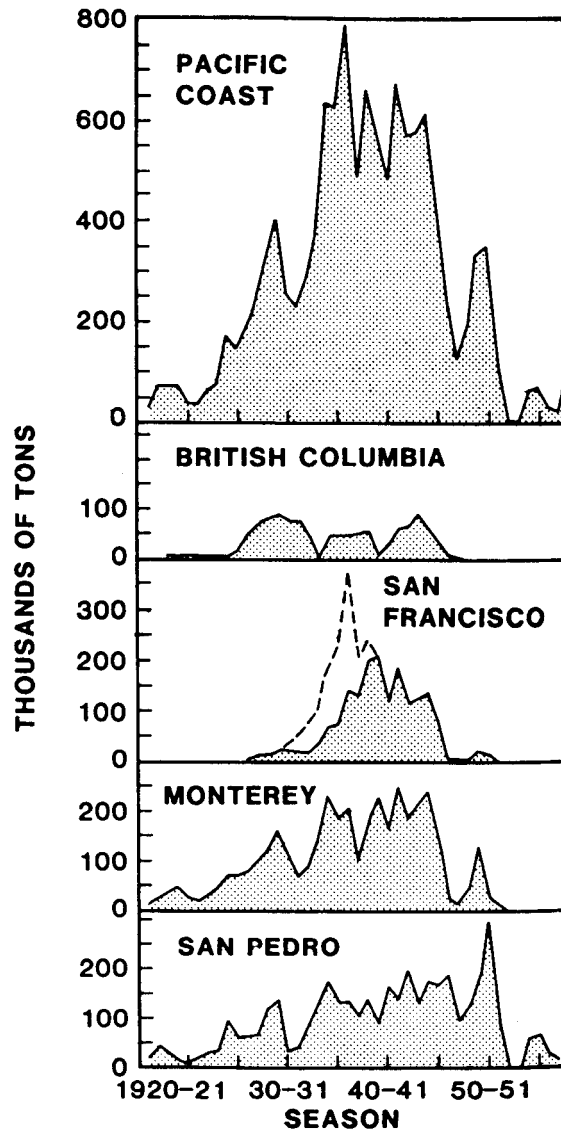
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FIG. 2. North American Pacific coast sardine landings. The dashed line in the San Francisco panel indicates landings made at high seas plants (after Marr 1960).

what we have come to expect from clupeoid fisheries today, can be seen by comparing similar catch records from other clupeoid fisheries. As one example, 1936 was also a peak year for the catch of the Japanese sardine, *Sardinops melanosticta*. Its disappearance was almost complete by 1945 with a small resurgence in 1951-53 (Fig. 3). Similarly, Hempel (1978) has shown that the North Sea herring (*Clupea harengus*) has seen, if not a disappearance of the fishery, a huge decline in catch from a high of 1.2 million t in 1965 to about 200 000 t in 1975 (Fig. 4). Other North Atlantic clupeoid fisheries have shown similar rapid declines (see Schumacher 1980), as has the pilchard (*Sardinops ocellata*) off Namibia, Africa (Troadec et al. 1980).

While collapses are common, so too are recoveries. Most notable in recent years have been the increased
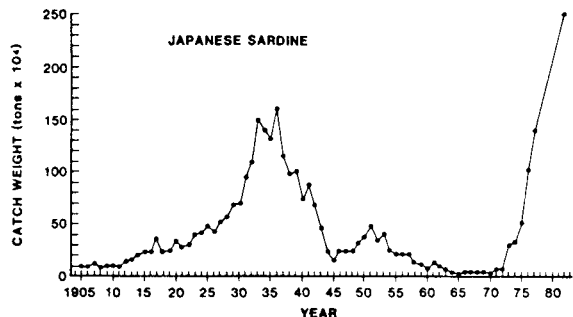

FIG. 3. Catch of the Japanese sardine (after Kondo 1980; and K. Kondo, Tokai Regional Fisheries Research Laboratory, Tokyo, Japan, personal communication).
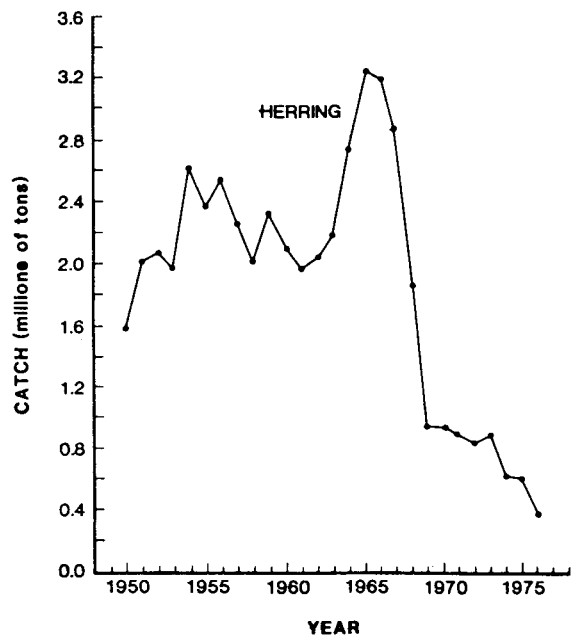
fisheries on the Japanese sardine, *S. melanosticta*, (Kondo 1980), and the Peruvian–Chilean sardine, *Sardinops sagax* (O. Rojas, Instituto de Fomento Pesquero, Santiago, Chile, personal communication). At its peak in 1936, the catch of the Japanese sardine was slightly over 1.6 million t. After its decline, very few sardines were caught from 1960 through 1972. Figure 3 illustrates the dramatic comeback made by this species, with the 1981-82 catch at about 2.5 million t. Kondo (1980) has said that this resurgence is attributable to the outstanding success of the 1972 year-class. Lea documented a similar outstanding year-class (1904) of herring (*Clupea harengus*) which sustained the North Sea herring fishery for many years (cited by Hardy 1959).

The loss of the Peruvian (and Chilean) anchoveta fishery is being offset, albeit not completely, by an increase in the catch of the Peruvian–Chilean sardine (Fig. 5). A comparison of Fig. 1 and 5 shows that the anchoveta declined in both Peruvian and Chilean waters simultaneously, coincident with a widespread El Niño condition, an unusual warming of the anchoveta habitat. Similarly the sardine catch has increased explosively in both countries. This is not to suggest that species from other fish families do not have similar dramatic ups and downs. Haddock (*Melanogrammus aeglefinus*) for example, has shown a remarkable increase in its North Sea population during a simultaneous collapse in the herring population (Hempel 1978).

While fishing is an obvious source of mortality, scientists who have studied the fluctuation of fish populations have not yet come to any definitive conclusion as to what degree fishing is the source of any clupeoid
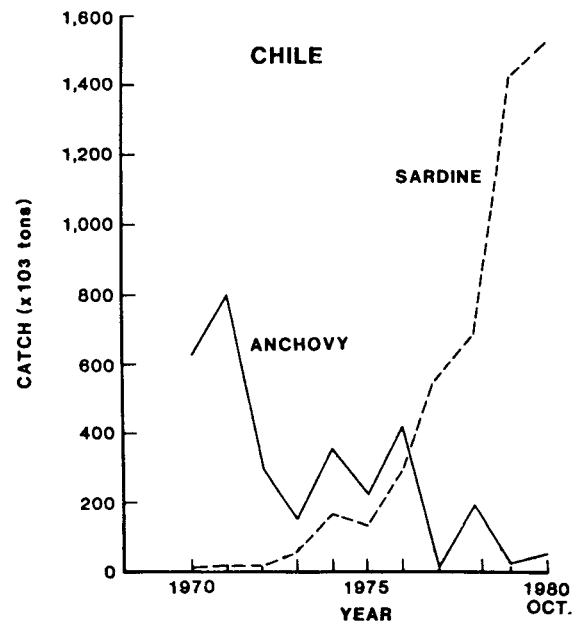

FIG. 4. Catch of the North Sea herring (after Schumacher 1980).

FIG. 5. The 1970-80 Chile catch of the Peruvian–Chilean anchovy and sardine (O. Rojas, Instituto de Fomento Pesquero, Santiago, Chile, personal communication).

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collapse. In an interesting paper, Clark and Marr (1955) argued for opposing viewpoints regarding the loss of the Pacific sardine. Clark believed that each Pacific sardine year-class was related to stock size and was density dependent. Marr, on the other hand, argued that poor year-classes were due to adverse environmental factors (chiefly temperature affecting spawning time) and caused the sardine's disappearance (density independence); however, he added that at the smallest stock sizes year-class size is a function of spawning stock size. Logically, some form of density independence must be operative to account for fish population outbursts, but neither Clark nor Marr commented on what might induce a successful year-class at low stock levels.

In an elegant paleoecological investigation, Soutar and Isaacs (1969, 1974) sought to reconstruct a history of the fluctuations in some of the common fish populations off California by identification of fish scales in undisturbed sedimentary cores from local anaerobic basins, such as the Santa Barbara Basin near Los Angeles. Figures 6 and 7 show nearly 2000 yr of apparent biomass fluctuations for Pacific sardine and northern anchovy (*Engraulis mordax*). Figure 8 shows that ex-

treme biomass fluctuations, both precipitous declines and rapid increases, are common where no fisheries have ever been present.

A few years after the Pacific sardine collapse, the northern anchovy *Engraulis mordax* began to increase in California and Baja California waters. By 1960, the sardine was virtually gone, but egg and larval surveys indicated that the anchovy had become the abundant clupeoid in California waters. By 1965, the anchovy spawning biomass exceeded 4.5 million t. Except for a brief period in the early 1950s, there was no substantial fishery for this species until 1966. A substantial decline in the population occurred between 1975 and 1978. Although a small fishery (ca. 200 000 t) was established during those years, only a tiny fraction of the decline from 3.5 million t to 1 million t could be accounted for by fishing. Studies over the past decade on the northern anchovy off California and Baja California have allowed the development of some generalizations which may be applicable to the fluctuation of clupeoid populations in general.

Ecological Requirements for Larval Survival

Hjort's (1913) original suggestion pinpointing the early first-feeding larva as the most vulnerable stage in the life history of fishes is still the basis for many interesting hypotheses. He believed that the presence or lack of food at larval first-feeding decided the size of the year-class in annually spawning herring. This idea has been resurrected from time to time in the literature, and has received experimental support from a number of investigations where the laboratory food requirements of fish larvae have been compared with available food under natural conditions. For example, laboratory work on anchovy larvae in California (O'Connell and Raymond 1970) indicated that first-feeding anchovy larvae require higher food densities (as determined in the laboratory) than has been usually reported from its habitat (Beers and Stewart 1967); (see review by Hunter 1977).
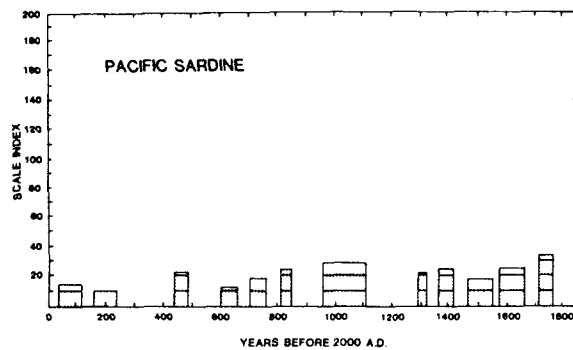

Fig. 6. Soutar and Isaacs' (1969) population indexes for Pacific sardine derived from the number of scales found in anaerobic sediments from the Santa Barbara Basin (modified after Soutar and Isaacs 1969).
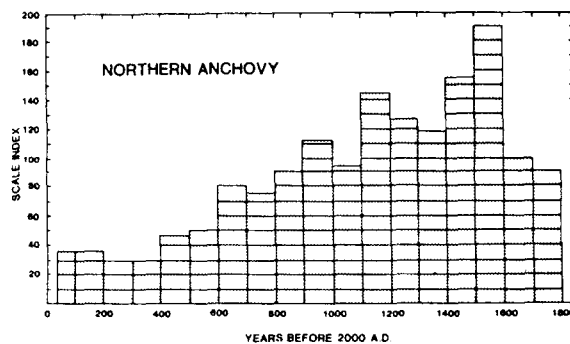

Fig. 7. Population index for northern anchovy derived from numbers of scales found in anaerobic sediments from the Santa Barbara Basin (modified after Soutar and Isaacs 1969).
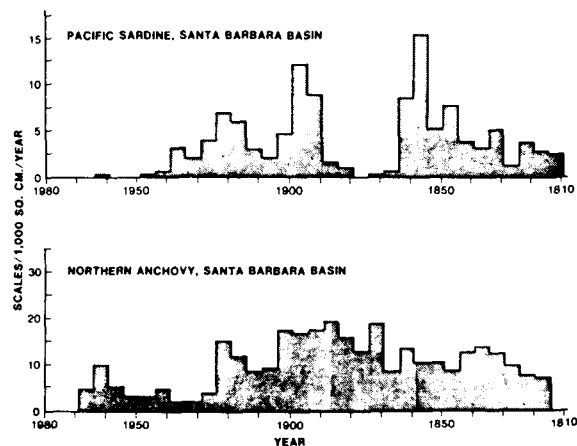

Fig. 8. Recent scale deposition rates for the Pacific sardine and the northern anchovy.

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In a series of papers, Lasker (1975, 1978, 1981a) showed that food is indeed present at high enough concentrations, usually in coastal waters, at local densities sufficient to insure feeding in a high proportion of first-feeding anchovy larvae. Furthermore, he indicated that survival may be a function of ocean stability (Lasker 1981b) where maintenance of high numbers of food organisms is dependent on the lack of water turbulence. When turbulence is strong, due to storms, upwelling, etc., concentrations of food organisms may be dispersed reducing the number of food particles to below feeding-threshold densities, and making it impossible for newly feeding anchovy larvae to survive. The kind of food available is another factor, since some foods would not support growth in anchovy larvae.

Egg Mortality and Larval Production

Mortality of northern anchovy eggs has only recently received much attention in relation to subsequent larval survival. Hunter and Kimbrell (1980) determined that anchovy adults, because of their filter-feeding capability, can and do strain out and ingest congregated as well as isolated anchovy eggs. The patchiness of eggs (prey) and the schooling behavior of the adults (predators) make the coincidence of predator and prey particularly important in determining the number of eggs that will survive. Probably other schooling organisms, e.g. sardines and euphausiid shrimps, (Theilacker and Lasker 1974) can reduce the number of surviving offspring.

In 1980 and 1981, very similar overall egg production rates occurred, but egg mortality rates were very different in the two successive years (Table 1). This resulted in a very much higher number of early larvae in 1981 than in 1980. At this writing (July 1982), the 1981 year-class seems to be a very poor one. Thus, environmental factors having little to do with the number of larvae produced seem the more likely explanation for the resultant year-class size in this case.

Recent studies by Methot (1981) incorporating birth date determination of anchovy recruits in which he used a precise aging technique, otolith daily annulus counts (Brothers et al. 1976; Methot and Kramer 1979), permit the determination of relative survival through the spawning and larval production period. Northern anchovy have a protracted spawning period from December through May. Peak spawning, however, is confined to the February–March–April period. By age-dating recruits resulting from the 1978 and 1979 spawning period, a relative picture of larval survival was obtained and comparisons could be made with the abiotic factors prevailing during the larval period. Methot (1981) showed that in 1978, despite the heaviest larval production in late February, the majority of recruits were born in March and April (Fig. 9). Lasker (1981a) attributed this to the series of severe storms that swept through the anchovy spawning grounds in December 1977 through February 1978 and ceased only by mid-March 1978. Turbulence from these storms appeared to reduce larval food concentrations below threshold for first-feeding and should have resulted in reduced larval survival. However, data from 1979 showed a reversed pattern with higher survival in winter relative to spring (Fig. 9). Methot (1981) favors the idea of Parrish et al. (1981) that spring upwelling may result in transport of larvae offshore where they are lost to the main population.

Correlations between menhaden year-class strength and Ekman transport characterize the interesting work of Nelson et al. (1976). Because of the estuarine dependence of menhaden larvae, these must be carried into estuaries from offshore spawning grounds in order to survive. Nelson et al. (1976) showed that indexes of westward transport toward U.S. east coast estuaries from offshore spawning areas were positively correlated with indexes of yearly survival.

Larval drift has also been implicated in excessive larval mortality of other species, for example by Parrish and MacCall (1978) who studied Pacific mackerel (Scomber japonicus) year-class survival in relation to upwelling indexes. They found strong negative correlations between upwelling and good year-classes. The Kondo (1980), Nelson et al. (1976), Methot (1981), Parrish et al. (1981), and Lasker (1981a) conclusions, while arrived at by different approaches, all depend on Hjort's (1913) idea that it is lack of food that affects larval survival and assumes the effect of predation on eggs and larvae to be minimal or constant.

TABLE 1. Variability of standing crop of larvae due to differential mortality.

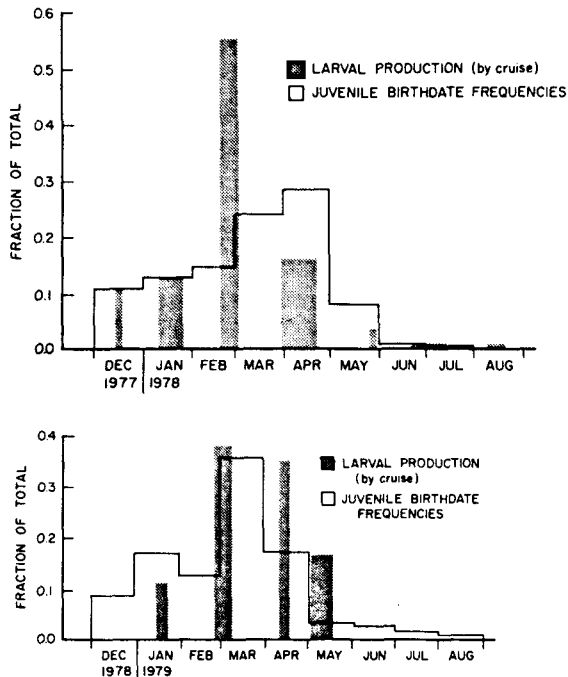| Year	Specific egg production $\left(\dfrac{eggs}{g \cdot d}\right)$	Survival to hatch	Exponential mortality rate for larvae (d^{-1})	Calculated specific standing crop of larvae $\left(\dfrac{larvae}{g \cdot d}\right)$	Larval abundance from surveys $(10^{12}$ larvae$)$
1980	30.65	0.359	0.168	65.5	18.11
1981	32.60*	0.705	0.164	140.1	28.60

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FIG. 9. Birthdate frequencies of juvenile anchovies compared to the larval production. Hatched bars indicate each of seven cruises (after Methot 1981). Top, December 1977–August 1978; Bottom, December 1978–August 1979.

Differential Fecundity

Compounding this complexity is the differential fecundity of the northern anchovy from year to year. For as yet unknown reasons, the northern anchovy increased its egg production per gram of female per day by 30% in 1981 over 1980. Thus the interplay of a variety of factors must determine eventual recruitment; (1) female fecundity and egg production; (2) egg mortality which depends on the number and coincidence of egg predators including the spawners themselves; (3) larval food availability and physical ocean factors including turbulence and drift; and (4) larval mortality (including starvation and predation). To what degree each of these contributes to larval survival is as yet unknown.

Cannibalism and Stock Expansion

Fishery management usually relies on conventional "black box" models of overall population dynamics such as production models or stock–recruitment relationships (SRR). These models are assumed to represent an integration of local mechanisms over the extent of the stock in space or time. Rarely are specific mechanisms identified and integration actually performed. However, when this is attempted, the results may differ from conventional models.

Behaviorally, anchovy spawning appears to be a risk-spreading strategy of covering all possibilities. Individual anchovies may spawn at 6- to 7-d intervals, or

about 20 times in a season (Hunter and Leong 1981), so that an individual's eggs encounter a wide temporal range of environmental conditions. Within the geographic limits of spawning, eggs occur ubiquitously.[2] As a result of this widespread temporal and geographic coverage, conditions favorable for larval survival, although relatively unpredictable, tend to be utilized wherever and whenever they occur.

Murphy (1977) observed that clupeoid fishes characteristically expand and contract their range with changes in overall stock abundance. This behavior is demonstrated clearly by the distribution and abundance of anchovy larvae off southern California (Fig. 10). Mac-Call (1980a) has shown that this geographic behavior is a logical consequence of density-dependent habitat selection, given the following assumptions: (1) the spawning habitat is most favorable near the center of the range, and deteriorates toward the periphery; (2) the local spawning habitat becomes less favorable as local density of spawners increases, for example, because of cannibalism (e.g. Hunter and Kimbrell 1980); and (3) fish individually attempt to spawn in the most favorable locations. The resulting distribution of spawner abundance should approach the "ideal free distribution" of Fretwell and Lucas (1970) wherein all fish experience approximately the same quality of spawning habitat. At low stock abundances the fish are concentrated in the most favorable localities. At high abundances the density increases in those previously favorable areas, but due to a density-dependent decrease in the quality of those habitats, the stock also expands into surrounding previously unoccupied areas of marginal quality. Thus, in terms of the risk spreading spawning strategy, the expected reproductive success in formerly poor peripheral areas now is equally attractive to the expected reproductive success in central preferred areas that have a high risk of cannibalism. While fish are probably unable to sense these risks directly, information such as water temperature and food abundance (which responds to grazing intensity) may be sufficient to govern adaptive geographic movements.

The overall effect is expansion of the range as stock abundance increases. Local density (and consequently, density-dependent effects) increases more slowly than does total abundance. If fishermen concentrate their activity in areas of highest density, catch per unit effort (C/f) will be insensitive to changes in total abundance even if C/f accurately reflects true local density. MacCall (1976) suggested that Pacific sardine C/f varied as a power function of stock abundance (N), $C/f = aN^b$, where $-1 < b < 0$, as is consistent with the above geographic behavior.
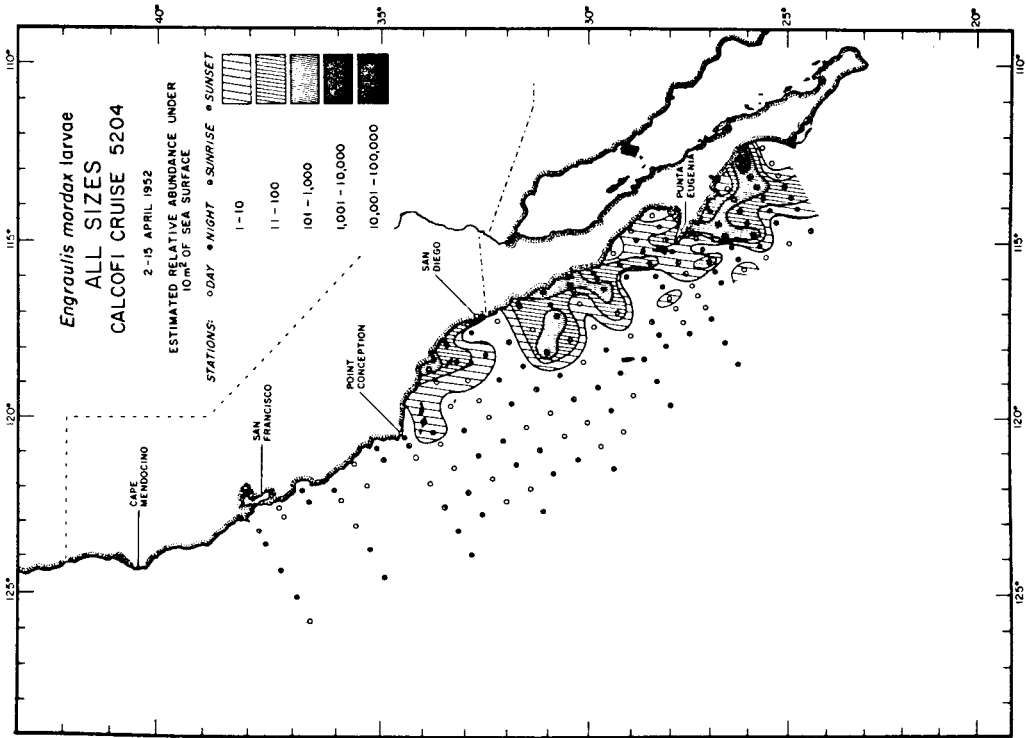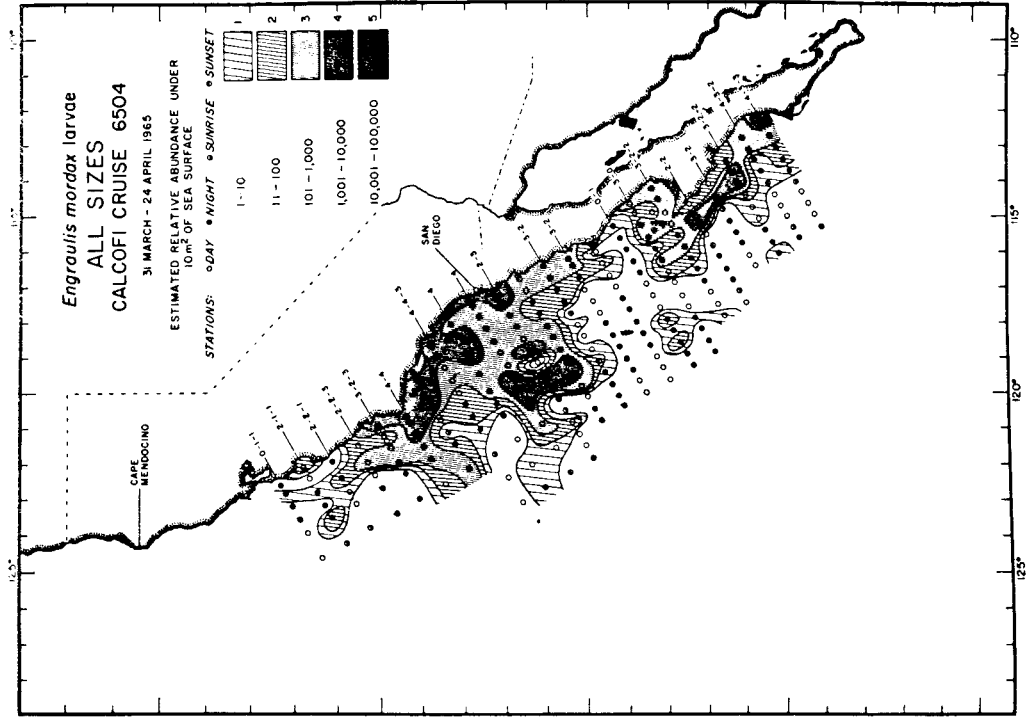
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FIG. 10. Geographic distribution of northern anchovy larvae at low and high population sizes.

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This geographic expansion model produces some surprising departures from the traditional fishery models. Gulland (1977) reports a production model originally developed by W. W. Fox Jr. wherein C/f varies according to the above power function. The resulting production model predicts stock collapse at levels of effort only slightly above that producing maximum sustainable yield (MSY). Also, depleted stocks would have difficulty recovering from this collapse unless effort is reduced drastically. Csirke (1980) describes a stock–recruitment model of Ricker form, where egg production is proportional to abundance, but subsequent survival is a function of mean adult density (measured by C/f) rather than total abundance. Csirke's model is therefore consistent with the above geographic expansion model. While local dynamics show decreasing recruitment at high density, geographic expansion offsets this local decrease, so that the overall stock–recruitment relationship (SRR) loses much of the domed shape characteristic of the traditional Ricker model. The resulting SRR appears almost asymptotic (Fig. 11).

The shape of the general clupeoid SRR has been open to debate. Harris (1975) distinguished between stock-dependent (intercohort) processes, which tend to produce a domed SRR, and density-dependent (intracohort) processes, such as competition among larvae, which tend to produce a less curved, asymptotic SRR. Cannibalism has often been suggested as the most likely regulatory mechanism for filter feeding clupeoid fishes (Murphy 1967; Csirke 1980), but as noted above, this mechanism produces a domed SRR. Cushing's (1971) empirical observations of clupeoid SRRs indicated that they are not domed, but only slightly curved. Stock and recruitment data on California sardines and anchovies are in agreement with Cushing (MacCall 1979, 1980b). According to Harris' (1975) criteria, Cushing's contention that clupeoids lack a strongly domed SRR would require that cannibalism not be a major regulatory mechanism.
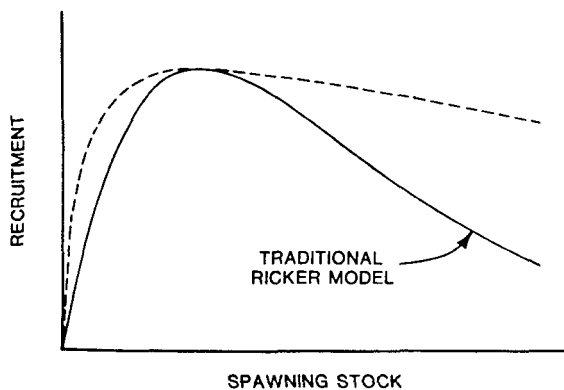
Hunter and Kimbrell (1980) have compared abundances of eggs in northern anchovy stomachs with production of eggs from their gonads, and concluded that cannibalism may account for 32% of the egg mortality. An increased mortality rate of eggs at larger anchovy population sizes also can be inferred from the relationship between egg abundance and production of hatched eggs or larvae (Fig. 12). Egg abundance is calculated as a regional census estimate according to the method of Smith (1972). This abundance was divided by the mean time to hatching as indicated by the mean water temperature. Larva production is derived from the time-zero intercept of abundance upon larval age (Hewitt 1982). At large population sizes, production of larvae per egg decreases as can be seen by the deviation of the relationship from proportionality in Fig. 12. Due to the inactive nature of eggs, this differential mortality is more likely stock dependent than density dependent (sensu Harris 1975, see above).

The geographic expansion model allows reconciliation of a stock-dependent regulatory mechanism and a slightly curved SRR. If accompanied by adaptive changes in geographic distribution and utilization of habitat, a stock-dependent process such as cannibalism need not produce a strongly domed SRR. The less curved SRR which results implies weaker regulation of abundance (i.e., weaker density dependence). As a corollary, studies of clupeoid fishery productivity which wrongly assume the strongly density-dependent Ricker curve will tend to overestimate MSY, underestimate the biomass necessary to produce MSY, overestimate the fishing effort necessary to produce MSY, and generally overestimate the resilience to overfishing.

FIG. 11. Modification of the Ricker stock–recruitment relationship due to geographic expansion at increased abundance (dashed line).
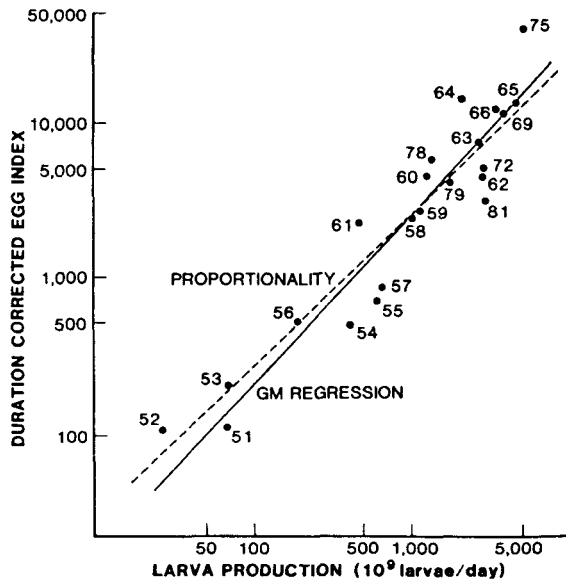

FIG. 12. Relationship between anchovy egg abundance (corrected for temperature-specific duration) and production of hatched larvae. The probability that the two variates are proportional is approximately 10%.

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Reconsideration of Paleosedimentary Evidence and Sardine–Anchovy Competition

Fish scales preserved in anaerobic sediments of the Santa Barbara Basin have provided several clues to the nature of the sardine–anchovy relationship (Soutar and Isaacs 1969, 1974). Unfortunately, interpretation of these clues has been equivocal. The evidence has been of two types: scale deposition rate (SDR) is assumed to be indicative of fish abundance, while the size (width) of the scales is assumed to be indicative of fish size.

Soutar and Isaacs (1974) show scale deposition rates for thirty-one 5-yr periods (pentads) from 1810 to 1965 A.D. (Fig. 8). The most prominent feature of these time series as shown by Smith (1978) is much lower variability of the anchovy population relative to the sardine population. This has been taken to be evidence that the sardine has been the more variable of the two, but this conclusion must be tempered by our knowledge of the geographic behavior of clupeoid stocks. The Santa Barbara Basin is near the central area of preferred anchovy habitat, so we must expect local anchovy abundance to be "buffered," that is, to vary much less than relative abundance of the total central stock (cf. Fig. 10). Soutar and Isaacs' (1974) calibration of anchovy SDR (Fig. 13) confirms this tendency toward a "buffered" response to changes in central stock abundance. Thus anchovy abundance is likely to have been more variable than is suggested by the time series of its SDR in the Santa Barbara Basin. We know less about the preferred habitats of sardines in the absence of fishing, and whether the Santa Barbara Basin is central or marginal. The SDR would correspondingly reflect a buffering or exaggeration of the total stock abundance. Soutar and Isaacs' (1974) calibration to sardine biomass (Fig. 13) is imprecise, but suggests a slight tendency toward exaggeration of changes in total abundance.

Soutar and Isaacs (1974) conclude that the low sardine SDR from 1865 to 1880 is similar to those following 1940 (Fig. 8), making the latter decline indistinguishable from previous natural fluctuations. While this interpretation superficially appears justifiable, we must note that sardine abundance has not recovered in the past 40 yr, contrary to the pattern of the 1870s. Soutar and Isaacs' (1974) calibration of sardine SDR loses definition at about 700 000 t biomass, where zero counts become common (Fig. 13). Thus the sardine biomass could have ranged from 0.5 to 1 million t during the "disappearance" in the 1870s. In contrast, recent sardine abundance has been less than 10 000 t (MacCall 1979). In view of this supplementary information, the scale deposition data do not support the previous conclusion that the recent decline in sardine abundance is indistinguishable from natural prefishery fluctuations. Also, sardines took 15 yr or less to recover from the relatively low abundance of the 1870s. It is reasonable to expect a similar capacity for recovery nowadays off California, if sufficient reserve biomass were to be maintained by an appropriate program of fishing restraint.

In an attempt to define the nature of sardine–anchovy interactions, Soutar and Isaacs (1974) calculated a Spearman rank correlation coefficient of +0.34 between sardine and anchovy SDR. The negative correlation that would be expected from the commonly assumed competition between these species is not evident at the 5-yr or longer time scale. Rather, there appears to be a slight tendency toward parallel variation, perhaps due to similar responses to large-scale environmental conditions. This allows a speculation that the increase in anchovy biomass from 1950 to 1975 could well have been accompanied by an increase in sardine biomass, had there not been an intense fishery on the latter. Therefore we invoke a density-dependent explanation for potential long-term recovery, although random, density-independent effects dominate over the short term.
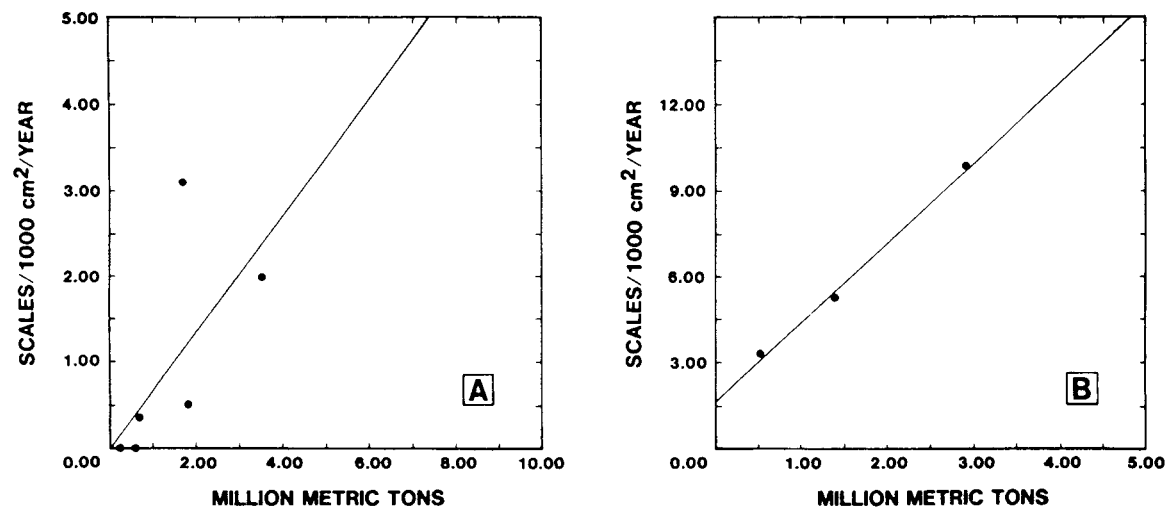

Fig. 13. Relationship of fish scale deposition rate to stock abundance off California. A. sardine, B. anchovy (adapted from Soutar and Isaccs 1974).

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The evidence from scale sizes is more suggestive of possible sardine–anchovy interactions. Previous attempts to infer individual fish lengths from scale widths have been confounded by the range of scale sizes on individual fishes. However, we can more safely infer relative changes in the distribution of fish lengths from relative changes in the distribution of scale widths, under the usual assumption that scales grow in proportion to fish length. The 31 pentads from 1810 to 1965 contained 326 anchovy scales for which widths could be determined (data provided by A. Soutar). If these scales are separated into two groups corresponding to high and low anchovy SDR (respective weighted mean SDRs are 16.9 and 9.7 scales/1000 cm²/yr), the two scale width distributions are nearly identical. However, if the scales are separated into groups corresponding to high and low sardine SDR (respective weighted mean sardine SDRs are 7.0 and 1.2 scales/1000 cm²/yr, weighted mean anchovy SDRs are both 13.3 scales/1000 cm²/yr), the width distributions are significantly different (Fig. 14, Kolmogorov–Smirnov D Statistic: $P < 0.01$). The mean anchovy scale width during periods of high sardine SDR is 4.94 mm, while during periods of low sardine SDR, the mean width is 5.71 mm. Assuming a cubic relationship between mean scale width and mean fish weight, the average anchovy is approximately 54% heavier during periods of low sardine SDR.

While this size–abundance relationship is consistent with the competition hypothesis, it is not the only explanation. It is possible that environmental conditions favorable to sardine abundance are associated with low growth rate, higher mortality rate, or a relatively more offshore distribution of small anchovies. Anchovies have exhibited some of these phenomena since the late 1970s in southern California, where they have tended to

be smaller, younger, and now mature at a relatively small size (Mais 1981; Hunter and Macewicz 1980). Coincidentally, sardines are showing signs of increased abundance (R. Klingbeil, California Department of Fish and Game, Long Beach, CA, personal communication), but are still much too scarce to have a significant impact on anchovies. These phenomena, whose causal relationships are unclear, are consistent with the paleosedimentary patterns. Unfortunately, the paleosedimentary record provides little evidence on causal mechanisms driving the patterns of apparent fish abundance.

Appreciation

Clupeoid fisheries have been studied intensely for nearly half a century. While some of the ideas presented in this paper may be new, others have existed in various forms for many years. Nonetheless, we feel that clupeoid fishery biology is approaching a new synthesis which will allow better understanding of stock fluctuations. Yet even this synthesis is not completely new: almost all the components appear in Sette's (1943) conceptual outline of the relationships among fish life history stages, fisheries, and the biotic and abiotic features of their environment (Fig. 15). Sette's paper has been a foundation of much of the subsequent research on clupeoid fisheries of California. The success of that research must be attributed, in part, to the completeness of Sette's original vision.
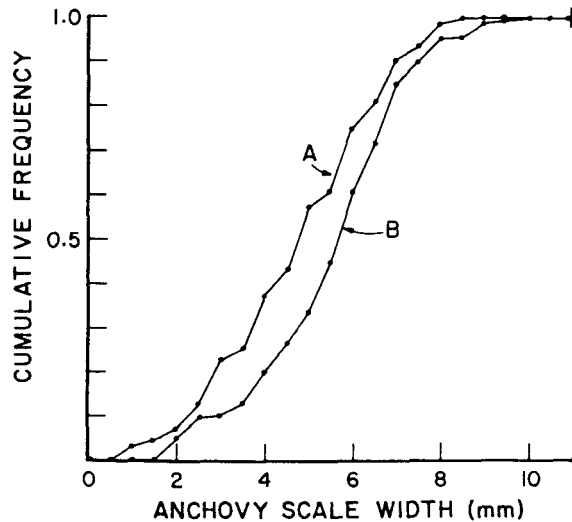

Fig. 14. Cumulative frequency distributions of anchovy scale widths from anaerobic sediments of the Santa Barbara Basin. A. Periods of high sardine scale deposition rate. B. Periods of low sardine scale deposition rate.
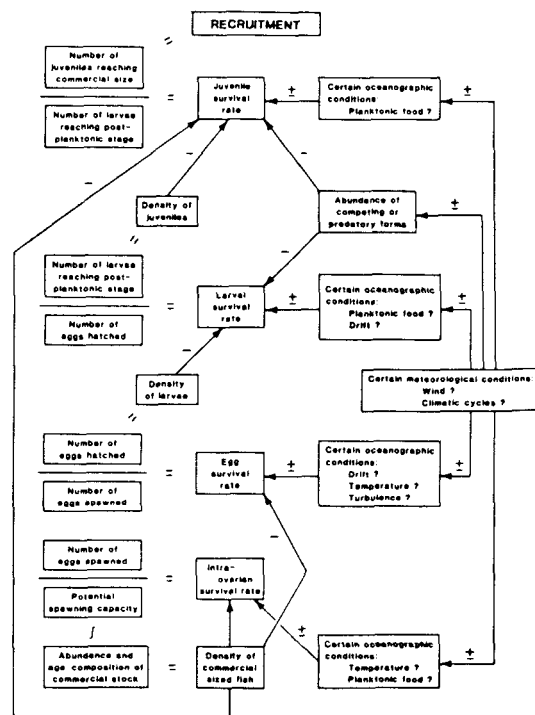
Fig. 15. Sette's (1943) research plan for studying recruitment of the Pacific sardine.

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