OCEANOGRAPHY AND VARIATIONS IN THE PACIFIC SARDINE POPULATION

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The Pacific sardine fishery has produced catches ranging from 789 thousand tons in the 1936-37 season (Schaefer et al, 1951) to 10 thousand tons in the 1953-54 season (Felin et al, 1954). Fishing pressure has remained sufficiently constant so that most of this fluctuation can be safely interpreted as the result of variations in abundance and availability of the sardines themselves.

With respect to abundance the basic variable is year class size, and the most readily available estimates of year class size are the virtual populations, that is the summation of those individuals actually taken by the fishery. These have ranged from over seven billion fish for the 1939 year class (Clark and Marr, 1955) to a low of .1 billion fish for the 1949 year class (estimated from published and unpublished catch statistics). This is a range of 70 times but the virtual population can be severely distorted by variations in availability, particularly during the second, third and fourth years of life. Variations in availability (in the sense of Marr, 1951) are difficult to document precisely. The results of one study (Widrig, 1954) suggest that availability might have had a range of five times during the period 1941-50, and the inclusion of more recent years would undoubtedly increase this range.

In terms of the fishery the obvious need is to understand and predict these fluctuations in abundance and availability. This may also be viewed as a problem in ecology; that is, the response of a population to its changing environment. The California Cooperative Oceanic Fishery Investigations is inquiring into these fluctuations, and attempting to define the relative role of nature and man in influencing the size of the population.

The objectives and general results of the programs have been documented in a series of six progress reports (Marine Research Committee; 1950, 1952, 1953, 1955, 1956, 1958), which include bibliographies of completed scientific papers so there is no need to report general results here. Rather, I wish to discuss certain aspects of the oceanographic material that seem to bear most directly on the problem of abundance.

AVAILABILITY AND ABUNDANCE

Before examining some of the facts it is well to consider the theoretical basis underlying the application of oceanography to fisheries problems. The fishery problem may be conveniently separated into availability, defined as the accessability of such sardines as exist to the commercial fishery, and abundance,

defined as the absolute magnitude of the sardine population or some segment of the population such as a year-class.

By and large, availability is a reflection of the momentary response of the population to the environment. This response takes the form of variations in distribution and behavior. Oceanographic studies related to availability generally include estimating the appropriate parameters of the environment of the fish population in question. As the studies progress, attempts are made to predict where and when environmental patterns associated with high availability will occur. Examples of this type of study are described by Sette (1955) who discussed several environmental mechanisms occurring in mid-Pacific Ocean that are associated with high concentrations of tuna, and Cushing (1955), who was able to relate the distribution of herring to changes in the food supply. All such studies suggest a more or less instantaneous response of the fish population to a parameter in the ocean.

In contrast to availability studies, investigations of abundance must consider the integrated response of the population to the environmental pattern over a period of time. The inherent difficulties of this approach are suggested in figure 1. Four curves are shown, each representing the relative change in instantaneous survival rate (Z) needed to reduce a particular initial survival rate (S) over a fixed period of time. The abcissa is the ratio of the initial survival rate (indicated on the curve) to any given lower survival rate. On the ordinate is a scale of the ratio of
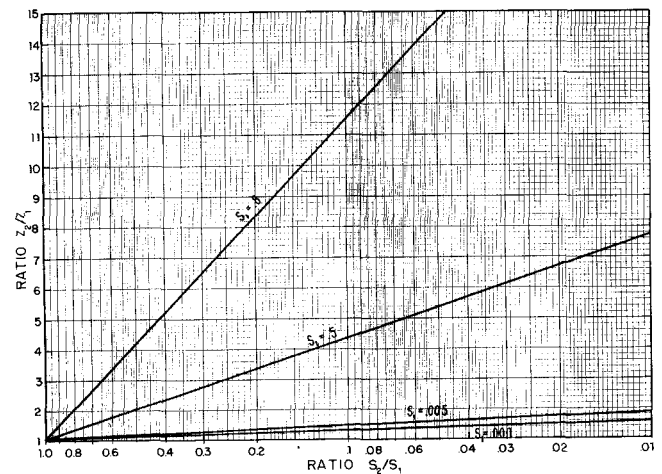

FIGURE 1. Diagramatic representation of the relation of changes in survival rate (S) to changes in the instantaneous mortality rate (Z), that is $S_2/S_1 = e^{-(Z_2 - Z_1)}$.

the instantaneous mortality rate associated with the initial survival rate to the instantaneous rate associated with the lower survival rate. For example, taking the curve representing $S = 0.8$ at initial survival, a change to $S = 0.08$, a reduction to $\frac{1}{10}$, would be associated with an 11.5 times increase in the instantaneous mortality rate.

Unfortunately when studying the California sardine we must deal with survival rates in the order of .001 during the first 45 days of life and of course much lower if a longer time-span is considered. At this initial level of survival (.001) an increase in the instantaneous rate of 1.6 times results in a hundred-fold decrease in the number of survivors.

In terms of an investigation we can hope to measure survival at some point(s) in the life of the sardine (the result of integration) but we cannot measure an integrated environmental effect; all that it is possible to measure is an instantaneous value of the factor(s) contributing to the mortality rate. In practical terms a large change in the integrated results, i.e., a spectacular change in survival, may be associated with very small changes in the instantaneous measure of the environment as suggested above. Thus the problem of understanding the relation between changes in the environment and changes in survival of the California sardine may be much more difficult than an investigation of availability.

It would appear that it is necessary to identify precisely the operating factors because if small changes in the operator(s) result in large changes in survival, it will be nearly impossible to achieve success by measuring factors merely associated with the true operators; we must know the precise manner in which the operators affect the population in order to permit some form of integration either formal or conceptual, and there must be precise inventories of the fish populations at critical stages. The alternative is to content ourselves with a rather general approach to changes in the ocean and changes in the populations without serious consideration of cause-effect relations. This is an analogue of the water mass approach of explaining the geographical distribution of animals with time substituted for space. For certain purposes this is not without profit but it falls short of being fully satisfying.

Historically, many attempts to relate the environment to survival have centered around the larval period because the major reduction in the numbers of a given year class occurs then. Moreover, it is at this stage of the life of the sardine, prior to its acquiring the ability and motivation to aggregate, that the factors responsible for mortality are most likely to operate in a density-independent manner; this should simplify the analysis.

The fundamental support for the assumption of density independence is that sardine eggs and/or larvae are a very small fraction of the biomass. For instance, sardine larvae comprised only four percent of the total fish larvae during 1955 and 1956 (Ahlstrom and Kramer, 1957, Ahlstrom, 1958) and, of course, a much smaller portion of the plankton in general. This statement seems to hold true even in

areas where spawning has been heavy. For instance at a moderately high density station (117.50, Cr. 5602, Ahlstrom, 1958) there were about 800 eggs, with a volume of about 2.5 ml. per 1000 m^3 of water. At this station the total catch of small plankton in the tow net was about 100ml. and total plankton was 425 ml. (Thrailkill, 1957). Eggs were therefore about 1/40 of the biomass of small plankton. If the water added to the perivitelline space after spawning is deducted from the egg mass the fraction is reduced to about 1/120, and, of course, if all the plankton were caught and considered, the fraction would be much smaller. Finally, random dispersal of the suspended eggs should serve to rapidly reduce such high concentrations.

Food is frequently considered the key to larval survival but in the instance of the California sardine this does not seem likely. Arthur (1956) showed that
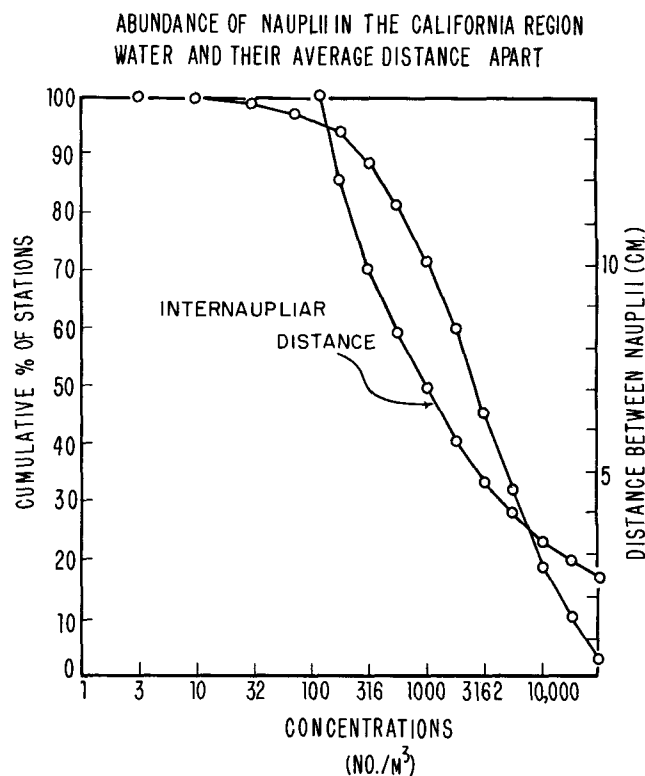
ABUNDANCE OF NAUPLII IN THE CALIFORNIA REGION WATER AND THEIR AVERAGE DISTANCE APART

FIGURE 2. Cumulative summary of the density of the nauplii of micro-copepods in the California Current, and the computed mean distance between nauplii associated with each density assuming they are randomly distributed in the water column, (after Arthur, 1956).

the standing crop of potential food organisms was 1,000 m^{-3} or greater in 70% of his stations and 3000 m^{-3} or greater in 50% of his stations in the general area of sardine spawning (figure 2). Referring to the high density station discussed above, the ratio of larvae (if all eggs survive to hatching and there is no dispersal, and if all eggs were assumed to be in the top 50 meters) to food organisms would have been 1 to 500 or 1 to 1,500 or greater in 70 percent or 50 percent of the station respectively.

Arthur also shows that the mean distance between food organisms was 10 centimeters or smaller at 70% of his stations and 7 centimeters or smaller at 50% of his stations. The mean distance between a larva and a food organism would be one half this. Because of motion of food and larvae, only a very short time need pass before a larva has a food organism within easy reach. This information suggests that there is little or no competition among sardine larvae for food, and that there is always or nearly always sufficient food within easy reach of the larvae. The qualifications in this statement stem from the fact that occasional tows reveal concentrations of eggs about 10 times as great as the high density station under consideration. Maximum observed concentrations of larvae in a given year, however, are about the same as the above described concentration of eggs. Variations in food supply may not then be a significant factor in larval survival, except in rare instances.

The arguments above are based on what amounts to an instantaneous view of the numerical and spatial relations of the larvae and their food. Their validity turns on whether or not it is possible to regard this instantaneous picture as a sample from a system in a reasonably steady state. That is, the implicit assumption is made that the observed food supply at a given instant is the integrated steady state result of its renewal rate, its "death" rate from predation, and its growth to a size too large to serve as food for the larvae. Though it is difficult to prove the assumption formally, the fact that an apparently favorable supply of food seems generally to prevail lends strong intuitive support.

Predation remains for consideration. It seems reasonable that fish larvae will be subjected to roughly the same rates of predation as are other organisms in the plankton possessing their same general dimensions and behavioral characteristics. I am unaware of precise data on this point but the rates appear to be extremely high. For instance, Cushing (1955) concluded that over 90 percent of the diatoms produced during the period April 10 to May 16 in his study area were consumed. Because the larvae are typically a small fraction of the biomass it seems unlikely that variation in their numbers results in variations in the population of predators. Presumably the arrival through hatching and departure (through growth) of a relatively few sardine larvae elicits little or no special response from the population of predators, suggesting that predation is density independent.

The arguments above indicate that environmental data should be examined in the light of three working assumptions. (1) The sardine egg-larva is a minor element in the pelagic fauna and therefore the factors affecting the survival rate operate in an essentially density-independent manner. (2) Food supply is not an important survival factor, but rather (3) the intense predation typical of the plankton community is responsible for the rapid decline in numbers of the sardine larvae, and variations in this rate of predation are primarily responsible for variations in the rate of larval survival. How observed changes in the California Current System can operate to vary the

rate of predation will be considered in the next section.

OCEANOGRAPHY AND LARVAL SURVIVAL

The most conspicuous variable likely to affect animals directly or indirectly in the California Current System has been temperature. Reid, Roden, and Wyllie (1958) have summarized certain aspects of these changes. The years prior to 1944 were characterized by more or less alternating positive and negative anomalies from the mean. From 1944-1956 the anomalies were predominantly negative, and from 1957 to the present (1960), they were mainly positive. The variations in temperature are essentially the result of the interaction of the strength of the California Current, upwelling along the coast, and the strength and character of the countercurrent. Because the historical record suggests that warm years tend to be associated with good year-classes, and cold years with poor ones (see Clark and Marr, 1955, Reid et al. 1958, and Marr, in press), I wish to examine the possibility that cold temperatures can act to increase larval mortality through predation and/or that cold temperatures are associated with other phenomena that adversely affect the sardine population.

Ahlstrom (1954) has presented evidence indicating that survival during the first 45 days of life is approximately .001 (figure 3). The mean instantaneous mortality rate associated with this is 6.9. Graham (1956, p. 244) suggested, but did not elaborate, that colder temperatures might prolong the larval phase, lengthening this period of high mortality, and therefore decrease survival. Ricker and Foerster (1948) conclude that mortality of sockeye fry is a function of growth rate. In their data, growth is accelerated or retarded as a function of population density, but the operator is predation, mortality being greater as the length of time spent at small, very vulnerable sizes is prolonged. Certain aspects of this problem are also treated in Beverton and Holt (1957, p. 55), and Ricker (1958, p. 263). Ahlstrom (1954) finds little evidence of serious mortality in the egg stage, which might well be associated with the extreme transparency of the eggs, and I have already noted that eggs are not aggregated densely enough to attract filter feeders. Thus the mortality (99.9%) under consideration occurs after hatching and before the stages at which the larvae are no longer sampled in the routine plankton hauls (a period of about 45 days).

If these high mortalities after hatching are simply a reflection of the larva's belonging temporarily to the relatively helpless plankton community, mortality will be sharply reduced or enhanced if the period of this association is altered. The only way a sardine can escape this community is by growth and this is a function of food and temperature, and larval food seems to be adequate for survival though the supply may not always be adequate for maximum growth. Thus, if predation is held to be the main source of larval mortality its effect can vary with the density of predators, and the duration of the vulnerable stages. The latter can be a function of food, temperature, or both. There is some indication (Reid et al.

FIGURE 4. Hatching time of sardine eggs as a function of temperature. The numbers along the curve represent the relative hatching time taking 15°C. as a base, (adapted from Ahlstrom, 1954).
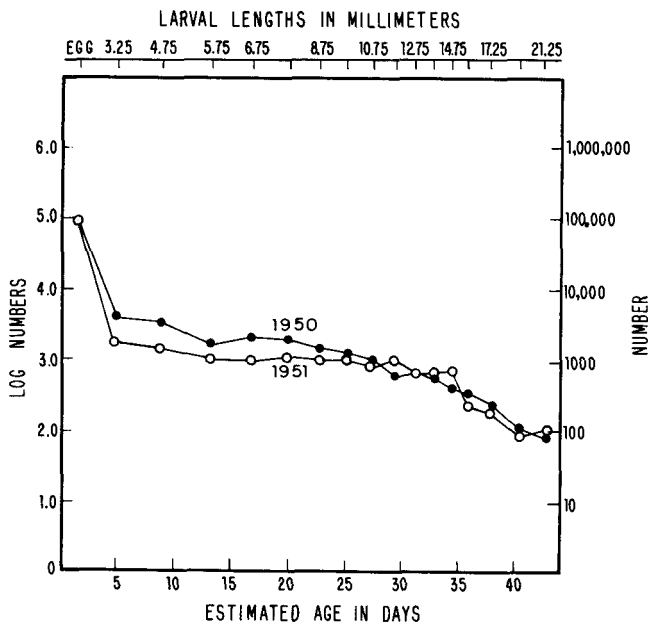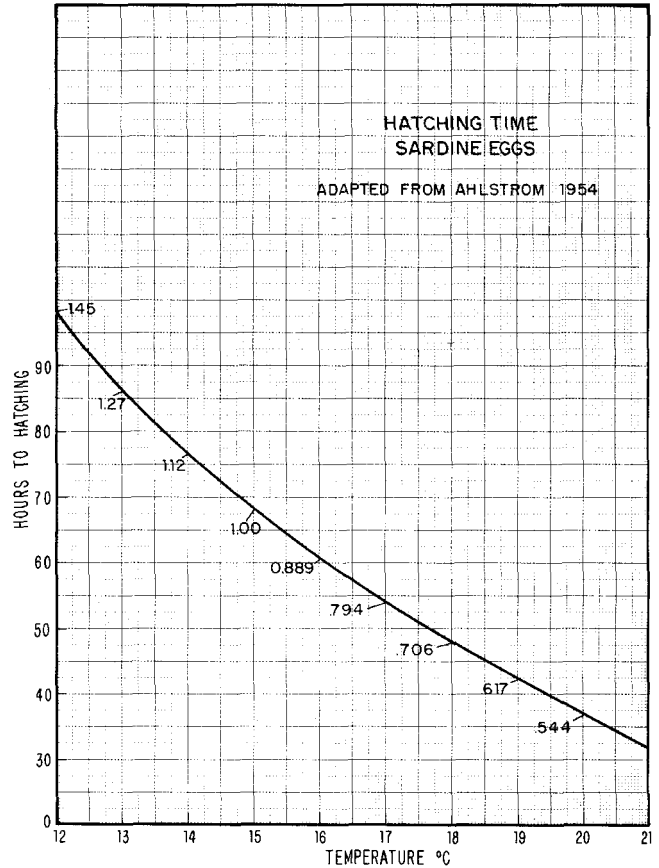

FIGURE 3. Apparent mortality curve of sardine larvae, (after Ahlstrom, 1954).

1958) that food was more abundant during the cold years associated with poor year classes so it seems logical (though not necessarily correct) to discount food, and examine the associations among temperature, larval growth, and the density of predators.

Temperature, through its control of the metabolic processes, can alter the growth and development rate. Data from Ahlstrom (1954) show that eggs hatch in 54 hours at 17°C, 60 hours at 16°C, 68 hours at 15°C and 77 hours at 14° C (figure 4). If these rates are projected into larval development which, at least in part, is an extension of embryonic development,

we can estimate the relative larval survival from the equation:

$$S = e^{-Zt}$$

where S denotes survival, Z is the mortality rate and t denotes time. Because the survival to 42 days or 24 mm (Ahlstrom, 1954) was based on years in which the average temperature was about 15°C, I use this temperature as the base setting 42 days as $t = 1$. Simple computation then gives the following relative survivals to 24 mm.

Temperature (C)	Relative Survival
14.0	0.43
15.0	1.00
16.0	2.12
17.0	4.14

Thus a three degree range of temperature, approximately the difference between warm and cold years in the California Current during the spring months (Reid and Roden and Wyllie, 1958), might result in a 10 fold variation in survival. The effect of growth on survival is clearly shown with respect to one predator (a plankton net) in figure 5.

Other effects of lower temperature on the survival of the sardine larva can be postulated. For instance, Brett, et al (1958) have shown that the swimming speed of small fish varies with temperature. Tempera-
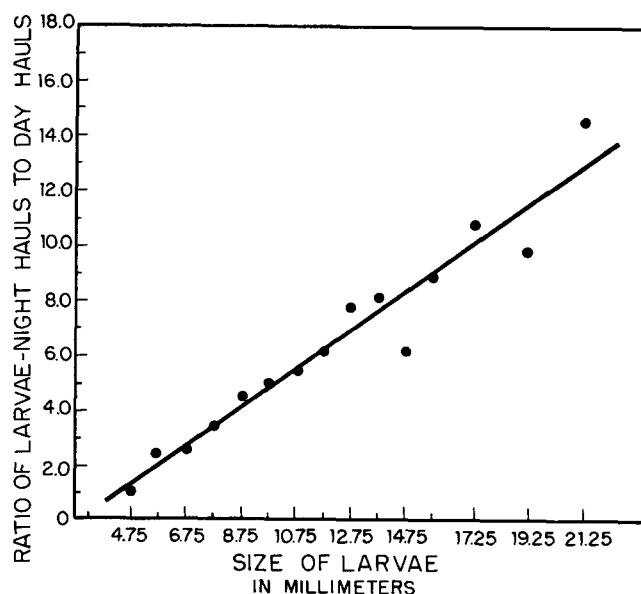
FIGURE 5. Relative efficiency of the one meter net in capturing sardine larvae between day and night as a function of larval size, (adapted from Ahlstrom, 1954).

tures below the optimum for sardines would place them at a disadvantage, particularly in the face of cool water predators.

Possibly even more important, in the California Current region a decrease in temperature has been accompanied by an increase in the standing crop of zooplankton (Reid et al, 1958). For example, off southern California the temperature during February to August ranged from 14.3° to 15.4° Centigrade among the years 1949 to 1956. The zooplankton volumes varied from about 50 to 800 ml. per thousand cubic meters, larger volumes being associated with cooler temperatures. This must be accompanied by an increased rate of predation, depending, of course, on the qualitative composition of the net zooplankton. Assuming the type of organism to be constant, the instantaneous mortality rate from this source might vary as much as 20 times judging by the variations in plankton abundance. Thus, lower temperature, in addition to prolonging the duration of the larval stages, and hence the vulnerable period with respect to predation, seems to be accompanied by an increase in predators. Because of the relationships shown in figure 1 only a fraction of the combined effects could easily produce more than the total observed range in sardine year-class strength. The increased food that must accompany the lower temperatures and higher plankton volumes might operate in the opposite direction, though probably not strongly enough to overcome the adverse effects. Definitive examination of the problem awaits, among other things, point-by-point examination of the in situ environment of the eggs and larvae.

A third effect associated with temperatures arises from the fact that in general lower temperatures are associated with a more vigorous California Current and more vigorous upwelling. If there is any loss of larvae due to the drift into unfavorable locations offshore and/or to the south, this loss would tend to be greater during years of cold water. At the present, however, it is impossible to state whether this is a major or minor source of mortality. The fact that the larva develops the ability to elude the plankton net at an early age argues against it. However, the cooler temperatures attendant on vigorous coastal upwelling would tend to induce the sardine to spawn further offshore, seemingly, increasing the likelihood that larvae will be swept to unfavorable areas. A full discussion of this problem is included in Sette (In press).

Finally, of course, cooler temperatures would tend to favor northern fishes, some of which might be competitors or predators of the sardine. With respect to the larval state during which sardine mortality is assumed to be density independent, the larvae of a more northern form such as the anchovy, which presumably is better adapted to cool temperatures, might grow relatively faster, and as a byproduct might prey on the sardine larvae. At the moment this is conjecture, and in any event it would simply be a special case of the general predation by the plankton community. A hypothesis involving the anchovy (some of these ideas together with documentation) has also been advanced by Marr (In press), but his working assumption is that the anchovy larvae affect sardine survival by competing for food in a density dependent model.

JUVENILES AND ADULTS

Almost nothing is known concerning the sardine between age 45 days and age six months. During this period they develop the schooling habit, and apparently move inshore (Phillips and Radovich, 1952). Because of this they will then be a significant element of the fauna at their points of aggregation, and the sizes of the past catches (nearly a million tons) suggest they are a significant element in the general biomass of their habitat. Mortality must be now assumed to be at least partially density dependent. Direct competition may exist among young sardines and between the young sardines and the young of other fishes. It also suggests that predation might operate in a density dependent manner. The only positive indication of a density dependent effect on record is a study by MacGregor (1959) which showed that condition factor of the catches of adults varies inversely with population size suggesting competition for food.

Because of the scarcity of data, reliance must be placed on the general principle that as the range of an animal is decreased for a protracted period during density dependent stages of its life, its numbers will decrease. The sardine is an inshore, pelagic, south-

temperate form. The southernmost end of its range abuts on tropical water and this boundary is relatively steady geographically because of the nature of the eastern Pacific circulation. The northern end of its range is near Vancouver Island but this can vary greatly. Between these limits flow is generally parallel to the coast and temperature isotherms and other physical attributes tend to parallel the coast. If we assume that the population spreads over its available range, with the limits set by its own inherent responses to the physical environment, and by competition, the stage is set for large fluctuations in the population. For instance, a change in the temperature regime will be transmitted down the coast, as far as the relatively constant southern limit of the California Current, thus producing a large change in the habitat available to the sardine.

Regulation of the population during a shift from warm to cool conditions can then be postulated as follows: A regime that cools the waters "pushes" the adults south. Their southern boundary remains relatively fixed thus temporarily increasing the density of large fish in the now restricted habitat, a phenomenon that must result in increased mortality until the population adjusts to a new appropriate size. Following or paralleling this, recruitment is reduced by the several effects associated with lower temperatures on larval survival, because of the reduced extent of the inshore nursery area and because of competition from species better adapted to the altered environment.

EFFECT OF THE FISHERY [1]

Though it is not appropriate to consider the fishery in detail, for the sake of continuity it is necessary to review briefly how the fishery might affect the natural "environmental" regulation of the population size. The effects of a fishery can be expressed qualitatively with reasonable exactness; the difficulties emerge in attempting to quantify these effects. Hence, this discussion will be in the main qualitative, and for this reason will do little more than attempt to identify the problems.

The fundamental effect of a fishery on adult sardines is to increase the mortality rate of the fished stocks. This results in four secondary effects: (1) the numbers of eggs spawned each year are reduced; (2) the total biomass of the population is reduced; (3) the average age of the population is reduced; and (4) the size of the population relative to the sizes of the populations of competitors is reduced.

Effect number 4 is not necessarily characteristic of all fisheries, and is perhaps one of the fundamental reasons why the changes in the sardine population have been intractable to the usual fisheries theory. Conventional theory was largely established on stocks of fish that seem to lack serious competitors such as the Pacific halibut, or on relatively non-selective fisheries such as North Sea trawling. An extreme, of course, is a mono-specific fish population in a pond.

Here, clearly, competition with other species is absent in the sense of the fisheries problem.

Taking each of the four points in turn, in the light of the earlier discussion, it is clear that reducing the numbers of eggs reduces the numbers of sardines passing through the density independent mortality stages, during which mortality is postulated to be largely a function of predation. The problem then narrows down to whether the combination of egg number times a density independent survival rate provides enough individuals to occupy efficiently the available environment during later stages when survival is expected to be density dependent. The term "efficiently" requires definition. For this discussion it means to occupy the environment to the extent that the addition of more individuals to a year-class at the beginning of the density dependent stage will not significantly increase the year-class when it enters the fishery.

Reduction of the size of the population by the fishery also interacts with the environment, because the *amount of environment* available to an organism is a function of the absolute amount of environment available and the numbers of individuals competing for that environment. Thus a fishery should enhance the survival of those individuals remaining and those individuals in a pre-recruit stage. Or paraphased the classical formula: a (annual mortality) $= m$ (fishing mortality) $+ n$ (natural mortality) $— m n$ will not apply in a predictive sense to the extent that a reduction in population decreases n. It can be concluded that a fishery exerts a positive effect on year-class size by relieving density dependent environmental pressures. Possibly the size of the 1939 year-class (the largest on record) was in part a function of this effect, as it was produced by a population that had been heavily fished for several years.

Reduction in the average age of the population as a result of a fishery has the general effect of making the size of the fishable population less stable, simply because the size of the adult or fishable population tends to become a function of the size of only the most recently recruited age class, and thus the population becomes more sensitive to short term changes in the environment. So long as environmentally induced fluctuations in year-class size coupled with the effect of the fishery do not reduce the population below the level at which it can provide sufficient recruits to the density dependent phases of sardine life, and so long as the time scale of the environmental fluctuations is short, the effect of a decreased average age will be to increase the amplitude of the fluctuations in population size, but it will not necessarily reduce the average size of year-classes. They may, in fact, be increased. If the time axis of the environmental changes is long compared to the average age of the adult population, the relative amplitude of the fluctuations will tend to be the same in the presence or absence of a fishery, the effect of the fishery induced mortality being confined to affecting the shape of the curves, particularly by steepening a decline.

The fourth effect of a selective fishery such as that on the sardine is to reduce the numbers of the population in relation to its competitors and predators. In

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[1] This and subsequent sections of this discussion were not presented at the symposium because of time limitations. They have been freely revised since the symposium.

the absence of competitors or significant predators this effect will, of course, be zero. This does not seem to be true in the instance of the sardine which has predators and probable competitors. Projection of the effects is difficult. There is little insight to be gained by reference to agriculture or pond culture, or even forestry, for here man is able and does intervene to counteract some of the adverse effects of the heavy mortality he induces. It would appear more appropriate to refer to the principles of evolution and survival for guidance.

In nature, most of the attributes acquired by a population are probably directed at one goal, survival of the species at a maximum commensurate with the environment. In nature there is no survival significance in maximizing annual production of protein at the species level, though there may be at the community level. What we interpret as potential production in a virgin stock may be the energy utilized by the species to maintain itself in the ecosystem. If the particular population in question either by accident or design has no significant predators or competitors man may then utilize this potentially available surplus production, e.g., a fish farm or a wheat field. If, again by accident or design, the population has predators, but no competitors, i.e., is the sole occupant of its trophic level, man may still safely utilize the potentially surplus production though to a lesser extent for he is simply competing with another predator, and the population of that predator will probably shrink to a size commensurate with the now smaller prey population.

In the instance of the Pacific sardine it appears that there need not be great concern over species that simply prey on the adults. If man reduces the population of sardines these predators will eventually reduce their predation, either by becoming less numerous, or by utilizing alternate foods. Competitors are another matter, particularly in the instance of a selective fishery. The sardine's range greatly overlaps that of species that share its diet in large part, share its living space, and prey on the sardine at some stages in its life, e.g., jack mackerel, and anchovies. Such species as these, though they obviously do not occupy precisely the same niche as the sardine, are potentially its serious competitors. To the extent that a proportion of the productive potential of the sardine which was "wasted" was in fact necessary for its survival in the presence of its competitors, removal or reduction of this "buffer" by a selective fishery will be detrimental to the species.

To some extent, then, the increased opportunity for survival of younger stages that man provides by thinning down the adult sardine population may be more than countered by increases of other species which occupy the space made available. Carried to a logical extreme, in the face of increasing pressure by man the selected species (in this instance the sardine) would ultimately be restricted to an ecological range and population size such that its ecological niche involved little or no overlap with other species at its trophic level.

It seems doubtful that this would ever occur in nature. More likely is the possibility that the selective pressure on the population by man might "sensitize" the Pacific sardine so that slight changes in the environment in unfavorable directions would tip the scale in favor of some other species or combination of species at the same trophic level, and thus precipitate a decline much greater than would be expected from the environmental change alone.

APPLICATION TO DECLINE OF THE PACIFIC SARDINE

The first section of this discussion sought to show specifically how recent changes in the California Current System, particularly cooler temperatures and associated changes, could adversely affect the Pacific sardine. In the second section an attempt was made to determine qualitatively how a fishery might modify the effect of the environment on the population, and it was shown that the minimum effect would be to make the population more responsive to environment changes, particularly because the sardine fishery acted selectively within the trophic level. By way of a summary, this section will review the history of the sardine population and fishery to see if the approach fits the facts. Temperature will be used in the discussion, not in the sense that it is the sole operator, but rather as a convenient index of the oceanographic information.

Very briefly, cooler temperatures along the California Current are associated with accelerated southward transport, and more vigorous upwelling with its attendant offshore movement of water. Plankton densities are increased. Warmer temperatures are associated with the converse of the above, as well as greater influence of southern water and/or the warmer water to the west.

Schaefer, Sette, and Marr (1951) described the growth of the fishery from 1916 to 1942. They found that the growth pattern could be fitted to a logistic curve with an upper limit of about 600,000 pounds. Though they attributed this growth primarily to economic factors, they also concluded, from biological information available, that this limit was close to the productive potential of the then existing population. In addition they suggest that, "Indeed, the limit attained, about 600,000 tons, may have been the result of a series of years during the late 1930's, which were exceptionally favorable for reproduction and survival of the pilchard, in which event the average maximum stabilized yield may be expected to be lower than this value." In point of fact, the largest year class by a factor close to 2 resulted from the 1939 spawning, during the period of heaviest exploitation.

In the light of present knowledge oceanographic conditions during the late 1930's and very early 1940's were generally warm (Reid et al 1958) and judging from the year classes produced appear to have been favorable for sardine spawning, and the adult population was certainly large and well distributed over the spawning grounds. Finally, heavy cropping by the fishery must have served to some ex-

tent to increase the habitat for the pre-recruitment sardines. Thus it appears that the fishery, by making the population more responsive to the *favorable environment*, was a positive factor with respect to the production of large year-classes during the period of favorable environment, and because a young population is more efficient with respect to food conversion, growth, and natural mortality, the standing crop of adult sardines may well have been larger than during earlier years.

Beginning in 1944-45 the northern fisheries (British Columbia, Oregon, and Washington) began to decline (Clark and Marr, 1955). These were somewhat cooler years, and years when the salinity at La Jolla suggested little influence of tropical water, so this decline, which initially resembled earlier fluctuations, may have been caused at first by inhibition of the seasonal northward migration of the sardines by cooler water and accelerated flow.

The decline, unlike earlier dips, continued; the far northern fisheries virtually ceased to exist after 1946; the Monterey-San Francisco fishery virtually ended in 1950; and the southern California fishery declined in 1953 to about one percent of its peak, later rising to fluctuate around 50,000 tons a year until 1958.

Coincident with this, the cooler than normal temperatures in 1943 and 1944 strengthened and persisted through 1956 (Reid et al, fig. 18) instead of oscillating between cold and warm anomalies as in the past, though there was a slight warming in 1946 and 1947. In 1944 and 1945 quite poor year-classes were produced and the catch fell dramatically during 1946-48. During 1946-48 moderate sized year-classes were produced and the catches rose to over 300,000 tons in 1949 and 1950, though nearly all the catches were made off Southern California. Among other things, this series of events illustrates the sensitivity of a young, heavily fished population to fluctuations in year-class size which may have been caused by environmental changes.

During earlier years the Pacific sardine ranged from lower Baja California to British Columbia. By 1950 the population was essentially confined between lower Baja California and Point Conception, roughly a 50 percent reduction in range. Most generally, a reduction in the range of an animal must be accompanied by a reduction in numbers. One critical question is which came first. A reduction in numbers does not necessarily involve a dramatic change in range; the population may simply become more thinly dispersed. In the present instance the coincidence of the contraction in range with cooling of the ocean climate lends support to the thesis that a change in the environment restricted the habitat of the sardine, and that the population adjusted to a new level commensurate with its new range.

The reduction in range could have come about simply because the adults were unable, in the face of swifter currents and/or keener competition, to occupy their range. This probably was one of the factors, but more significant is the probability that the contraction in the range was a result of failure of northern spawning because of the environment. Felin (1954)

and Radovich (in press) show that the relative significance of a year-class to the fishery, especially the Monterey-San Francisco fishery, is a function of the apparent origin of the year class as judged by the relative catches when they are one year olds; those originating in Central California weighing more heavily in the catch, in particular the Central California catch during subsequent years. Thus it seems that sardines spawned to the north have a predilection to occupy the northern part of the range, and vice versa. The last northern year-class (by Felin's and Radovich's definition) was that of 1947, apparently the progeny of a fairly small stock of spawners judging by the distribution of the fishery that year.

The Monterey fishery collapsed in 1950 and 1951, three and four years later, that is when these 1947 fish were three and four year olds. Since they contributed heavily to the southern California catch those years (in fact, the 1947 year-class made its greatest contribution in southern California as three year olds during 1950-51, strongly suggesting that its distribution changed), it must be concluded that the environment altered their normal northerly oriented distribution during those fishing seasons. It thus appears that contraction of range was brought about by failure of the adults to migrate as far north as usual during the spawning season which of course would in itself preclude a northern year-class, and also was caused by failure of spawn to survive in the north, a phenomenon that feeds back into the first operator.

After 1949 the sardine population was essentially confined to the area from Point Conception south. Substantial catches (over 300,000 tons) were made during the fall of 1949 and 1950, so there must have been substantial spawning in the spring. Yet, the resulting year-classes were apparent failures. A further major effect of the environment with respect to these year-classes is suggested by their catch curves. The 1949 year-class shows pronounced negative mortality between ages 4 and 5, the catch of five year olds being six times as large as the catch of four year olds, and almost as large as the catch as of two year olds. Previous to this year-class the typical pattern was for maximum contribution as two year olds or three year olds. Similarly, the 1950 year-class made its maximum contribution at age four. From this record it is obvious that the virtual population method markedly underestimates their size relative to other year-classes though there is no evidence they were large year-classes. Perhaps more important the catch curves clearly show that the time-space distribution of these year-classes with respect to the fishery clearly departed from the normal, presumably in response to the same kinds of environmental changes that altered the distribution of the 1947 year-class after its second year of life.

The ocean climate remained cold until 1957, and the now reduced population remained centered in the south. During these years, the southern California fishery, instead of being located in the center of the range of the species, was stationed at the northern edge of the range, and since the fishery has the essential character of a day fishery it was exceedingly sensi-

tive to minor changes in the north-south distribution of the sardine, the landings ranging from 3 to 76 thousand tons. From 1957 through 1959 the ocean climate warmed and the sardine population ranged farther north in 1958 and 1959 (as far as San Francisco), though the catches have not suggested a significantly larger population.

The recent warming of the California Current and slackening of its speed is the reverse of the events that were associated with the decline, so presumably a recovery should ensue if the oceanic climate continues to be favorable. If the recovery follows a course which is the reverse of the decline it should proceed as follows: (1) more northerly distribution of existing adults and more northerly spawning (already underway but involving very small numbers of sardines), (2) maturity of northerly spawned fish, and a spawning by them, and (3) growth of these northerly spawned fish to commercial age (2 year olds). Obviously this will take time, and a real recovery could not be expected before 1961 at the earliest. In the meantime the population of competitors such as the anchovy should decline as a result of the shift in ocean climate and increased competition from the sardine.

In conclusion, it is possible to divide the natural pressures that regulate the Pacific sardine into three groups. The first is the physical-chemical environment and trophic levels below the sardine. These seems to affect the sardine directly in a density independent manner and indirectly in a density dependent manner by contracting the available habitat. The second is the within-trophic level competition. This involves the sardines themselves and such species as anchovies. These would seem to exert their effect in a density dependent manner either by competition for food and space or by specialized predation, e.g., adults eating larvae, large larvae eating small larvae, etc. The third is predation of various sorts from higher trophic levels. The rate of this source of pressure may well be density dependent and self-adjusting, and perhaps this regulatory mechanism is of secondary importance. (Man, of course, preys heavily on many of the potential predators tending to produce a compensatory effect.)

Finally, there is the role of the fishery. It seems clear that the minimum effect of the fishery is to sensitize the population to environmental changes. It is equally clear that the growth-mortality regime of the sardine leaves little to be gained by manipulating a year-class after it enters a fishery (Clark and Marr, 1955). This leaves the question as to whether or not the fishery has or will reduce the pre-spawning population to a point that there are not enough survivors through the density independent mortality stages to efficiently utilize the environment during density dependent stages. Even a positive answer to this question leaves unresolved the problem of the practicality of population manipulation through regulation of the catch.

The fact that at this writing it is possible to identify environmental changes that parallel changes in the sardine population along the Pacific Coast (and else-

where in the world, Proceedings of the World Sardine Conference, in press), and for which it is possible to assign a logically significant effect on the Pacific sardine, suggests that the environment has played the major role in the regulation of the population. In a purely negative sense, the impossibility to date of being able to satisfactorily apply any of the existing and in some instances highly successful mathematical models of fish populations to the excellent series of catch statistics on the sardine is evidence that the environment is playing a major and possibly dominant role, and that the fishery's chief but not necessarily exclusive effect is to make the population more responsive to changing environmental pressures.

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