LARVAL SARDINE AND ANCHOVY INTERRELATIONSHIPS[1]

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INTRODUCTION

This paper presents analyses of data on the size and numbers of sardine and anchovy larvae. The analyses are a selection from a larger number carried out by the author over the last several years, selected because of the insight that they provide or in some cases, because of the useful or intriguing questions that they raise.

The data employed are the length-frequencies of anchovy and sardine larvae collected over the years 1950–57 by the CalCOFI Program and measured and reported by the Bureau of Commercial Fisheries, La Jolla, California (Ahlstrom, 1950, 1951, 1952, 1956, 1957 and Ahlstrom and Kramer, 1953, 1954, 1955).

PURPOSES OF THE ANALYSES

The adult stocks and the entering year classes of sardines have fluctuated rather widely. In addition, the stocks of adult anchovies, as judged by their eggs and larvae, have increased greatly over the years 1950 to 1957 and later. It is quite possible that these fluctuations are determined by changes in larval survival or growth. In addition, the co-occurrence of the two species at the larval level may impose changes in the larval statistics indicative of interaction.

There is another important purpose to these studies. The numbers of larvae of a species that are taken in a survey, are dependent upon a number of poorly understood factors. These factors include net efficiency versus size of larvae, towing speed and light level; growth rate of the larvae; and larval mortality rate. Analyses were performed in an attempt to separate the effect of these factors.

RESULTS

An understanding of some of the factors of larval growth, mortality, and escape and of the developing anchovy-sardine interaction has been gained.

The increasing dominance of anchovies over sardines during the period is shown to have taken place with:

1. a rapidly increasing anchovy larval population and a slowly decreasing sardine larval population,
2. a rapidly increasing portion of the anchovy larval population free from association with sardines,
3. a slowly increasing portion of the sardine larvae free from association with anchovies and
4. an initially rapid increase in the numbers of anchovies associated with sardines, apparently becoming constant in later years at about 6 to 1.

Thus the anchovy simultaneously achieved not only increasing numbers, but also increasing freedom and association!

During the early portions of the period—about 1951 to 1953—the degree of mixing or association of larvae decreased with increasing larval size, whereas in 1954 and subsequently, the degree of association increased with increasing size.

The success of the year class of sardine larvae may be related to the degree of association with anchovies, perhaps indicating that areas with the best conditions are inhabited by both species.

A coherent picture of escape from the net, and growth rates and mortality of the larvae of both species has been derived.

The anchovy larvae is found to escape, probably through the webbing up to a size as much as 7.75 mm in length and to escape, probably out of the mouth of the net above 9.75 mm. The sardine escapes out of the mouth of the net above 14.75 mm.

Both species largely dodge the net in daytime. In the case of the sardine larvae the day-caught larvae are shown to be a measure of mortality of the population. From this, criteria of growth and survival are derived and are found to rank years in fair agreement with the sardine year class success as determined by the fishery. A similar treatment of the anchovy larvae could not be *directly* defended because of the brief sampling interval of these larvae. Nevertheless a treatment of the anchovy larvae in this way and derivation of anchovy growth and survival criteria results in a rational picture of the relationship between the two species. There is apparently some inverse correlation between the derived survival of the two species. The years strongly advantageous to one or the other species are clearly indicated by this analysis. For example, 1952 and 1956 are shown to have been relatively advantageous to the sardine; 1955 disadvantageous to both but relatively advantageous to the sardine and all other years in the series are shown to have been relatively advantageous to the anchovy with 1951 being the most advantageous.

It was found that a direct correlation exists between the criteria of growth and survival within each species. This accounts for the slightness of the variation between years of the slope of the length-frequency statistics, despite the changes in the growth and survival. In general, rates, which are derived from ratios, display more consistency than numerical survival. This argues that the sampling is more nearly adequate for representivity than for census, as must always be the case in such sampling programs.

[1] All figures appear at end of paper, pages 114 to 140.

The calculated survival of sardines appears directly correlated with the size at which the larvae of the anchovy cease escaping through the mesh of the net. This is believed to result from either some inverse correlation of sardine survival with the "condition" of the anchovy larvae, a direct correlation with some associated entangling material in the catch that early prevents anchovy larvae escape through the mesh, or a direct relationship of vigor in both species.

There exists a direct correlation between survival of the sardine and the slope of the length-frequency of extremely rare, very high catches of the larvae. This indicates perhaps that significant survival occurs in very small patches of highly advantageous conditions.

An assumed *exponential* growth combined with the *real* numbers of larvae caught, results in a *linear* biomass growth for both species, and this can be extrapolated to the adult stocks within good agreement of their relative size over the period. This suggests that larval survival is the result of a limiting input, and that *biomass* growth is independent of larval size (that is $dw/dt \sim w$).

The algebra of the effect of growth on the length-frequency diagrams is developed.

ANALYSES

The analyses are discussed along with the presentation of the appropriate graphs or tables. In some cases no direct conclusions can be drawn but the analyses indicate peculiarities of the data that are provocative. These are merely pointed out.

In general, as will be established later, the significant size range of sardine larvae is about 5.75 mm to 14.75 mm and for anchovy larvae the significant interval is about 6.75 mm to 9.75 mm. Where slopes or integrations are performed the corresponding intervals are decreased 1 mm. Thus the data on the anchovy is severely limited in many cases.

SIZE OF CATCHES—FIGURES 1-8.

Numbers of sardine larvae taken in each net haul for each year are plotted versus length. Curve A is the average numbers of all positive hauls taking larvae at that length and Curve B is the median of all positive hauls.

For the larger larvae the numbers reported in the literature are in some instances influenced by aliquoting the samples. The largest number of large larvae found are usually the result of multiplying some very small number of larvae, (usually one), by the reciprocal of the aliquot fraction. This figure appears in the basic data, and there is no satisfactory statistical way to correct for it. Thus, the flattening of the curves from 15.75 mm on to greater lengths results from aliquoting and hence is not significant at the smaller sizes; where the larvae are more numerous, aliquoting introduces no such difficulty.

The following table summarizes the slopes of these curves.

TABLE 1

LOG SLOPES OF LARVAE CATCH DIAGRAMS

	(1) Slope Extreme	(2) Slope Upper N	(3) Slope ΣN_N
1950	0.94	1.01	0.84
1951	0.70	0.84	0.74
1952	0.49	0.87	0.82
1953	0.60	1.04	0.86
1954	0.74	0.90	0.86
1955	0.80	0.86	0.87
1956	(0.17) 0.57	0.92	0.85
1957	0.89	0.89	0.77
Average	0.717	0.917	0.827

Slopes, $\frac{\Delta \log N}{\Delta L}$

By way of explanation, the extreme was the extreme line that could be drawn through the uppermost separated points; the upper N was the average of the highest N number of samples in each size category, where N was the number of cruises in that year; and ΣN_N is the sum of all night samples at each length. (The slopes of the latter sum, are, of course, the same as the slopes of the night catch; i.e., from Figures 31–38, presented later.)

In the simple case, the slope of these lines might be thought of as a measure of mortality of some portion of the population. Hence, if larval survival were important to the development of a year class the years that were apparently years of relatively good year class survival (i.e. 1952 and 1956) would have small values of slope, and years that appear to be particularly poor years (i.e. 1950 and 1955) would have large values of slope. An inspection of the table of slopes indicates that none of these measures displays such relationships among the years, except for the slopes of the extreme. This, indeed, shows such a very flat slope for the year 1956 that the second extreme for that year is also recorded and it is still the second flattest slope in this series.

Perhaps the most intriguing aspect of these presentations is this existence of extremely high concentrations at a few lengths. For example, in Figures 3 (1952) and 7 (1956), there are several points that represent only a small decrease over the highest concentrations of very small larvae. These could be interpreted as the result of schooling behavior with increasing size. If this were the case, the effect of schooling should not be limited and it would seem reasonable to find occasional catches of large larvae that were *greater* than *any* catches of smaller larvae. Only in 1957 is there the suggestion of such a case but it involves comparison of only very small larvae. In most cases the extreme concentrations of large larvae is merely slightly less than the extreme concentration of smaller larvae.

An alternative explanation is that in these cases we are observing an occasional sample from a region of very high concentration and very high survival. It is not unreasonable that this might be so. The entire population of adult sardines easily could be re-

produced by extremely high survival in small patches that were much smaller than the grid of the survey pattern and hence only occasionally sampled. Such patches would presumably represent a maximum number of advantageous factors and a minimum number of disadvantageous factors.

That is, to explain these results we may suppose that the sardine survival results from small isolated patches a few square miles in extent where there is optimum food, a minimum of predators, a minimum of competitors, and other optimum conditions. If we consider the great number of factors that must influence the survival of larval sardines, and the spottiness of the distribution of these factors, there must be rare areas where an unusual concert of advantageous conditions is combined with a virtual absence of adverse conditions over a significant period of time.

That such circumstances could control the year class success is not so surprising.

If we were to try to reforest a great area by profligate seeding from aircraft we would not be surprised to discover most of the reproduction in very small well-defined areas where recognizable conditions greatly favored survival. It is by no means farfetched that similarly profound but virtually invisible conditions at sea lead to similar rare spots of unusual survival. Indeed if the apparent survival in these few extreme points is extrapolated to 180 mm by log linear extrapolation (i.e. Log $N' = CL$), the surviving fish are of the order of 10^{10}, quite in accord with the order of requirements of sardine recruitment. Add to this the superficial correlation of slope and apparent year class success between years and this hypothesis is not unattractive.

It should be noted that these rare large samples at early times are not a very large part of the total larval sardine catch. Their influence on the slope of the average curves is small and an average survival applied to these extreme concentrations will, of course, show only a slight survival.

An examination of the zooplankters associated with two of these high concentrations of sardine larvae reveals a mixed zoogeographical group of zooplankton. This group differs from adjacent stations in possessing fewer species of copepods including fewer predaceous species (Fleminger, 1963). This will be published later.

Later in this paper will be developed an hypothesis leading to the establishment of growth and mortality criteria for the general population of sardine larvae. These criteria are not derivable from single samples as they involve an interpretation of related day catches and night catches. However, there will be shown a correlogram (Fig. 65) of the mortality criterion for the year and the extreme slope. The correlation is reasonable, and especially so when one considers the rare nature of the samples upon which the extreme slope is based.

ANCHOVY AND SARDINE CATCHES—Figures 9, 10, 11, and 12

These figures consist of plots of all catches of sardine and/or anchovy larvae for the years 1950, 1952, 1955 and 1957. Numbers of larvae of each species for each catch are plotted against the numbers of the other species occurring in the same catch. The anchovy larvae were inadequately sampled in 1950, so this plot is somewhat biased toward sardine larvae. (In all drawings, points representing pure catches are sometimes "stacked" off the axis. The zero axis is intended in these cases.)

The trends over these years are conspicuous in these plots.[1] In 1952 there are many pure catches of sardines and many mixed catches as well as many pure catches of anchovies. The largest numbers of sardines are associated with anchovies! (Later it will be indicated that the high survival and growth of sardines may occur in the regions that the two species coinhabit.) As time progresses, however, as shown in 1955 and 1957, the diagrams rotate toward the anchovy axis. Large pure catches of sardine larvae decrease dramatically, mixed schools have a greater proportion of anchovies and the pure catches of anchovies increase greatly. During this period the surveys were increasingly concentrating on the areas where sardines were abundant and hence the indicated trend was undoubtedly even more extreme.

Apparently any competition between the species takes place with an association that is at least sufficiently intimate to allow their larvae to be taken in the same oblique plankton hauls very frequently.

ANCHOVY-SARDINE RELATIONSHIPS WITH LENGTH—Figures 13–19 and 20–26

Another parameter in this association of anchovy and sardine larvae is the relation of the association with length. These are shown in Figures 13–26, where all larvae from night hauls are compared both in total (labeled night) and those from night hauls in which the other species was also present. The two sets of curves are of course not wholly independent, for associated anchovies, of course, imply the existence of associated sardines. However, the sets of curves are not entirely dependent as each one reflects the *numbers* of the particular species involved, and not the numbers but only the presence of the other species.

In comparisons of numbers at related lengths in different years the significant interval of sampling, discussed above, is not necessarily pertinent.

It is seen that for both species the relative association tends to decrease with increasing length for the years 1951, 1952 and 1954, (that is, the curves diverge), where as the opposite trend (convergence of the curves) obtains for both species for 1953, 1955 and 1956. (The 1957 graph for sardines is a possible exception.) The simplest explanation for convergence of the curves is an increasing dispersion and mixing of both species and perhaps increased co-schooling with increasing age. In the cases (1951, 1952 and 1954) where the curves diverge it is difficult to conceive of a simple dominant process by which the two species can become *less* associated with increasing age.

[1] The particular years selected for these diagrams display the trends but not the range of variations between years. Figures 27–29 show 1951 to have been a critical year, and 1954 and 1956 interesting. Similar plots of these years will be undertaken later.

Several factors could, however, account for the trend, including an increasing relative growth rate or decreasing relative mortality of the anchovy versus the sardine with age. Such a relationship in these years does not appear in subsequent analyses, however. A dispersion of one species and a schooling of the other could also account for the trend.

The principal conclusions of these diagrams are: (1) that over the majority of years the association of the two species tends to increase with age, and (2) that over the period the anchovy at all lengths becomes increasingly independent of the sardine whereas the sardine remains closely associated with the anchovy. To say this latter in a somewhat different way: there develops a large, unassociated population of anchovies at all lengths but not one of sardines.

This conclusion is essentially the same as that derived from Figures 9–12, but shows those conclusions to apply to all the ages sampled rather than only to the population as a whole. (See also footnote above.)

ANCHOVY AND SARDINE NUMBERS VERSUS YEARS—Figures 27–29

These figures demonstrate the onset and development of association even more dramatically. These figures cover the sums of larvae over only the length interval 6.75 to 9.75 mm for both species (i.e. the length interval of adequate sampling for the anchovy).

In Figure 27 the basic data are presented. It is seen that the numbers of pure sardines increase slowly over the period while the numbers of pure anchovies increase rapidly. The numbers of associated sardines and the numbers of sardines decrease with a two-year oscillation, the numbers of anchovies and pure anchovies increase throughout the period. Associated anchovies reach a peak in 1954 and level off subsequently.

Figure 28 shows these data as simple ratios. The number of associated sardines as a proportion of the total sardines decreases with a similar two-year oscillation, and with peaks above the trend in 1951, 1952, 1954 and 1956. The number of associated anchovies as a proportion of total anchovies similarly decreases. However, the ratio of the associates of the sardine larvae (i.e. associated anchovy larvae plus total sardine larvae) to the sardine larval numbers increases constantly with a sudden minimum in 1956. (This latter ratio reflects the average environmental pressure on sardine larvae from the combined larvae and/or adults of the two species.)

Thus the anchovy larvae achieve an increasing freedom and an increasing association with the sardine larvae simultaneously!

Figure 29 demonstrates the increasing dominance of both associated and total anchovies to associated and total sardines. These ratios with a brief respite in 1956 reach continuously higher levels.

The third curve of Figure 29 is the average of the ratio of these two previous ratios. This ratio is a comparison of the degree of association of the two larvae in the total area. (That is:

$$\frac{N_{aa}}{N_a} = K \frac{N_{sa}}{N_s}$$; where K is this third ratio.)

It is seen that this ratio varies between about 0.4 and 0.7 through 1955 and then declines abruptly for 1956 and returns to a higher level in 1957. The anchovy thus had only about half the degree of association as did the sardine during the years and much less in the year 1956. This is clearly another portrayal of the "breakthrough" of the population of anchovies which achieved increasing independence, while still maintaining a high level of competition.

It will be indicated later that the sardine may have suffered high larval mortality and slow growth in the year 1955. In 1955 the anchovy also apparently did not have an increasingly successful year. The anchovy subsequently recovered, however, and the sardine subsequently declined. (The year 1955 was the coldest year in a cold persistent period.)

At this point it should be noted that if the interactions of the two species were a purely random overlap of the two populations without serious effect on one or the other, the value of K should be a ratio of the magnitude of the environment occupied by the sardine larvae (and spawning adults) in respect to that occupied by the anchovy. This follows from the following argument.

Let E_s, E_a and E_{as} be some appropriate quantitative measure of the size of the environment for the sardine, anchovy and the overlapping populations respectively.

Then $$\frac{N_s}{E_s} = \frac{N_{sa}}{E_{as}} \text{ and} \tag{1}$$

$$\frac{N_a}{E_a} = \frac{N_{aa}}{E_{as}} \tag{2}$$

Thus $$\frac{N_{aa}}{N_a} = \frac{E_s}{E_a} \times \frac{N_{sa}}{N_s} \tag{3}$$

and $$\frac{E_s}{E_a} = K \tag{3.1}$$

If, however, the overlap were still random but both of the larvae were equally interacting in the region of overlap (including the effects on the larvae of the presence of the adults of the two species) in a manner similar to some limiting effect on the separate populations, then:

$$\frac{N_s - N_{sa}}{E_s - E_{as}} = \frac{N_{sa} + N_{aa}}{E_{as}} \tag{4}$$

and $$\frac{N_a - N_{aa}}{E_a - E_{as}} = \frac{N_{sa} + N_{aa}}{E_{as}} \tag{4.1}$$

solving, $$\frac{E_s}{E_a} = \frac{N_s + N_{aa}}{N_a + N_{sa}}$$

It would be intriguing to compare such models with some quantitative measure of the environments occupied by the two species. The difficulty in doing this stems from selecting a measure. The environment of a pelagic creature can thin, thicken, spread or contract. Thus area is probably a poor measure of extent of the environment. This particular difficulty would be corrected by selection of a volumetric criterion. The plankton nets, of course, sample volumetrically, but this in no way guarantees that the volume sampled in a series of positive hauls has described the volume of the environment, for the appropriate environment can occupy only a portion of the depth range sampled. Even were the appropriate volume to be sampled adequately, the environment is not necessarily measured by the volume of water but may concentrate or attenuate in disregard to the quantity of water present.

Despite these difficulties, it would be interesting to compare the models suggested above (along with others that can be developed) with possible measures of the environment.

In respect to the first of the two models it is difficult to imagine that the "size" of the environment of the sardine has only varied between 0.4 and 0.7 of that of the anchovy, for the relative *areas* occupied by the two species have changed much more than this. Despite the inadequacy of area as a criterion, very large changes in area are undoubtedly significant. The second model varies only somewhat more (about 0.3 to 0.6).

Thus, the *prima facie* appearance is that neither model holds and thus the region of overlap is not random. Whether or not the two species interact is not determined by this particular analysis.

LENGTH-FREQUENCY ANALYSIS—Figures 30–56

Figures 30–47 show the catches of the two species (sardines and anchovies respectively) plotted as numbers versus length. Curve A is the total catch. Curve B are those larvae taken in daytime hauls [2] and Curve C are those taken in nighttime hauls. (Numbers have been halved where the length interval was two mm i.e., 17.25, 19.25, and 21.25 mm.)

The remainder of this discussion will concern itself almost solely with some of the numerous matters derivable from this set of graphs.

In the case of the sardine it is seen that the curve of the day catch (B) begins at a greater number than the night catch (C) and then drops rapidly always falling below the night catch by the second or third size category. The night catch, however, shows an early maximum at the second or third size category.

In the case of the anchovy the day catch is often practically a straight line from the beginning and is larger than the night catch only in the case of 1952. The night catch passes through a maximum at a larger but still early size category. The day catch only twice shows a maximum subsequent to the first point.

As will be shown later for *sardine* larvae, the day catch is a measure of mortality. Thus an inferred explanation of this portion of the *anchovy* curves is as follows. The anchovy eggs and the small anchovy larvae are known to escape through the webbing of the net. This mode of escape becomes impossible for all cases at a size of about 7.75 mm. At night very few of the larvae can dodge the net. Most of these larvae are vigorous and the small ones can escape by wriggling through the webbing. During the day, however, most larvae dodge the net. Those that are caught are not sufficiently vigorous to escape through the webbing and hence show no maximum at the point where this mode of escape becomes impossible. An added factor in producing the higher night catch undoubtedly is the fouling effect of the greater mass of other plankton in the net, which prevents escape of many larvae.

There is considerable variation between years of the point in the night curve of anchovy larvae at which escape through the webbing apparently ceases. One is tempted to attribute this to some factor of larval condition. That is, poorer larvae escape at a greater length than do fatter larvae, or, conversely, more vigorous ones escape at a greater length than do the feebler larvae. The years rank as follows (length at termination of escape is shown in brackets):

1955, (3.50); 1953, (4.75); 1951, (5.75); 1950 and 1954, (6.75); 1952 and 1956, (7.75) with 1957 indefinite.

This "condition" factor will be compared to a criterion of *sardine* larvae survival that will be developed below and it will be found to be directly correlated.

Before discussing the curve marked D in these sets, it should be noted that in many cases of the sardine larvae the day Curve B has the characteristics of a first differential of the night catch, Curve C! The veracity of this relationship was tested in two ways. First the slope of the night curve was compared to the *total* value of the day curve at each point. Night curve slopes were computed across the interval employing the two adjacent points. These correlations are shown in Figures 48–56, and it is seen that the correlation is very high and with a slope of about unity. The combined results of the eight years, Figure 48, displays a particularly close correlation.

A further test of this relationship is shown in Curve D of Figures 30–38, sardines. Here, beginning at 5.75 mm, a successive summation of the day curve is added to each value of the night curve. The mathematical results of this, if indeed the day curve is a measure of mortality, should be to reconstitute the population as it would be *sampled* in the absence of mortality. In the absence of a changing growth rate, this sampled population should be constant. An inspection of Curve D for sardine larvae

[2] The total number of dayhauls has differed only a few percent from the number of nighthauls (i.e. ~ 3%). There has been no correction for this small difference.

Table 2

TIME CHANGES IN SARDINE LARVAL GROWTH

	1950	1951	1952	1953	1954	1955	1956	1957
Time change	−0.13	−0.005	−0.165	+0.075	+0.028	+0.077	−0.308	−0.058 (−0.20)
Relative time	(0.87)	(0.995)	(0.835)	(1.075)	(1.028)	(1.077)	(0.692)	(0.942) (0.80)
Relative growth rate	1.15	1.01	1.19	0.93	0.97	0.92	1.44	1.06 (1.22) (average 1.14)

shows that Curve D is almost constant, with variation between years from a somewhat ascending slope to a descending slope.

A *sampled* population in the absence of any mortality will show a variation in numbers between given length intervals that depends inversely upon the comparative growth rates across the various length intervals. Thus a descending slope in Curve D is attributable to accelerating growth with increasing length and an ascending slope in Curve D is related to decelerating growth.[3]

In like fashion a changing growth rate will alter the slope of the correlation in Figures 48–56.

For the sardine the factor required to bring each point from 6.75 to 13.75 mm of Curve D to a constant value has been calculated and the averages of their change across the interval are shown in Table 2.

This time change factor can be considered as a *change in the time* ($\triangle^2 t$) required for the sardine larvae to cross a length interval as length increases. Thus values less than zero indicate accelerating growth, zero unchanging growth and values greater than zero decelerating growth. Adding unity to this value (as shown in brackets) results in a relative time across a length interval. The reciprocal of this is the growth rate criterion.

The growth rate (dL/dt) is not derivable from any simple analysis of these data.[4]

In Figure 57 this growth rate criterion of the sardine is shown for each year.

The growth rates for 1957 are much more complex than in any other year of the series. At small sizes there is decelerating growth and rapidly accelerating growth at larger sizes. The average time change for 1957 is thus indefinite and could be as much as —0.2. An average relative growth rate of 1.14 will be used. The data for this year will be later tested to ascertain if it is compatible with some specific growth law.

An hypothesis to explain this curious relationship of the day-caught and night-caught larvae of the sardine is that the relationship of these larvae to their food and predators is a highly visual one. At night the plankton net acts unlike a predator, and adequately samples the population up to a larval length of 15.75 mm. During the day, however, it acts much like a predator. Most larvae above 5.75 mm dodge the net, and the larvae that are caught are a measure of their availablity to predation. This would be expected to include disproportionate numbers of the less active and visually alert, starving, maimed, moribund, and dead larvae. This category should closely represent the fraction of the population that is being removed by natural mortality.[5]

In regard to this relationship as it applies to the anchovy larvae, it has been pointed out that the anchovy larvae apparently escape from the nets at all sizes greater than 9.75 mm. In addition, as mentioned in the previous discussion, they escape *through* the net up to sizes of as great as 6.75 mm. Thus only about four intervals of length can be considered adequately sampled for the anchovy larvae. For determinations of slope the two limiting sizes must not be considered, leaving only three intervals for slope analysis. This is inadequate for a demonstration of the correlation between Nd/Nn and mortality, similar to that of the sardine. The Curves D for the anchovy uniformly display a downward slope with the exception of 1955, which is also irregular in other respects. There thus appears to be no presently satisfactory *direct* manner in which the veracity of growth and mortality measures can be demonstrated from the field data for anchovy larvae. However, the analysis *can* be *applied* to the anchovy over the limited length interval without the direct demonstration of its veracity.

In this hypothesis the length-mortality rate of the larvae is simply measured by the proportion of day-caught to night-caught larvae at each interval (that is—N_d/N_N).

The length-mortality rate can be qualitatively altered to more closely resemble the probable time-mortality by dividing it by the growth rate criteria derived above. This qualitatively compensates somewhat for the change of time over which the mortality acts.

The values of the length-mortality rate, "compensated" mortality rate and compensated survival rates for the sardine averaged over the interval 5.75 to 14.75 are shown in Table 3.

[3] Curve D, of course, tends to be dominated by the large numbers associated with small sizes of larvae. The correlograms (Figures 48 to 56) show the relationship also to hold for the small numbers associated with large sizes.

[4] The measured time change across each interval $\triangle^2 t/\triangle L^2 \approx K$. The growth rate criterion is $1/(K+1)$. In differential form, the growth rate dL/dt would be $1/(KL+C)$. The criterion thus assumes unity for the unknown constant factor of all growth rates. Where a significant acceleration or deceleration exists, (i.e. $|d^2L/dt^2| > 0$), K dominates the growth rate after a few length intervals. Where, however, there is little acceleration or deceleration, the unknown constant continues to dominate. Thus sardine larvae growth rates in the years 1951 and 1954 may be poorly described by this criterion. 1954 is the conspicuous poorly correlated year in later analyses.

[5] Ahlstrom (pers. comm., 1964) has made the remarkably cogent suggestion that the larvae may dodge the net in daytime by a school-communicated response. Thus the day-catch may be an inverse measure of the degree of schooling (i.e. mainly isolated larvae are caught). The same larvae, of course, also are presumably more available to predation.

TABLE 3

DERIVED MORTALITY AND SURVIVAL FOR SARDINE LARVAE

	1950[1]	1951	1952	1953	1954	1955	1956	1957
Length mortality	0.276	0.276	0.213	0.349	0.202	0.344	0.153	0.333
Compensated mortality	0.243	0.275	0.178	0.375	0.207	0.371	0.106	0.313 (alt. 0.256)[2] (avg. 0.286)
Compensated survival	0.757	0.725	0.822	0.625	0.793	0.629	0.894	0.687 (alt. 0.744)[2] (avg. 0.715)

[1] The sampling in the year 1950 differed from that in subsequent years. It has not been used in some of the subsequent analyses.
[2] The average of the two 1957 possibilities will be used.

The survival criterion is obtained by subtraction of the above mortality from unity. Figures 58 and 59 are correlations between the two survival criteria and the growth criterion. It will be seen that correlation is excellent, 1954 being the exception, with high survival and low growth.

If these growth and mortality results were correct, one mysterious characteristic of the length-frequency diagrams of sardine larvae would immediately be explained. The slopes of these diagrams are almost unchanged from year to year, (see column 3, Table 1) despite the certainty that survival is quite different in various years. As shown in the previous discussion the hypothesis developed leads to the result that "good" years are characterized by an *accelerating* growth rate *and low* mortality whereas "poor" years are characterized by *decelerating* growth rates *and high* mortality. The effect of each of these combinations of parameters on the length-frequency diagrams is compensatory. For example, in a "poor" year a decelerating growth rate will result in the collection of successively more larvae in the samples than if the growth rate were unchanging. The effect of the associated high mortality, however, is successively to *decrease* the numbers captured, and, hence, qualitatively to compensate for the effect of growth.

If the hypothesis presented were correct, it is only through the independent measurement of mortality and growth by analysis via the day- and night-caught larvae that the differences in years become conspicuous.

The effect of growth rate on the sampled numbers is handled algebraically in later discussions.

At this point it should be noted that if the length-frequency diagrams of the larvae were truly of constant slope the assignment of a particular mortality to any year would *a priori* result in a compensatory growth history. To the extent that a constancy of slope prevails in the various years' length-frequency diagrams, the foregoing of the two sardine larvae parameters are not independent and ensue only from the mortality assumption N_d/N_N. Thus to some degree the weight of the case rests on the veracity of the ranking of the years as related to sardine success from other sources of information.

The spawning success in these years can be estimated from catch data. McGregor has estimated the size of the year class entering the fishery in billions of fish as follows: 1951—0.41; 1952—0.63; 1953—0.22; 1954—0.16; 1955—0.36; 1956—1.16; 1957—0.52.

Here the agreement with the survival rate criterion Figure 60 is fairly good with only the year 1954 poorly correlated as would be expected. The agreement with the growth criterion is better, (Fig. 61). The salient features of the history are in good agreement. The fishery statistics are, of course, incomplete and are heavily biased to the northern part of the present sardine range. Some disagreement is thus not unexpected.

A further study of these criteria as related to the stocks as determined by egg census is a logical step that is being taken.

In a final interrelation, all of the derived statistics concerning the sardine larvae growth and survival is shown in Table 4. Here for each year is calculated a number of survivors after some extrapolated period of growth.

TABLE 4

SARDINE—SURVIVAL

Year	Mortality Rate	Survival (M) Rate	Ns	Relative Time (g)	$\frac{Ns}{g}$	5g	m^{5g}	N′
1950	0.276	0.724	1490	0.87	1750	4.35	0.245	421
1951	0.276	0.724	2550	0.995	2562	4.97	0.200	514
1952	0.213	0.787	4040	0.835	4840	4.17	0.368	1777
1953	0.349	0.651	2160	1.075	2009	5.38	0.100	201
1954	0.202	0.798	3800	1.028	3690	5.14	0.312	1150
1955	0.344	0.656	1490	1.077	1382	5.38	0.104	144
1956	0.153	0.847	2896	0.693	4170	3.47	0.561	2340
1957	0.333	0.667	1665	0.942	1768	4.71	0.149	203
1957 (alt.)				0.800	2080	4.00	0.198	412

The calculation is as follows:

$$N' = \frac{N_s}{g} \times m^{ng}$$

where N′ are the extrapolated survivors from n growth periods; N_s is the total night-caught larvae for the year in the length interval 6.75–9.75 mm; g is the relative time criterion previously derived; m is the derived survival criterion. Since absolute time is unknown, five time intervals were chosen for n for all years so that the variation in final survival was of the order of 10, as observed in the year class from catch statistics.

In Figure 62 this calculated survival is compared to the year class. Again 1954 is poorly correlated but the salient features of the history are very well shown.

In Figure 63 this survival is plotted against the presumed measure of anchovy condition previously derived and in Figure 64 sardine growth rate is also plotted against anchovy condition. A direct correlation appears excellent. There are three possible explanations. (1) The anchovy "condition" truly represents the thinness of the preponderance of anchovy larvae, which is directly related to sardine success or (2) the escape of the anchovy larvae through the webbing is an inverse function of the quantity of certain other plankton captured by the net and the sardine success is inversely related to the quantity of this plankton or (3) the "condition" is directly related to the vigor of the anchovy larvae and also directly related to sardine success.

Before entering into the discussion of anchovy parameters, there should be presented the correlogram Figure 65 which relates the mortality criterion with the extreme slope of the individual catches of sardine larvae (see Table 1, column 1). As previously noted, the correlation is fair, especially at the extremes. It should also be noted that there is nothing incompatible between the idea of a general condition of the whole population being reflected in an exaggerated way in very small portions of the population. Thus these very small areas of high concentration of large larvae may contribute disproportionately to the ultimate entering year class.

It also should be noted that these very large concentrations are mixed with anchovies (see Fig. 9–12, in which, except for 1957, all the extreme concentrations of sardines are so mixed).

Figure 66 correlates sardine growth and mortality with the proportion of sardine larvae associated with anchovies. The correlation is low but direct—that is in the years in which associated sardine larvae represented a large part of the sardine larval population, growth and survival rates also were high. Referring to Figure 28, it will be noted that the factor Nsa/Ns decreases over the years. This may result from an increasing "chasing" of sardines in the survey program. Removing this possible "bias" from the Nsa/Ns ratio as shown on Figure 28 results in the correlation shown on Figure 67. The simplest bias line has been chosen—the correlation is good.

This may suggest that the waters occupied by both species are more suitable to the sardine than the waters that it occupies outside the anchovies association. Presumably this has obtained only in the recent years of the increase in anchovies.

An hypothesis that the anchovy larvae "dilute" the sardine larvae in the mixed population and buffer them from predation does not yield defensible statistical results.

ANCHOVY MORTALITY AND GROWTH—Figure 68

As discussed previously the brief length interval of sampling of this species precludes the direct demonstration of the veracity of the analysis. However, the analysis can be performed on the four length categories that appear to be properly sampled. The large numbers involved in the anchovy larvae may partly compensate for the small interval.

The results of the treatment are shown in Table 5.

As shown by Figure 68 the correlation between relative growth and survival of the anchovy is by no means as significant as that of the sardine. However, the years during which the anchovy apparently made high gains are clearly shown as well as those during which it made low gains.

There is a complete lack of correlation between anchovy "condition" previously described and either of the two anchovy criteria. This lends credence to the alternative that this "condition" is related to the entanglement in some other component of the catch that also influences sardine survival.

TABLE 5

ANCHOVY—MORTALITY, GROWTH AND SURVIVAL

Year	Mortality	Relative survival rate	Na	Growth criterion	Relative growth rate	Na × growth	5g	S^{5g}	Na′ survival
1951	0.127	0.873	8,930	0.745	1.34	12,000	3.73	0.603	7,250
1952	0.211	0.789	16,870	0.962	1.04	17,500	4.81	0.320	5,600
1953	0.164	0.836	25,750	0.953	1.05	27,000	4.77	0.425	11,500
1954	0.122	0.878	45,000	0.894	1.12	51,200	4.47	0.559	28,600
1955	0.490	0.510	30,000	1.037	0.97	28,900	5.18	0.031	895
1956	0.166	0.834	45,700	1.00	1.0	45,700	5.00	0.404	18,800
1957	0.181	0.819	44,340	0.979	1.02	45,300	4.89	0.369	16,700

COMPARISON OF ANCHOVY AND SARDINE GROWTH AND SURVIVAL—Figures 69–71

It is now possible to compare these derived parameters between the two species.

In Figure 69 is shown a comparison of relative growth rates of the anchovy and sardine. There appears to be some negative correlation. If we may except the year 1955, during which *both* species apparently did poorly, the negative correlation is rather good.

On this Figure 69 is marked the 1:1 line separating conditions relatively advantageous to one or the other species. The years are clearly separated in good agreement with the experience.

A similar comparison between survival rate of the two species is shown in Figure 70. Here the survival rate has been extended over five and ten length intervals in two plots. Again the years are separated in a rational way between those relatively advantageous to one or the other species.

Again excepting 1955 there appears to be a negative correlation in the five interval plot that is emphasized when extended to ten intervals.

All lines connecting points for the same year, of course, continue to diverge from the 1:1 line. Thus the inverse correlation would become stronger as the rates were further extended.

Figure 71 extends the growth and survival calculations to include the numbers of larvae sampled. The line separating relatively advantageous and disadvantageous conditions for the two species undoubtedly should be placed on the 1:1 position. However, this shows all years relatively advantageous to the anchovy, (as is undoubtedly the case). However a line is transferred from the relative survival graph (Fig. 70) along the 1:10 position to show relatively advantageous *conditions* over the period. This, of course, shows the relative advantages of the two species to vary much in the same fashion as do the previous comparisons.

These comparative studies of sardine-anchovy growth and survival appear to present a rational picture of the history with considerable agreement and little conflict with indications from other sources. This lends support to the veracity of the treatment and to its applicability to the anchovy data as well as to that of the sardine.

BIOMASS GROWTH OF SARDINE AND ANCHOVY LARVAE

The following discussion covers some exploration into the dimensional analysis of larval growth.

A. *Effect of growth on numbers sampled*

The length-frequency diagrams discussed above are a presentation of the numbers of larvae sampled (N_s) across a series of 1 mm length increments (or adjusted to 1 mm length increments).

However, for a given number of larvae developing in the environment (N_e) the numbers sampled at each increment will be influenced by the length of time that the larvae spend within each growth increment.

Thus for a given sampling effort

$$N_e \sim \frac{N_s}{\Delta T_L} \tag{1}$$

where $\triangle T_L$ is the time interval associated with a particular length interval. This is a reflective correction to an original bias in the data that is necessary to examine the implications of any assumed growth law.

Thus the general decrease of sampled numbers versus length can be made up of two components: one the true mortality of the larvae and the other a changing rate of growth of length as it affects capture of larvae within length increments. Note that an accelerating growth rate decreases the number captured at the greater lengths and a decelerating growth rate increases such numbers.

Thus, to reiterate, in a year of accelerating growth and low mortality, (which we might consider highly advantageous for the species) the length frequency diagrams are not much changed from a presumably disadvantageous year in which high mortality and low growth rate prevailed, for each of the two effects in each of the years rotate the length-frequency diagrams in opposing direction.

Mortality and growth rate could be placed in a more meaningful context if the numbers of larvae were converted to relative biomass.

For populations of a series of geometrically similar larvae this can be approximated by the following assumption:

$w \sim L^3$, where w is the weight of individual larvae. (2)

Thus

$N_s L^3 \sim W_s$, where W_s is the total biomass sampled (3)

during the reporting period; (actual laboratory measurements of sardine and anchovy larvae weight vs length result in exponents of about 3) (Figure 72).

In order to convert W_s into a measure of W_e, (the total biomass in the environment), it is necessary to measure or to assume some growth law.

ASSUMPTION OF A GROWTH LAW

A series of different models are assumed for the nature of the distribution of food in the sea and the nature of the larval feeding habits.

A further assumption is that larval growth rate is a linear function of the rate of food intake dQ/dt, that is:

$$\frac{dw}{dt} \sim \frac{dQ}{dt} \tag{4}$$

All models that assume food intake to be a function of a continuous swimming effort on the part of the larvae, result in growth laws of the form:

(5)

$\frac{dL}{dt} \sim L^n$, where the exponent n is 1/3, 4/3, or $-5/3$ or 10/9 for a filter feeding, and three selective feeding models respectively.

When swimming velocity of the larvae is considered non-restricting, and the food intake determined only by some portion of the larval capacity, $n = 1$.

or $\frac{dL}{dt} \sim L$, (5.1)[6]

$\frac{dw}{dt} \sim w$, (6)[6]

and this states *that each unit of mass in the larval fish population possesses an equal opportunity for growth regardless of the size of the larva of which it is a part.*

The several derived equations from this type of growth follow:

$\frac{\Delta L}{\Delta T} \sim L$; $\Delta T \sim \frac{\Delta L}{L}$ (7), (7.1)

$T = C + K \log L$, where T is progressive developmental time (age), and (8)

$w = w_o e^{Kt}$ (9)

It is possible to use the law in connection with the observed numbers in the following way:

$N_e \sim \frac{N_s}{\Delta T} \sim N_s L$ (ΔL being a constant) and, (10)

neglecting C in equation (8),

$T \sim \log L$ (11)

since also

$W_e \sim N_e L^3$ (12)

Then

$W_e \sim N_s L^4$ (12.1)

Within the above assumptions, therefore, it is possible to plot relative biomass in the environment versus age, by plotting the sampled numbers of larvae (N_s) multiplied by L^4, vs log L, as seen in Figures 73 and 74.

When this is done the curves assume a wholly new character. Both species display a steeply ascending straight line with a sharp peak, followed by a steeply descending straight line.

[6] In this context, it should be noted that if the presentation of larval data in the usual way (as numbers sampled vs equal intervals of length) were viewed as a mortality curve vs age, this is tantamount to the assumptions:

$\frac{dL}{dt} \sim K$, and $\frac{dw}{dt} \sim w^{2/3}$.

Figures for total years are shown for the two species.

The sharp maximum for sardines occurs at 14.75 mm and that of the anchovy at 9.75 mm. From other evidence it appears that the decreasing leg of the curve is the result of escape from the nets. This thesis can be examined (along with the veracity of a straight line extrapolation of the ascending portion of the curve) by the following argument:

1. Since all data used are night-catch only, escape from the net is probably related to the ultimate swimming speed of the larvae, and results from some tactic, such as swimming out of the net after entering.

2. The reason for a steeply descending curve of catch (rather than a complete cut-off), once a size is achieved at which some larvae can escape, may be due to variations in the speed of tow of the net.

3. If all of the above obtains, then the two species should "measure" the variations in net speed in the same way, and a plot of per cent escaping at each length measured from the extrapolated branch versus U as measured by $L^{1/3}$ (see appendix) should result in a pair of parallel curves for the two species (i.e., two curves related by a single constant).

The two curves are closely parallel, as shown in Figure 75. Thus, the results are not inconsistent with the assumptions that the ascending branch of the curve is a reasonable measure of biomass increase of the larval population vs time and can be extrapolated, and that the descending branch is the result of escape.

Two particularly important results should be emphasized:

1. A law of growth that results in exponential *growth of the individual* when applied to the *real numbers collected,* is almost exactly modified by these *real data* to show a *linear growth of biomass of the population!*

2. The presentation shows the biomass of the anchovy larval population increasing more rapidly than that of the sardine, as is apparent from other sources.

3. The straight line extrapolation of the total curves to 180 mm in length yields a ratio of biomass of anchovy to sardine adults of about 8.1 to 1, which is very close to estimates from other data for these years.

From these results a number of further questions can be asked. Do these results imply that there is a fixed limited rate of input of food material into the population? It is, also, intriguing to consider whether, over the *long term,* populations of clupeoids increase their biomass linearly with time up to sexual maturity; and also the related question: is the length at which sexual maturity is reached for the species determined by the penultimate length at which not-less-than linear biomass growth of the population can be maintained over the long run?

It is possible that this presentation of the larval data approximates the truth.

Some possible simple models are shown in Table 6.

TABLE 6

PARAMETERS OF GROWTH MODELS

(1) Usual Plot (Length-Frequency)	(2) Filter Feeding Mode	(3) Intermediate Mode	(4) Capacity or Food Source Limited
$\frac{dw}{dt} \sim w^{6/9}$,	$\frac{dw}{dt} \sim w^{7/9}$,	$\frac{dw}{dt} \sim w^{8/9}$,	$\frac{dw}{dt} \sim w^{1}$
$\frac{dL}{dt} \sim L^{0}$,	$\frac{dL}{dt} \sim L^{1/3}$,	$\frac{dL}{dt} \sim L^{2/3}$,	$\frac{dL}{dt} \sim L^{1}$
$T \sim L^{1}$	$T \sim L^{2/3}$	$T \sim L^{1/3}$	$T \sim \log L$

CONCLUSION

The salient results of this inquiry are included in the early portions of this paper.

The paper is essentially exploratory and, thus, throughout the paper various indications are pointed out. Many of these are somewhat contradictory, others require further statistical and field investigations to decide between alternatives or to verify the results.

Perhaps the most important development and verification required is that for the growth and mortality criteria that are apparently derivable from the remarkable relationship of day- and night-caught larvae.

In this connection, the analyses were based on the data from the critical years 1951 through 1957. Similar data for the years 1958 through 1963 have not been published. It will be important to carry on these analyses through this latter period. There is one possible difficulty, however. During this latter period the sardine larvae continued to decrease in numbers. Already in 1957 the numbers sampled were low and there is a concomitant irregularity of the length-frequency diagrams and the relationships derived from these. If this irregularity stems from the small numbers of sardine larvae sampled, increasing irregularity of relationships can be expected in the latter period, and an increasing uncertainty of the derived parameters.

Perhaps the best test of the veracity of these relationships will ensue not from the data of 1958 through 1963 but from some other data on pelagic fish larvae. The future CalCOFI surveys should perhaps be altered to obtain larger and more nearly representative samples of the two species, and the test of veracity can then be applied to these.

At the same time there is a requirement to place the analysis of these data on a sounder analytical basis. For example, the presented analyses of growth rate are limited to an estimate of the acceleration of the time rate of change of length. (i.e., d^2L/dt^2 the second differential of length with respect to time). Where this is significantly different from zero, the second differential greatly affects the rate after a short period. Where it is close to zero, (1954 for sardines for example), the lack of knowledge of the growth rate (i.e. dL/dt) is a more serious deficiency. An attempt will be made to arrive at a more sophisticated treatment of growth and mortality rates, and to fit the data into experimental and theoretical growth models. Included in this will be the biomass growth models explored in this paper.

Barely mentioned in the foregoing is any correlation between the growth and mortality criteria of the two species, their spawning stocks, the biological associates, and the oceanographic conditions. These growth and mortality criteria (expecially in relative form between the two species) constitute objective measures for comparison with the ecological factors. A great continuation of work needs to be carried out in this area, and is being undertaken.

Confirmation and further development of the day-night relationship would permit the management of a pelagic fishery on a year to year basis rather than by the slow accumulation of catch statistics. Independent inquiry into its veracity and applicability, thus, becomes an important matter.

ACKNOWLEDGEMENTS

This paper represents one of the results conducted under the Marine Life Research Program, the Scripps Institution of Oceanography's part of the California Cooperative Oceanic Fisheries Investigations, which are sponsored by the Marine Life Research Committee of the State of California.

The author wishes to acknowledge the great aid in many of the foregoing calculations of Paula Chambers, Nancy Begnoche, Sandra McArthur, Steven Goss and Ann Katherine Isaacs. He also gratefully acknowledges the patience and help of Lorayne Buck in multitudinous typing and retyping the manuscript; Julian Miller for the careful determinations of larval weights; and the interest and council of Dr. Elbert H. Ahlstrom, Dr. Milner B. Schaefer, Walter R. Schmitt, Garth I. Murphy and others.

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Appendix

POSSIBLE GROWTH RATES OF LARVAL FISH

A. GENERAL ASSUMPTIONS

1. Throughout a series of similar larvae, the power output per unit weight is a constant at any behaviorally similar speed (i.e. ultimate speed, feeding speed, etc.).

$$P \sim W \tag{1}$$

2. The hydrodynamic drag of a larva is determined by its area and the square of its velocity.

$$F_d \sim AU^2$$

3. In a series of similar larvae of different lengths all volumes and weights are related to the cube of length, all areas by the square of length and all dimensions by the length.

$$W \sim V \sim L^3 \tag{3}$$
$$A \sim L^2 \tag{4}$$
$$L_1 \sim L \tag{5}$$

4. The feeding velocity of a larva is a velocity at which the power output, P_o, is constantly related to the internal power capacity, P_i.

$$P_i = P_o \tag{6}$$
$$P_o \sim AU^3 \sim L^2U^3 \tag{6.1}$$
$$P_i \sim W \sim L^3 \tag{6.2}$$
$$L^2U^3 \sim L^3 \tag{6.3}$$
$$U \sim L^{1/3} \tag{7.0}$$

5. The time rate of weight growth is proportional to the time rate of food intake.

$$\frac{dW}{dt} \sim \frac{dQ}{dt} \tag{8.0}$$

B. ASSUMPTIONS OF FEEDING CONDITIONS AND FEEDING BEHAVIOR

Case No. 1

The ocean contains uniformly distributed fine particles. The larvae feed by swimming at some constant power-to-weight output and capture a fixed proportion of the particles in a column of water whose cross sectional area is proportional to the mouth area of the larva.

$$\frac{dQ}{dt} \sim AU \sim L^2\,L^{1/3} \sim L^{7/3} \sim w^{7/9} \tag{9.0}$$

$$C_1 \frac{dw}{dt} = L^{7/3} \tag{9.1}$$

$$C_1 \frac{d(C_2L^3)}{dt} = L^{7/3}$$

$$3C_1C_2L^2 \frac{dL}{dt} = L^{7/3}$$

$$3C_1C_2 \frac{dL}{dt} = L^{1/3} \tag{9.2}$$

$$T = 3C_1C_2\,(L^{2/3} + C) \tag{9.3}$$

Case No. 2

The ocean contains equal weight quantities of food at each size over the appropriate range. The larvae randomly select these particles at their feeding velocity without regard to the size.

$$C_1 \frac{dw}{dt} = L^{1/3}$$

$$C_1 \frac{d(C_2L^3)}{dt} = L^{1/3}$$

$$3C_1C_2 \frac{dL}{dt} = L^{-5/3}$$

Case No. 3

The ocean contains a continuous size spectrum of food particles with an equal density of *numbers* of particles of each dimension over the appropriate range. The larva selects particles of a size associated with the dimensions of its mouth at a time rate associated with his velocity.

$$\frac{dQ}{dt} \sim L^3\,U \sim L^3\,L^{1/3} \sim L^{10/3} \sim w^{10/9} \tag{10.0}$$

$$C_1 \frac{dw}{dt} = L^{10/3} \tag{10.1}$$

$$C_1 \frac{d(C_2L^3)}{dt} = L^{10/3}$$

$$3C_1C_2 \frac{dL}{dt} = L^{4/3} \tag{10.2}$$

Case No. 4

The ocean contains a continuous size spectrum of food particles with equal *quantities* (by weight) of each size. The larvae feed with the velocity associated with the length and select appropriate-sized particles at a range associated with the larval volume.

$$\frac{dQ}{dt} \sim \frac{L^3U}{L} \sim L^{7/3} \sim w^{7/9} \tag{11.0}$$

This case is equivalent to Case No. 1.

Case No. 5

The larva's food intake is not related to his swimming ability but only to his volume capacity.

$$\frac{dQ}{dt} \sim L^3 \sim w \tag{12.0}$$

$$\frac{dw}{dt} \sim w \tag{12.1}$$

$$\frac{dL}{dt} \sim L \tag{12.2}$$

$$T = C_1 \log L + C \tag{12.3}$$

FIG. 1 SARDINE

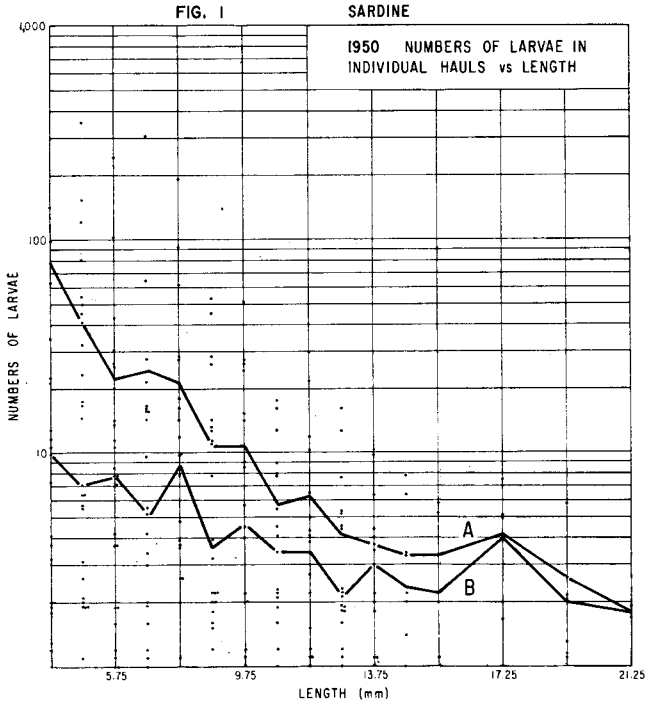


FIG. 2 SARDINE

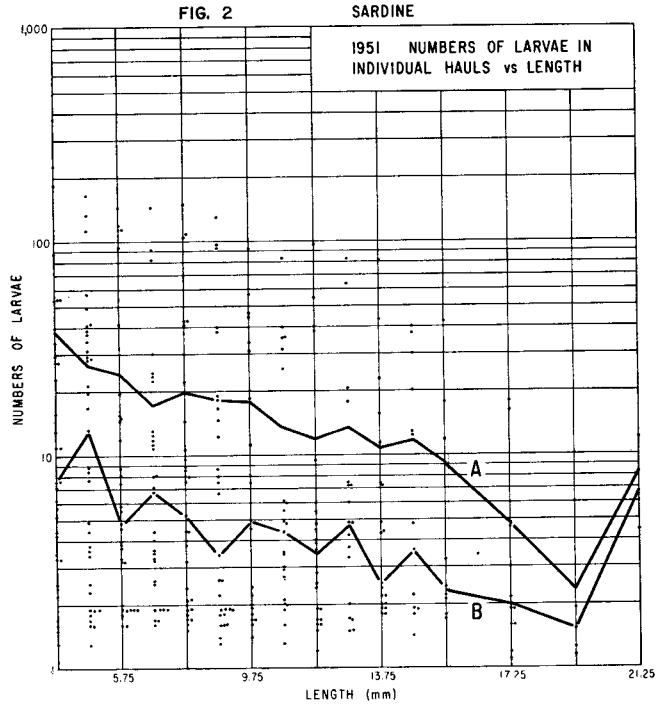


FIG. 3 SARDINE

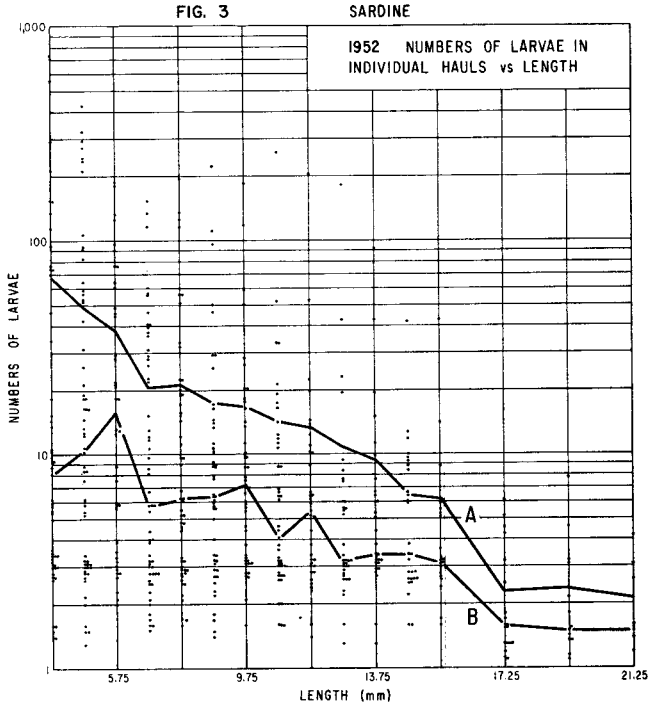


FIG. 4 SARDINE

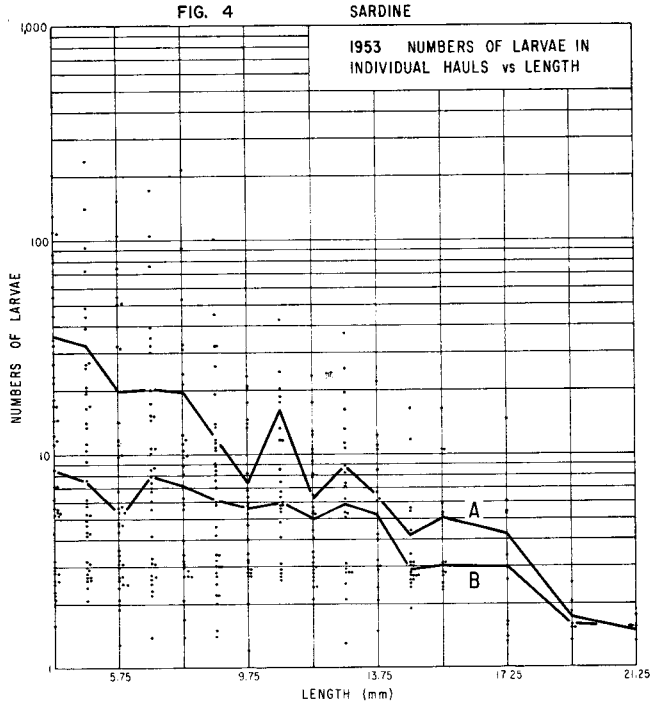


FIG. 5 SARDINE

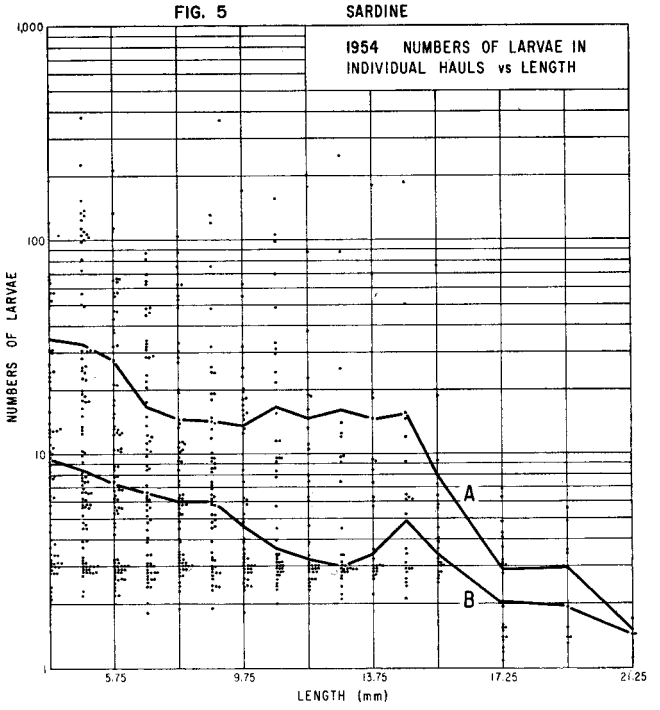


FIG. 6 SARDINE

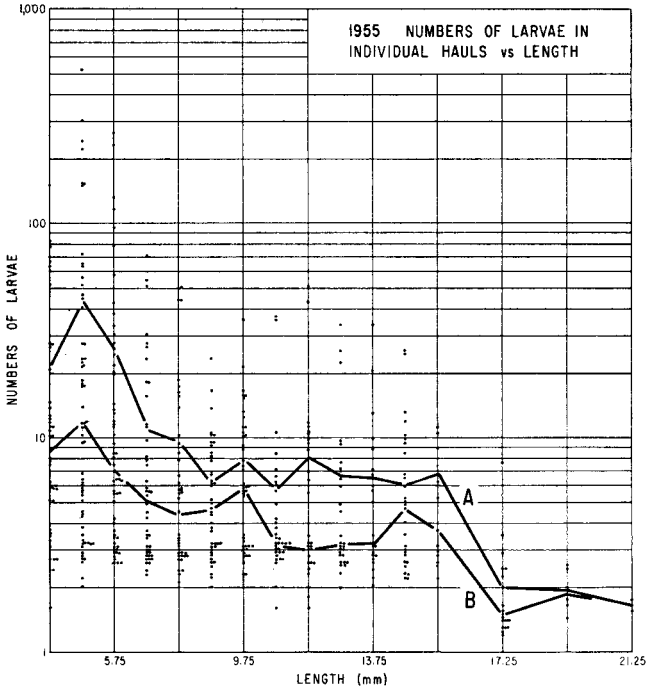


FIG. 7 SARDINE

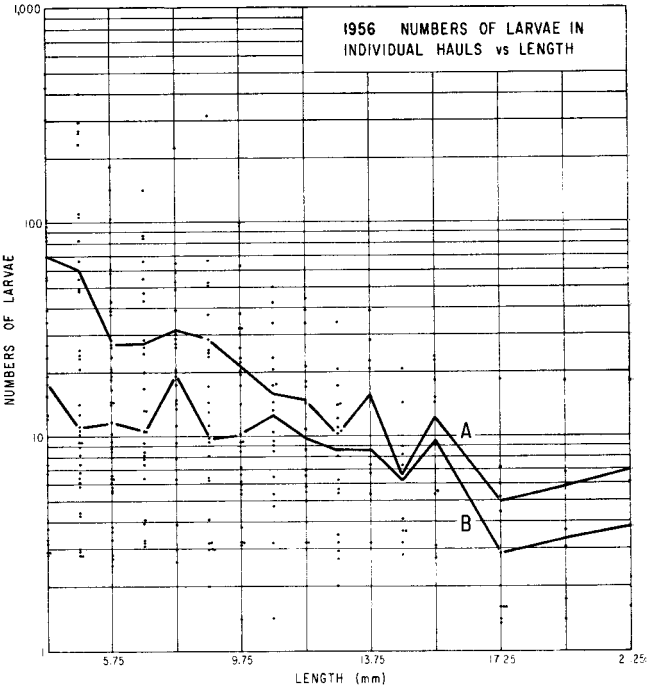


FIG. 8 SARDINE

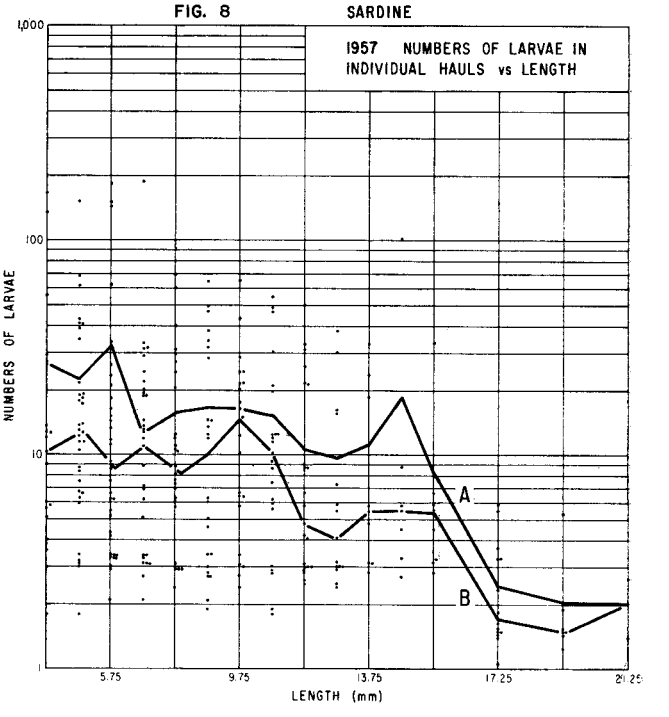


FIG. 9 SARDINES vs ANCHOVIES 1950

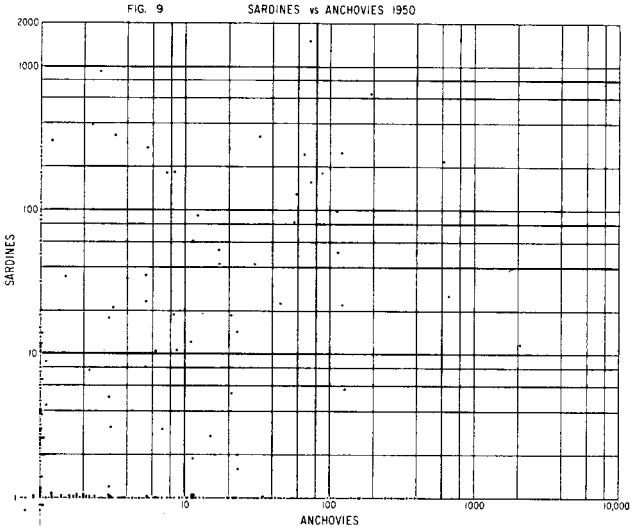


FIG. 10 SARDINE vs ANCHOVY 1952

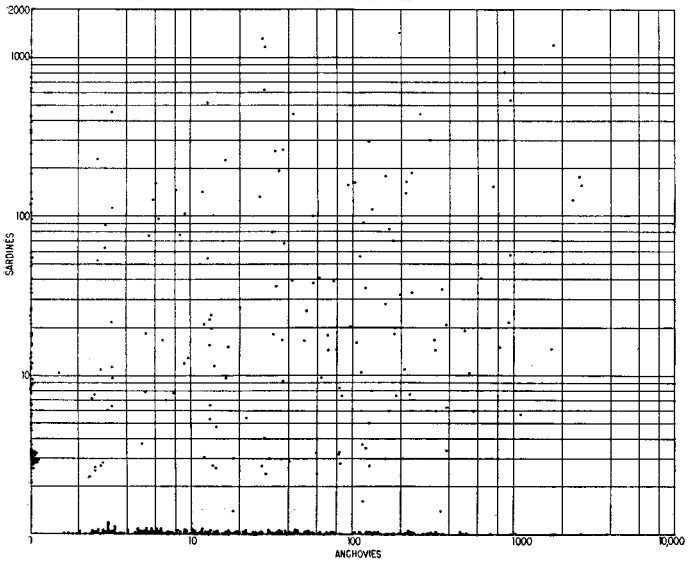


FIG. 11 SARDINES vs ANCHOVIES 1955

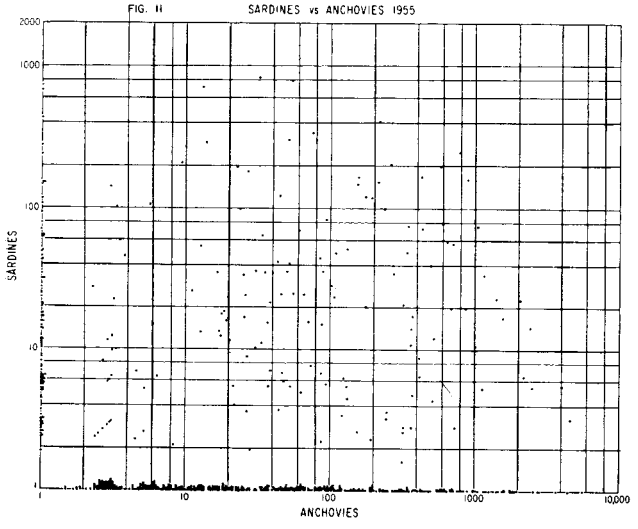


FIG. 12 SARDINE vs ANCHOVY 1957

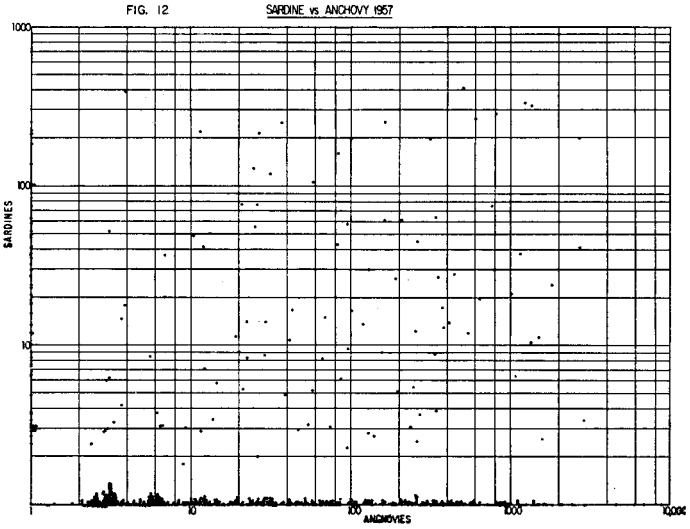


FIG. 13

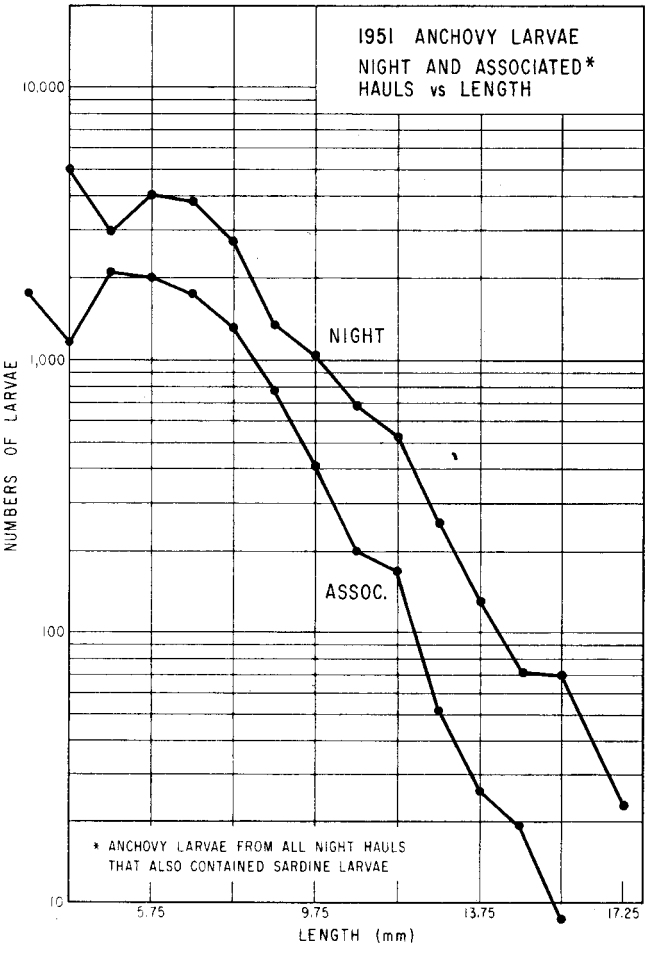


FIG. 14

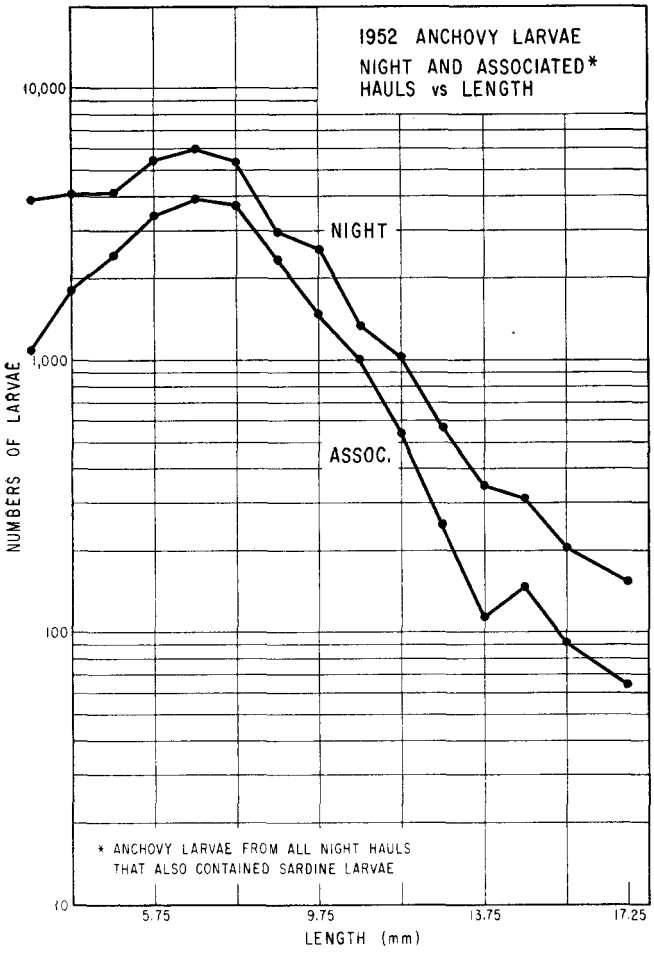

1952 ANCHOVY LARVAE
NIGHT AND ASSOCIATED*
HAULS vs LENGTH
NIGHT
ASSOC.
* ANCHOVY LARVAE FROM ALL NIGHT HAULS
THAT ALSO CONTAINED SARDINE LARVAE
NUMBERS OF LARVAE
10,000
1,000
100
10
5.75
9.75
13.75
17.25
LENGTH (mm)

FIG. 15

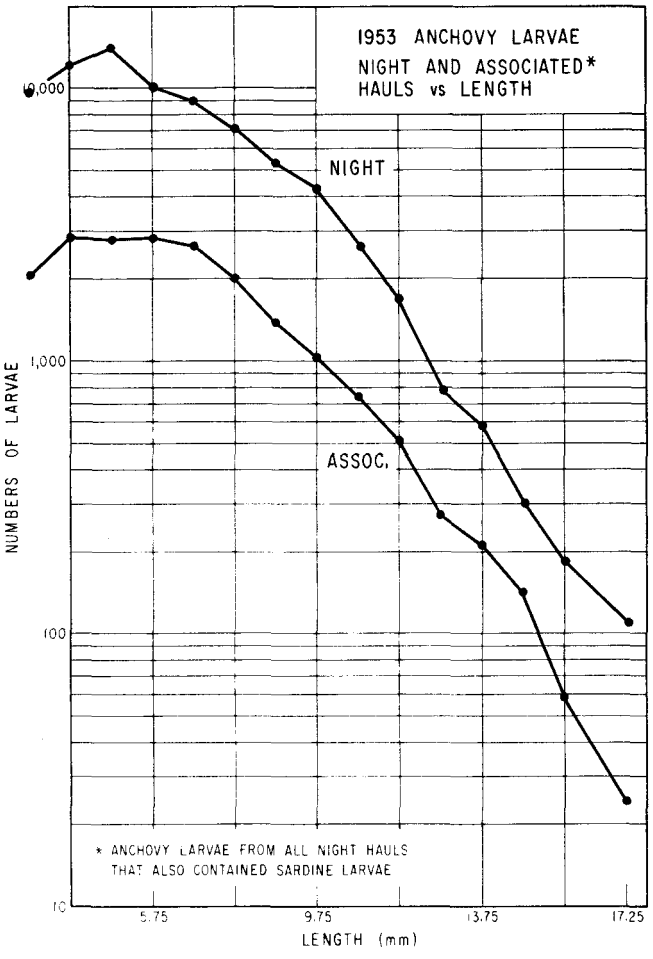

1953 ANCHOVY LARVAE
NIGHT AND ASSOCIATED*
HAULS vs LENGTH
NIGHT
ASSOC.
* ANCHOVY LARVAE FROM ALL NIGHT HAULS
THAT ALSO CONTAINED SARDINE LARVAE
NUMBERS OF LARVAE
10,000
1,000
100
10
5.75
9.75
13.75
17.25
LENGTH (mm)

FIG. 16

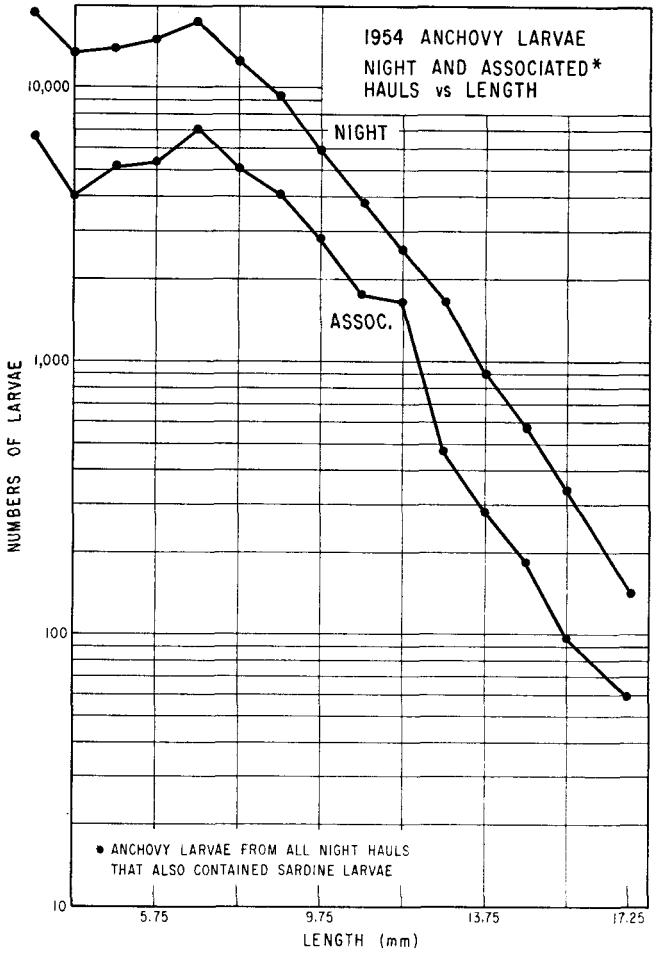

1954 ANCHOVY LARVAE
NIGHT AND ASSOCIATED*
HAULS vs LENGTH
NIGHT
ASSOC.
NUMBERS OF LARVAE
10,000
1,000
100
10
5.75
9.75
13.75
17.25
LENGTH (mm)
* ANCHOVY LARVAE FROM ALL NIGHT HAULS
THAT ALSO CONTAINED SARDINE LARVAE

FIG. 17

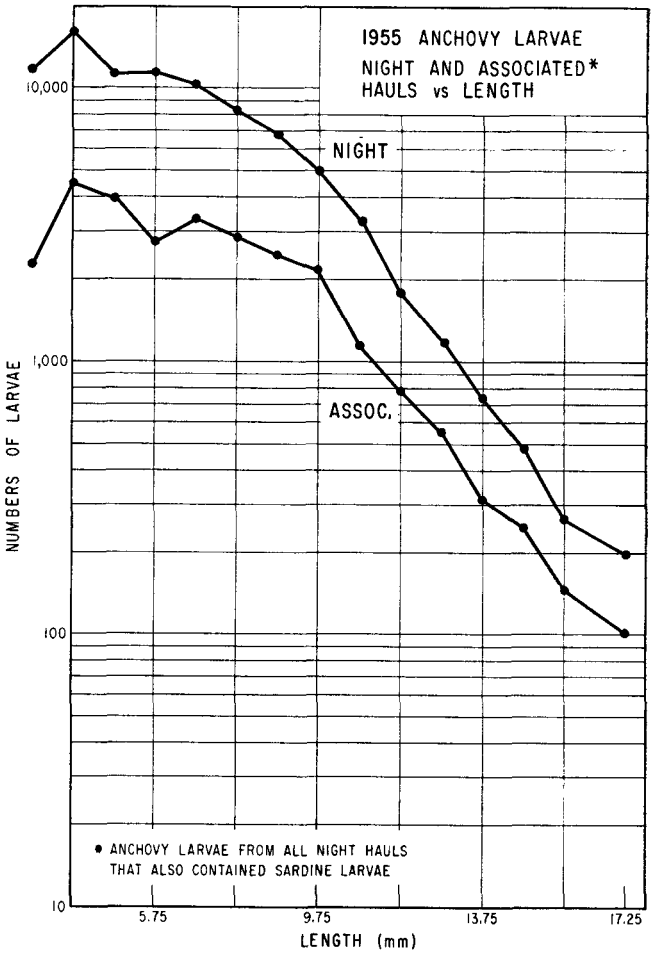

1955 ANCHOVY LARVAE
NIGHT AND ASSOCIATED*
HAULS vs LENGTH
NIGHT
ASSOC.
NUMBERS OF LARVAE
10,000
1,000
100
10
5.75
9.75
13.75
17.25
LENGTH (mm)
* ANCHOVY LARVAE FROM ALL NIGHT HAULS
THAT ALSO CONTAINED SARDINE LARVAE

FIG. 18

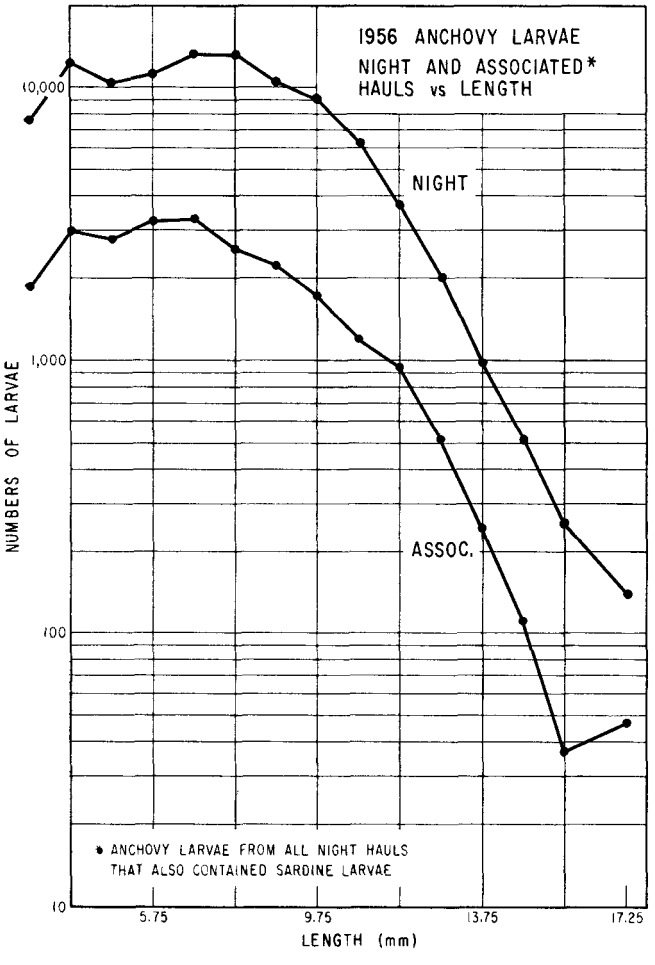

1956 ANCHOVY LARVAE
NIGHT AND ASSOCIATED*
HAULS vs LENGTH
NIGHT
ASSOC.
10,000
1,000
100
10
NUMBERS OF LARVAE
5.75
9.75
13.75
17.25
LENGTH (mm)
* ANCHOVY LARVAE FROM ALL NIGHT HAULS
THAT ALSO CONTAINED SARDINE LARVAE

FIG. 19

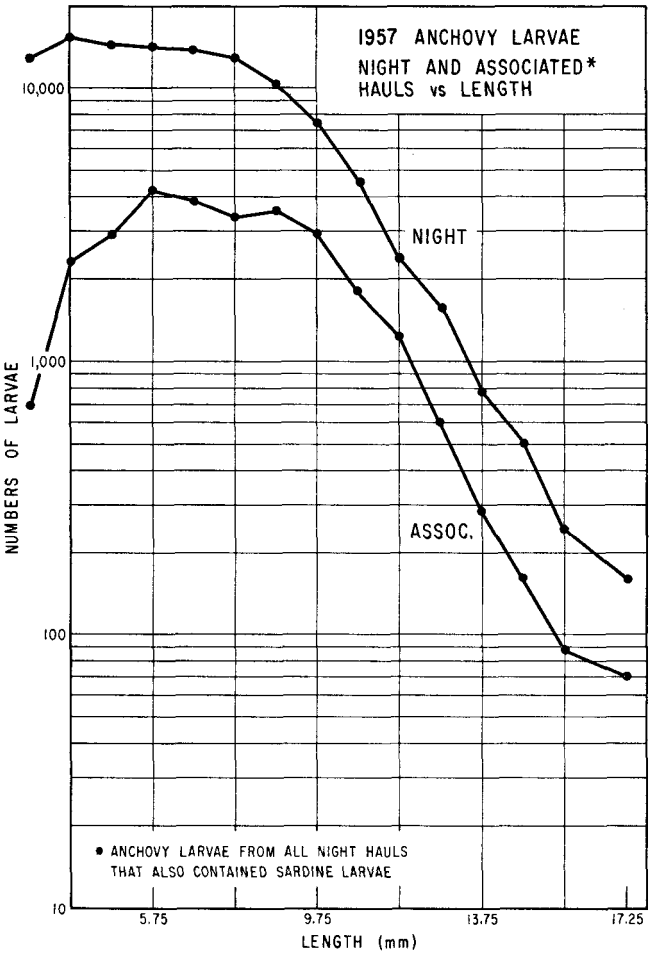

1957 ANCHOVY LARVAE
NIGHT AND ASSOCIATED*
HAULS vs LENGTH
NIGHT
ASSOC.
10,000
1,000
100
10
NUMBERS OF LARVAE
5.75
9.75
13.75
17.25
LENGTH (mm)
* ANCHOVY LARVAE FROM ALL NIGHT HAULS
THAT ALSO CONTAINED SARDINE LARVAE

FIG. 20

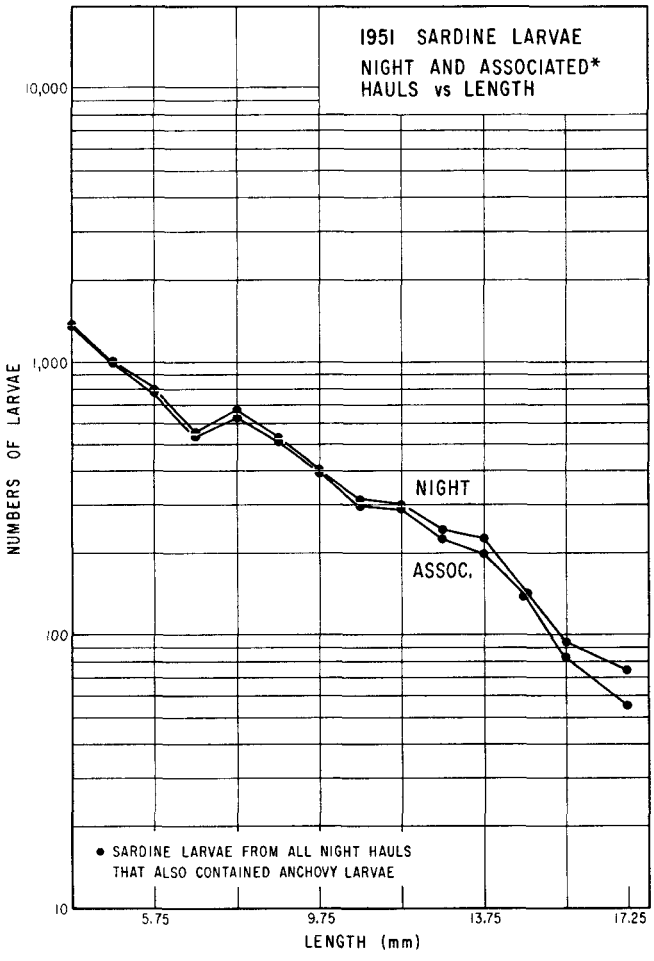

1951 SARDINE LARVAE
NIGHT AND ASSOCIATED*
HAULS vs LENGTH
NUMBERS OF LARVAE
10,000
1,000
100
10
NIGHT
ASSOC.
• SARDINE LARVAE FROM ALL NIGHT HAULS
THAT ALSO CONTAINED ANCHOVY LARVAE
5.75
9.75
13.75
17.25
LENGTH (mm)

FIG. 21

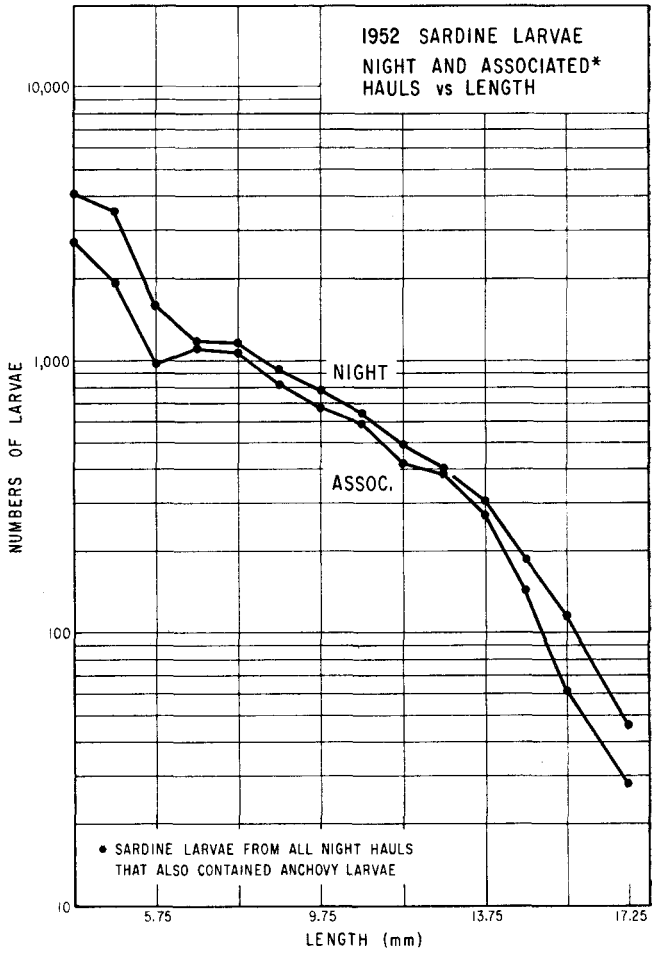

1952 SARDINE LARVAE
NIGHT AND ASSOCIATED*
HAULS vs LENGTH
NUMBERS OF LARVAE
10,000
1,000
100
10
NIGHT
ASSOC.
• SARDINE LARVAE FROM ALL NIGHT HAULS
THAT ALSO CONTAINED ANCHOVY LARVAE
5.75
9.75
13.75
17.25
LENGTH (mm)

FIG. 22

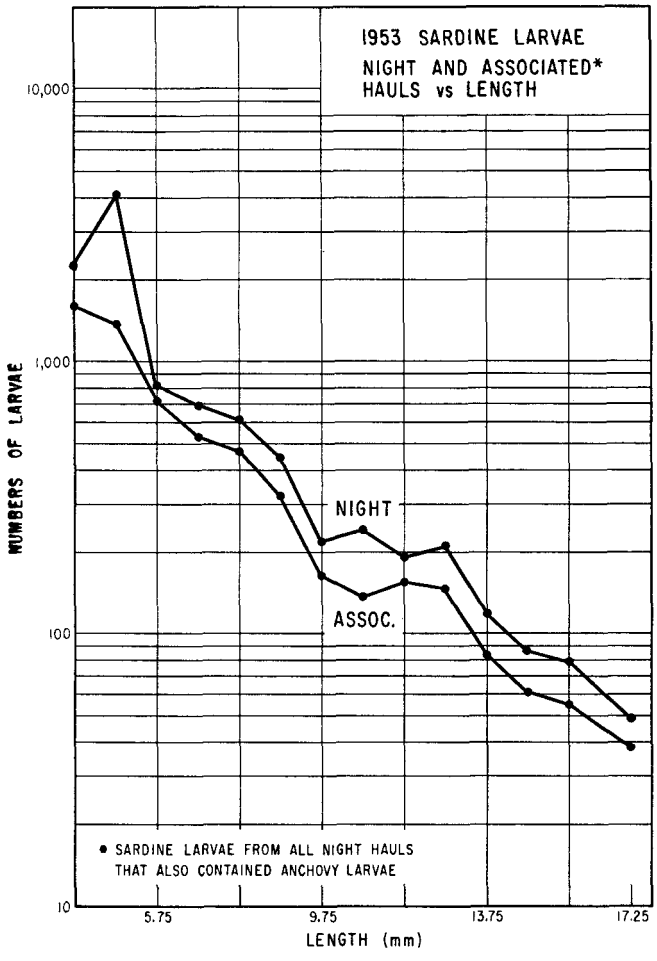

1953 SARDINE LARVAE
NIGHT AND ASSOCIATED*
HAULS vs LENGTH
10,000
1,000
100
10
NUMBERS OF LARVAE
NIGHT
ASSOC.
• SARDINE LARVAE FROM ALL NIGHT HAULS
THAT ALSO CONTAINED ANCHOVY LARVAE
5.75
9.75
13.75
17.25
LENGTH (mm)

FIG. 23

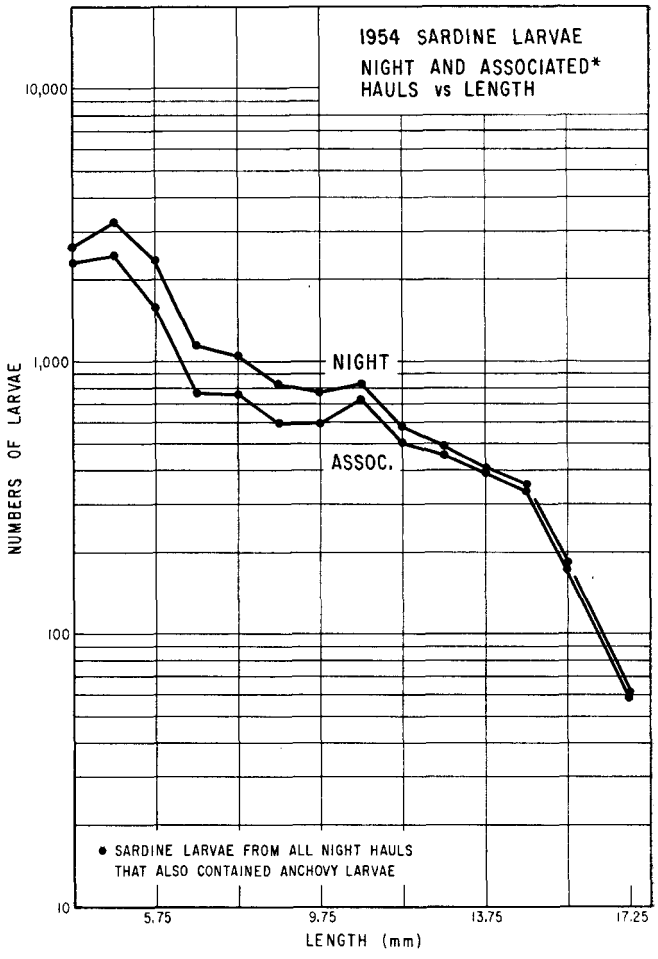

1954 SARDINE LARVAE
NIGHT AND ASSOCIATED*
HAULS vs LENGTH
10,000
1,000
100
10
NUMBERS OF LARVAE
NIGHT
ASSOC.
• SARDINE LARVAE FROM ALL NIGHT HAULS
THAT ALSO CONTAINED ANCHOVY LARVAE
5.75
9.75
13.75
17.25
LENGTH (mm)

FIG. 24

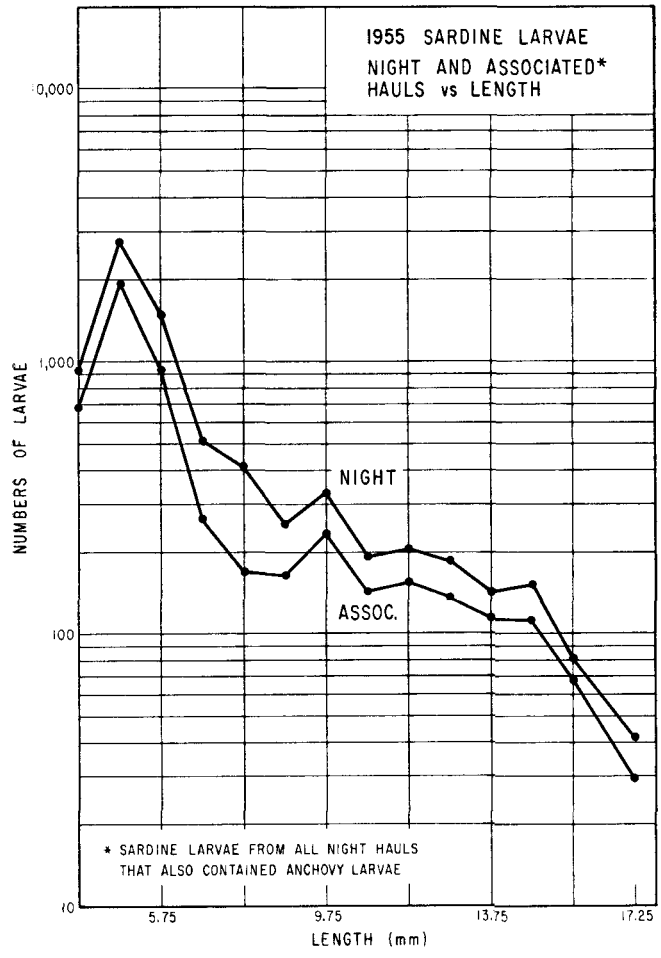

1955 SARDINE LARVAE
NIGHT AND ASSOCIATED*
HAULS vs LENGTH
NUMBERS OF LARVAE
10,000
1,000
100
10
NIGHT
ASSOC.
* SARDINE LARVAE FROM ALL NIGHT HAULS
THAT ALSO CONTAINED ANCHOVY LARVAE
5.75
9.75
13.75
17.25
LENGTH (mm)

FIG. 25

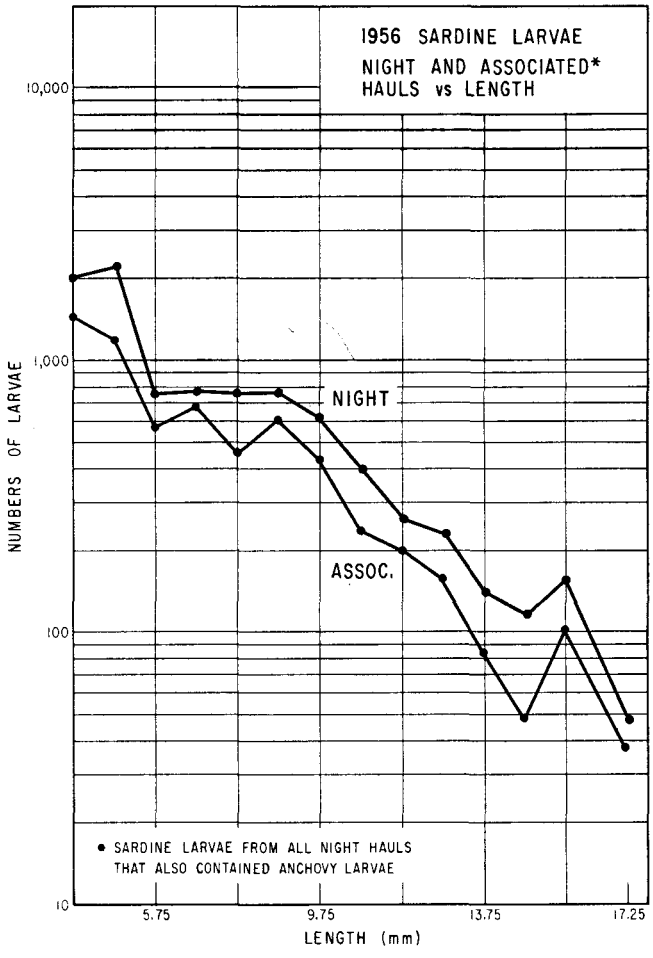
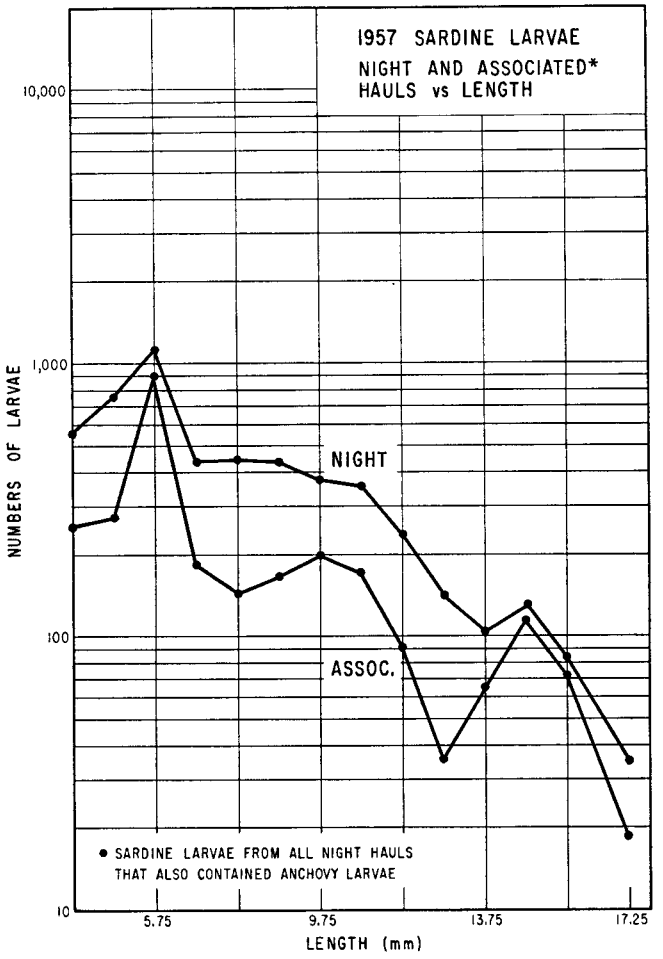

1956 SARDINE LARVAE
NIGHT AND ASSOCIATED*
HAULS vs LENGTH
NUMBERS OF LARVAE
10,000
1,000
100
10
NIGHT
ASSOC.
* SARDINE LARVAE FROM ALL NIGHT HAULS
THAT ALSO CONTAINED ANCHOVY LARVAE
5.75
9.75
13.75
17.25
LENGTH (mm)

FIG. 26


1957 SARDINE LARVAE
NIGHT AND ASSOCIATED*
HAULS vs LENGTH
NUMBERS OF LARVAE
10,000
1,000
100
10
NIGHT
ASSOC.
• SARDINE LARVAE FROM ALL NIGHT HAULS
THAT ALSO CONTAINED ANCHOVY LARVAE
5.75
9.75
13.75
17.25
LENGTH (mm)

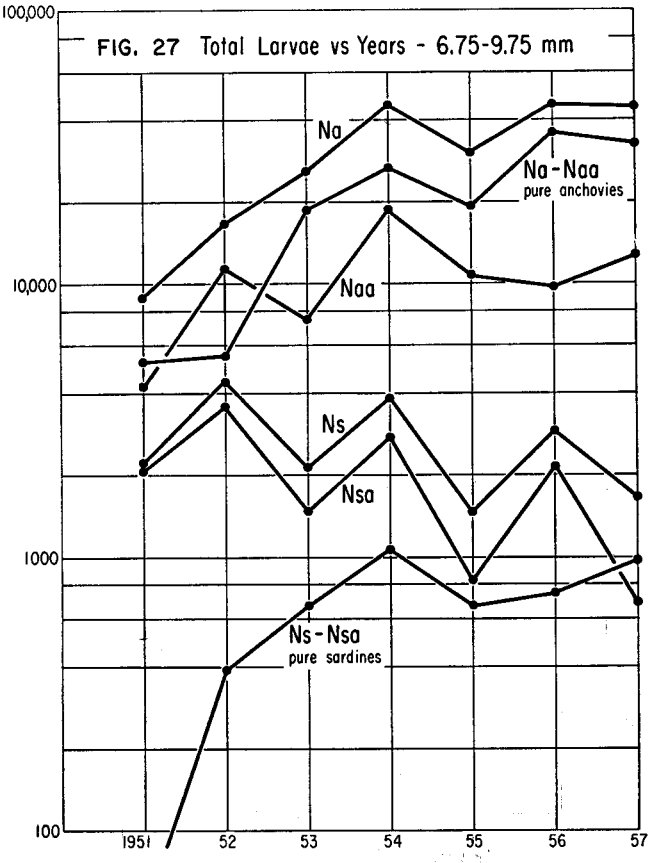


FIG. 27 Total Larvae vs Years - 6.75-9.75 mm
100,000
10,000
1000
100
Na
Na-Naa
pure anchovies
Naa
Ns
Nsa
Ns-Nsa
pure sardines
1951
52
53
54
55
56
57

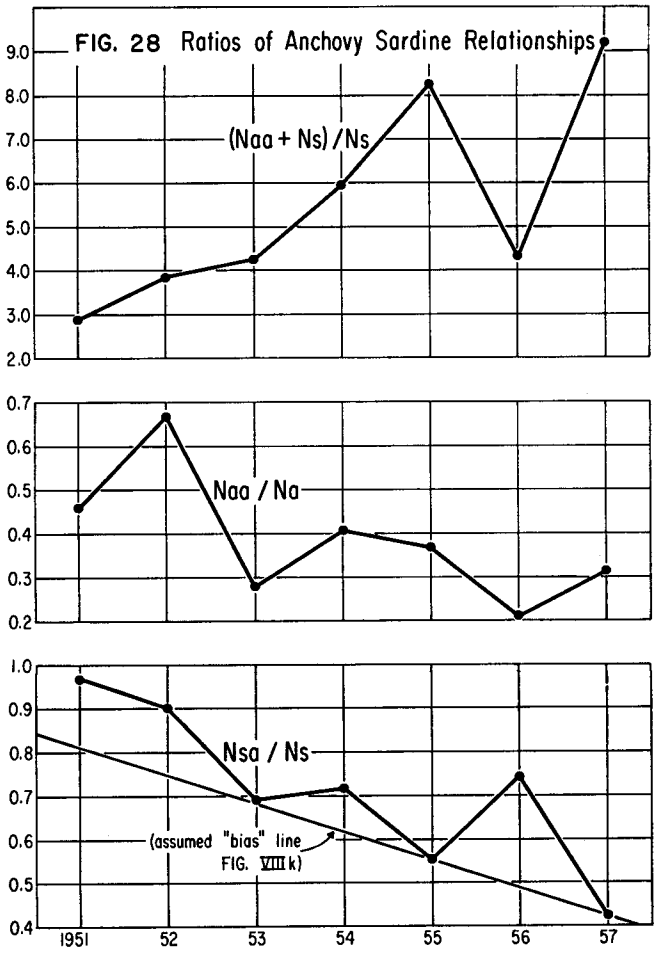


FIG. 28 Ratios of Anchovy Sardine Relationships
(Naa + Ns) / Ns
Naa / Na
Nsa / Ns
(assumed "bias" line FIG. VIII k)
1951
52
53
54
55
56
57

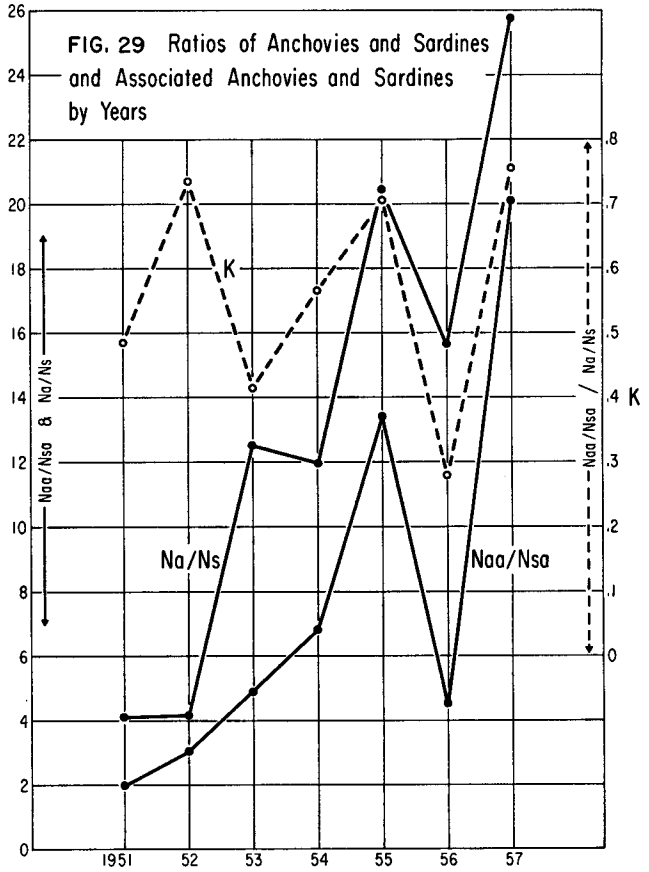


FIG. 29 Ratios of Anchovies and Sardines and Associated Anchovies and Sardines by Years
K
Na/Ns
Naa/Nsa
Naa/Nsa & Na/Ns
Naa/Nsa / Na/Ns
1951
52
53
54
55
56
57

FIG. 30

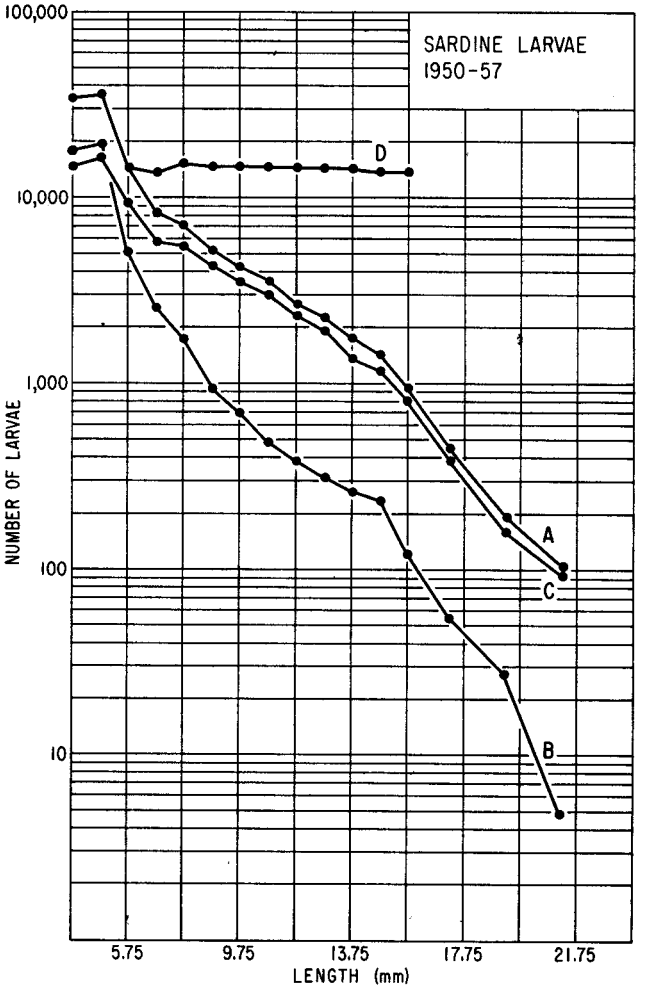

SARDINE LARVAE
1950-57
100,000
10,000
1,000
100
10
NUMBER OF LARVAE
D
A
C
B
5.75
9.75
13.75
17.75
21.75
LENGTH (mm)

FIG. 31

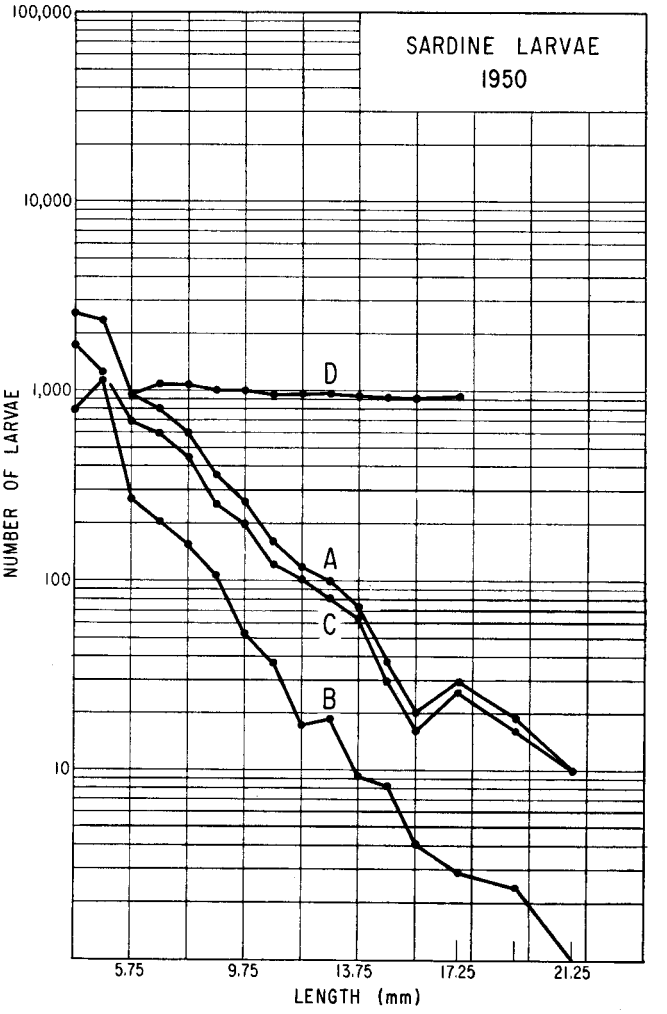

SARDINE LARVAE
1950
100,000
10,000
1,000
100
10
NUMBER OF LARVAE
D
A
C
B
5.75
9.75
13.75
17.25
21.25
LENGTH (mm)

FIG. 32

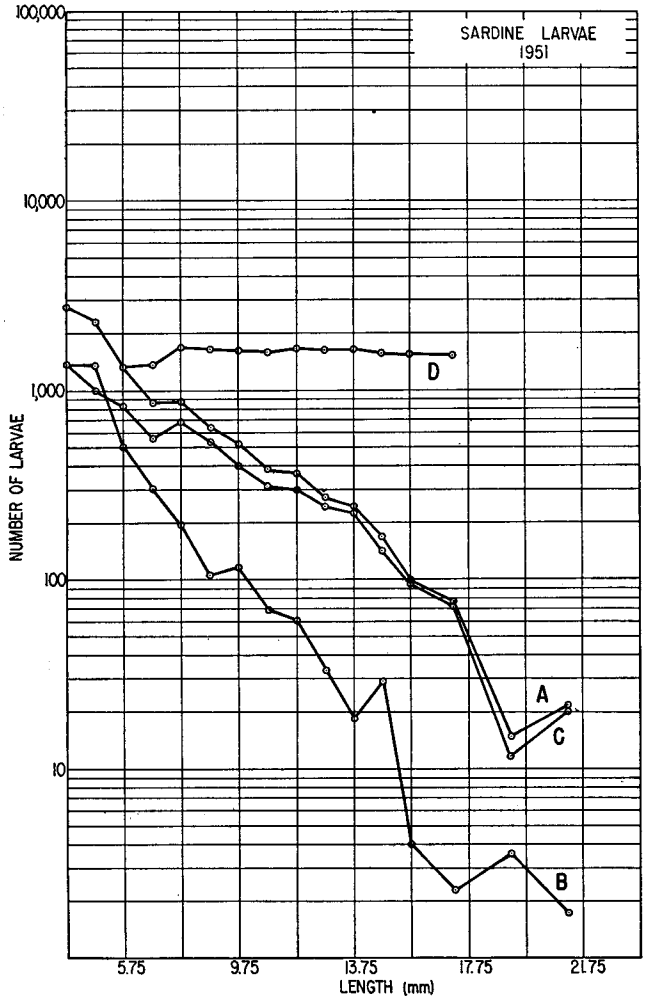

SARDINE LARVAE
1951
100,000
10,000
1,000
100
10
NUMBER OF LARVAE
D
A
C
B
5.75
9.75
13.75
17.75
21.75
LENGTH (mm)

FIG. 33

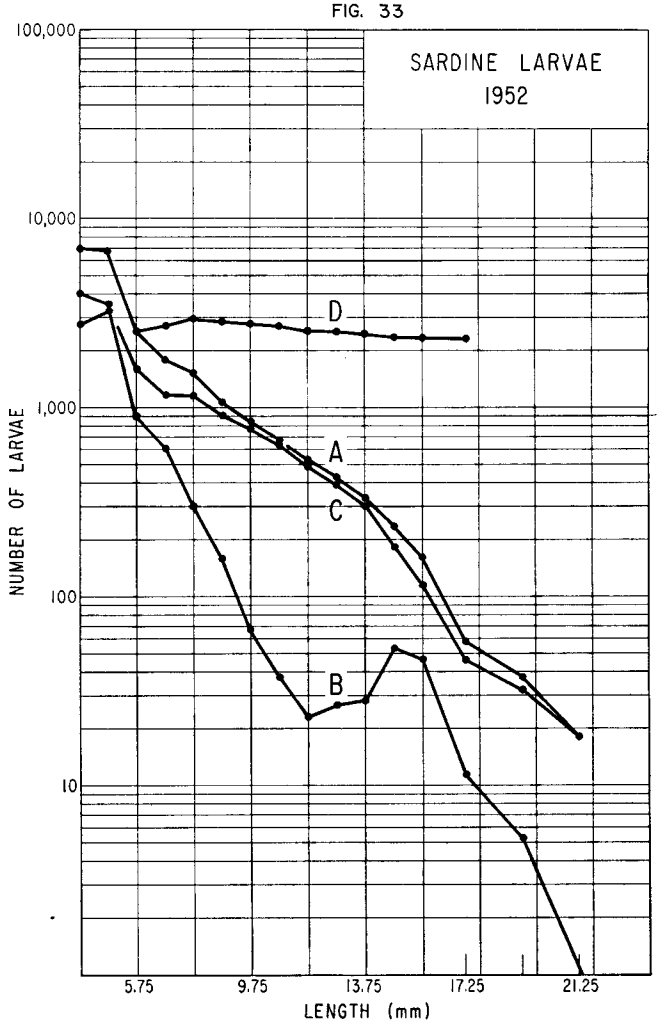

SARDINE LARVAE
1952
100,000
10,000
1,000
100
10
NUMBER OF LARVAE
D
A
C
B
5.75
9.75
13.75
17.25
21.25
LENGTH (mm)

FIG. 34

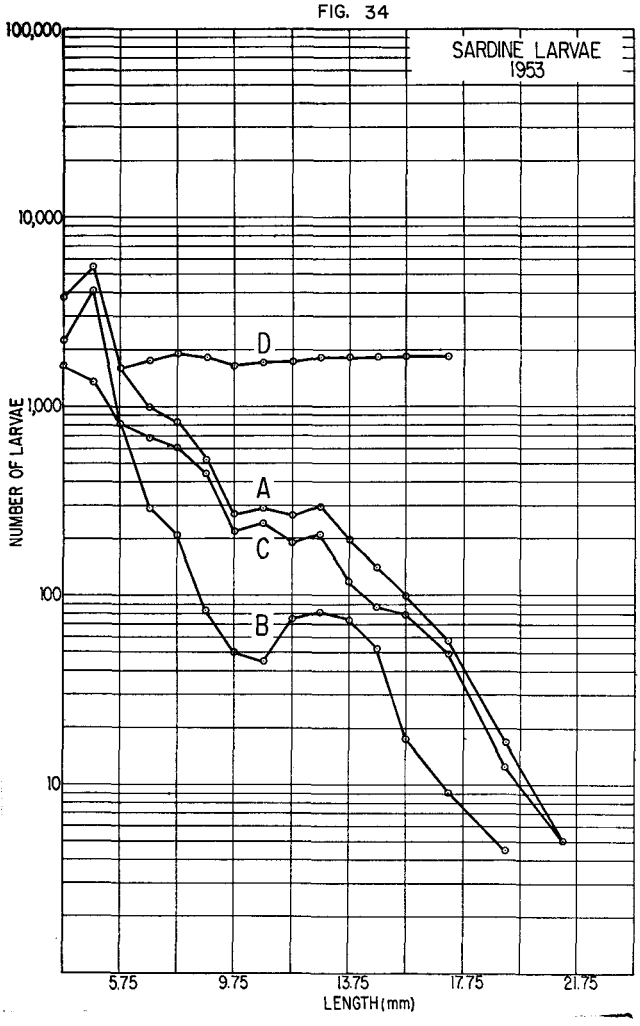

SARDINE LARVAE
1953
100,000
10,000
1,000
100
10
NUMBER OF LARVAE
D
A
C
B
5.75
9.75
13.75
17.75
21.75
LENGTH(mm)

FIG. 35

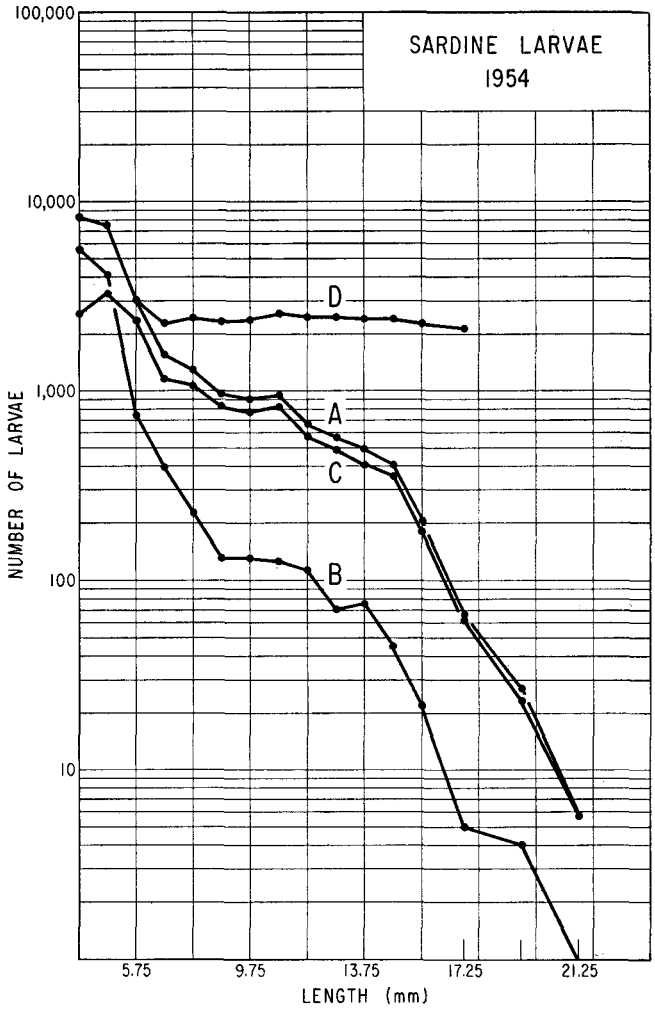

SARDINE LARVAE
1954
100,000
10,000
1,000
100
10
NUMBER OF LARVAE
D
A
C
B
5.75
9.75
13.75
17.25
21.25
LENGTH (mm)

FIG. 36

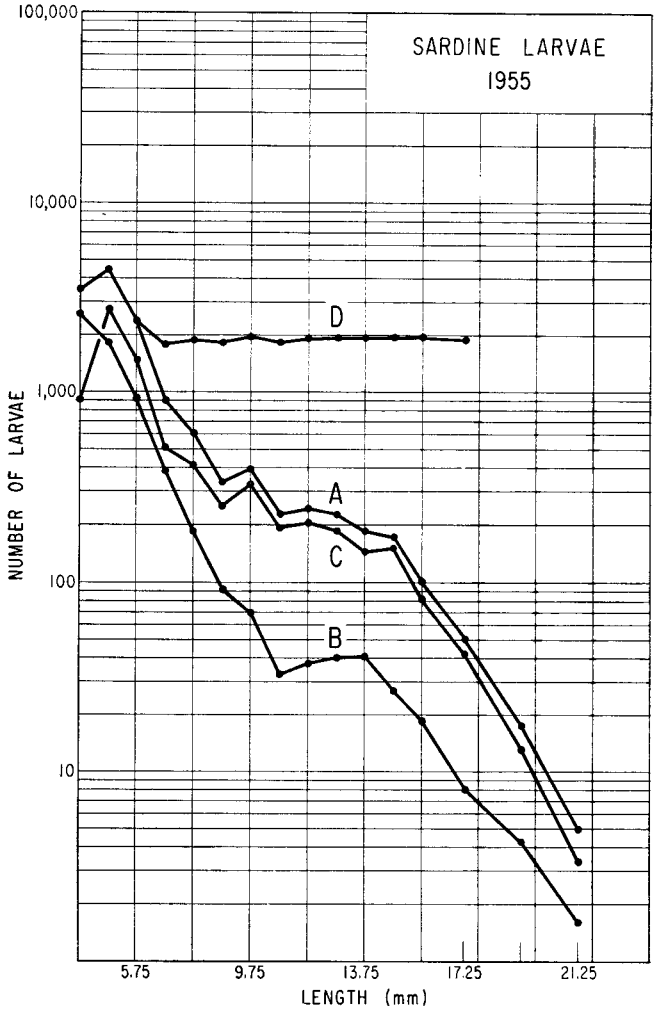

SARDINE LARVAE
1955
100,000
10,000
1,000
100
10
NUMBER OF LARVAE
D
A
C
B
5.75
9.75
13.75
17.25
21.25
LENGTH (mm)

FIG. 37

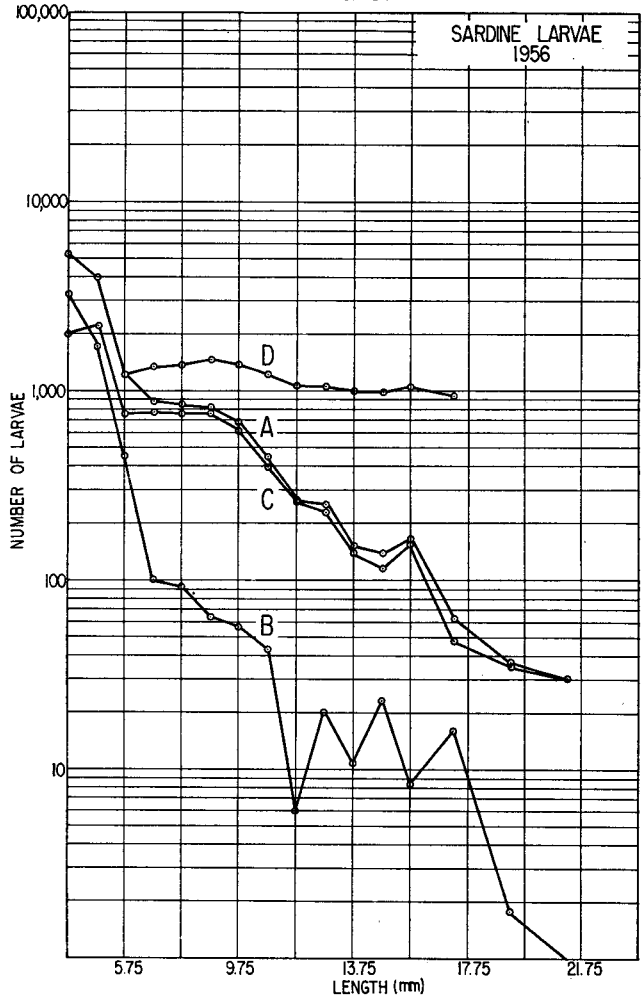

SARDINE LARVAE
1956
100,000
10,000
1,000
100
10
NUMBER OF LARVAE
D
A
C
B
5.75
9.75
13.75
17.75
21.75
LENGTH (mm)

FIG. 38

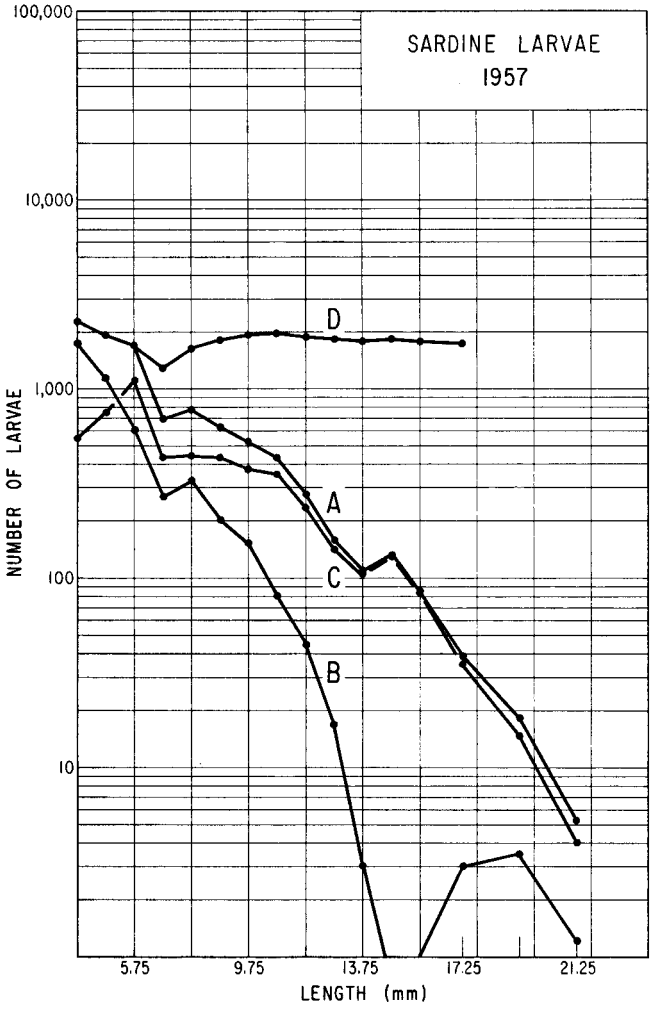

SARDINE LARVAE
1957
100,000
10,000
1,000
100
10
NUMBER OF LARVAE
D
A
C
B
5.75
9.75
13.75
17.25
21.25
LENGTH (mm)

FIG. 39

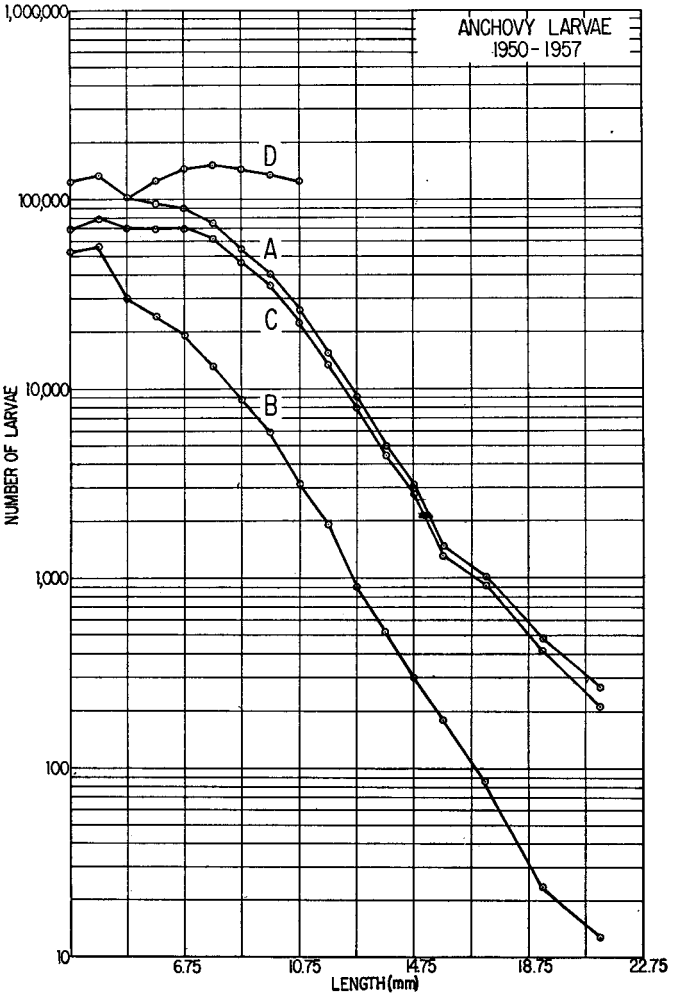

ANCHOVY LARVAE
1950-1957
1,000,000
100,000
10,000
1,000
100
10
NUMBER OF LARVAE
D
A
C
B
6.75
10.75
14.75
18.75
22.75
LENGTH (mm)

FIG. 40

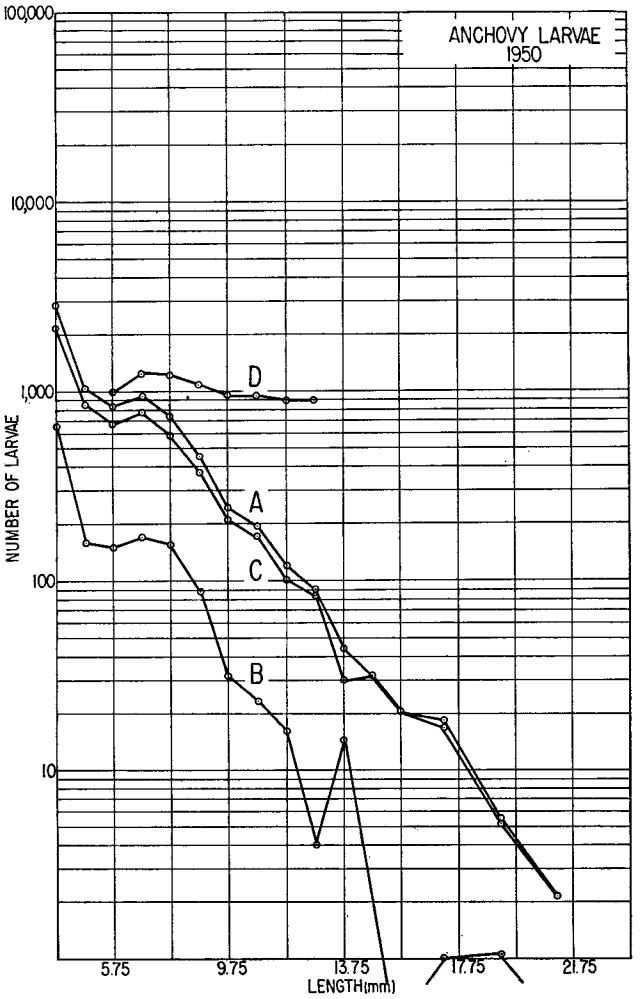

ANCHOVY LARVAE
1950
100,000
10,000
1,000
100
10
NUMBER OF LARVAE
D
A
C
B
5.75
9.75
13.75
17.75
21.75
LENGTH(mm)

FIG. 41

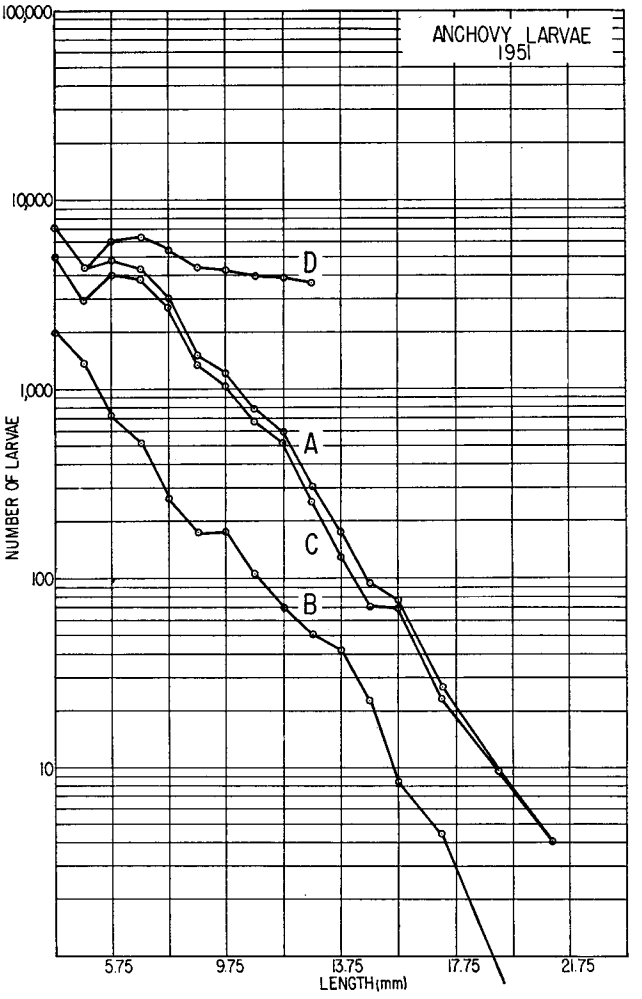

ANCHOVY LARVAE
1951
100,000
10,000
1,000
100
10
NUMBER OF LARVAE
D
A
C
B
5.75
9.75
13.75
17.75
21.75
LENGTH(mm)

FIG. 42

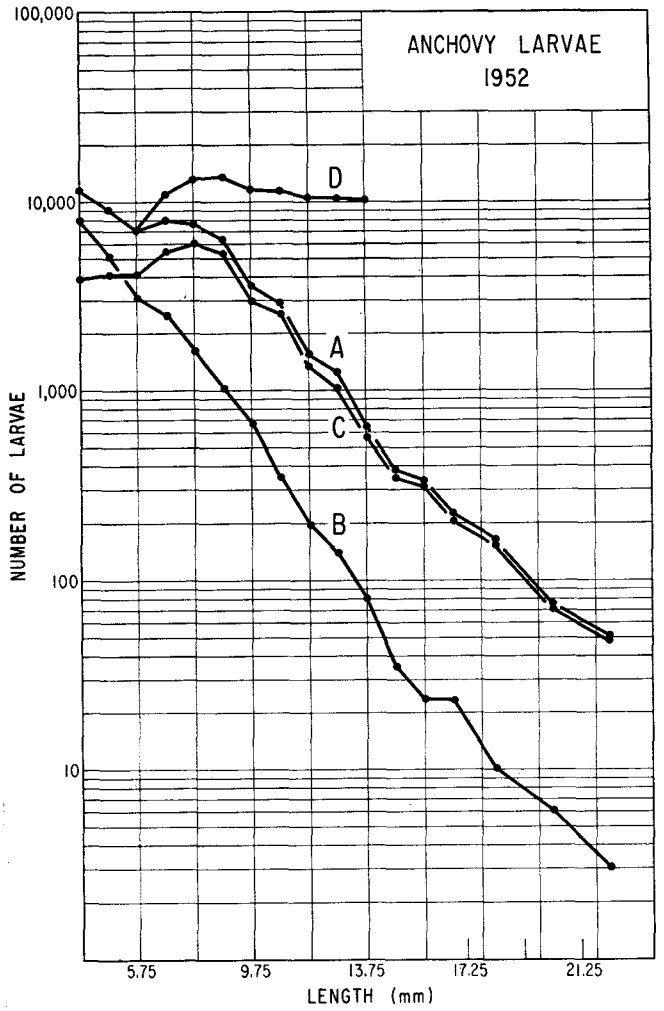

ANCHOVY LARVAE
1952
100,000
10,000
1,000
100
10
NUMBER OF LARVAE
D
A
C
B
5.75
9.75
13.75
17.25
21.25
LENGTH (mm)

FIG. 43

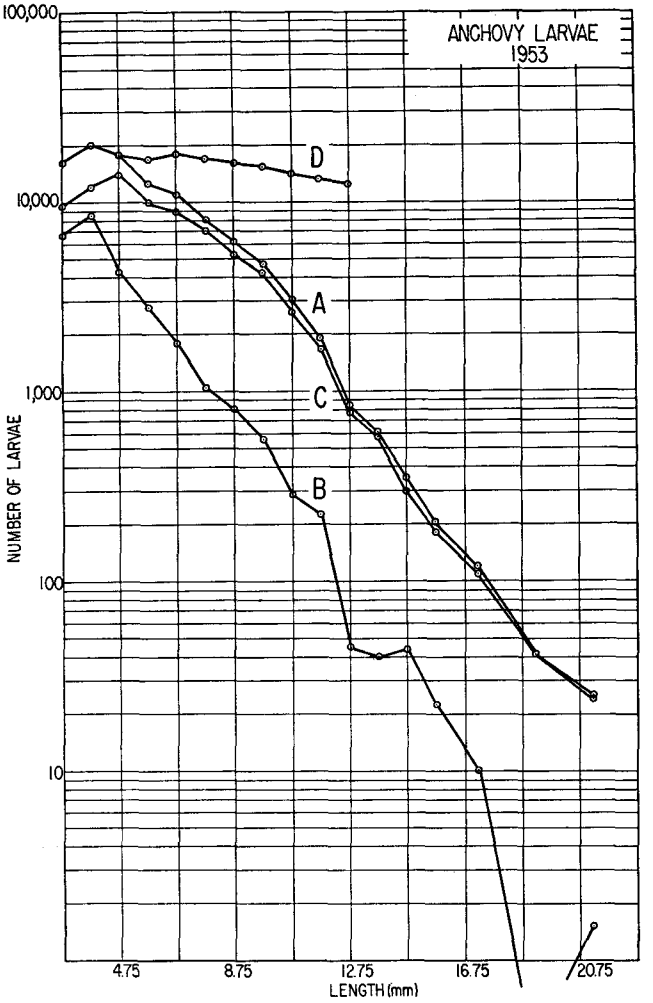

ANCHOVY LARVAE
1953
100,000
10,000
1,000
100
10
NUMBER OF LARVAE
D
A
C
B
4.75
8.75
12.75
16.75
20.75
LENGTH (mm)

FIG. 44

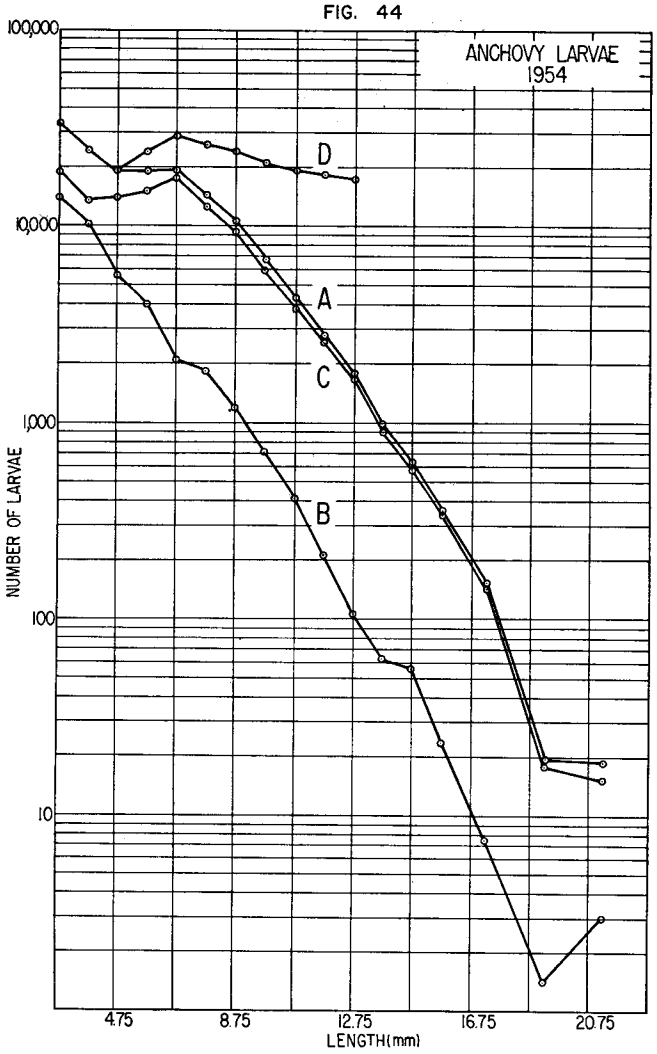

ANCHOVY LARVAE
1954
100,000
10,000
1,000
100
10
NUMBER OF LARVAE
D
A
C
B
4.75
8.75
12.75
16.75
20.75
LENGTH(mm)

FIG. 45

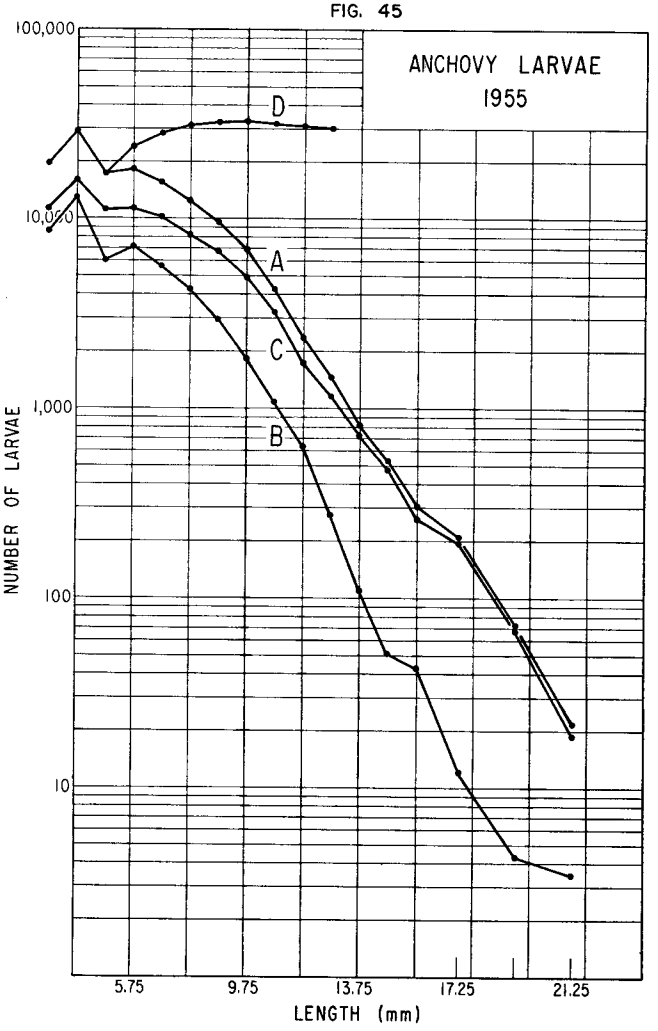

ANCHOVY LARVAE
1955
100,000
10,000
1,000
100
10
NUMBER OF LARVAE
D
A
C
B
5.75
9.75
13.75
17.25
21.25
LENGTH (mm)

FIG. 46

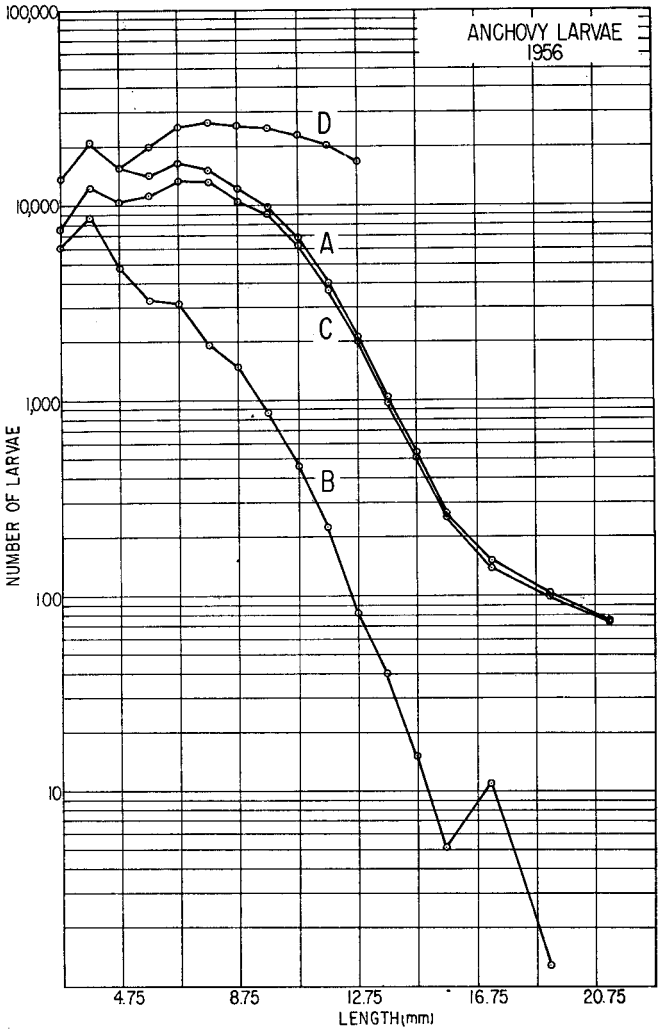

ANCHOVY LARVAE
1956
100,000
10,000
1,000
100
10
NUMBER OF LARVAE
D
A
C
B
4.75
8.75
12.75
16.75
20.75
LENGTH(mm)

FIG. 47

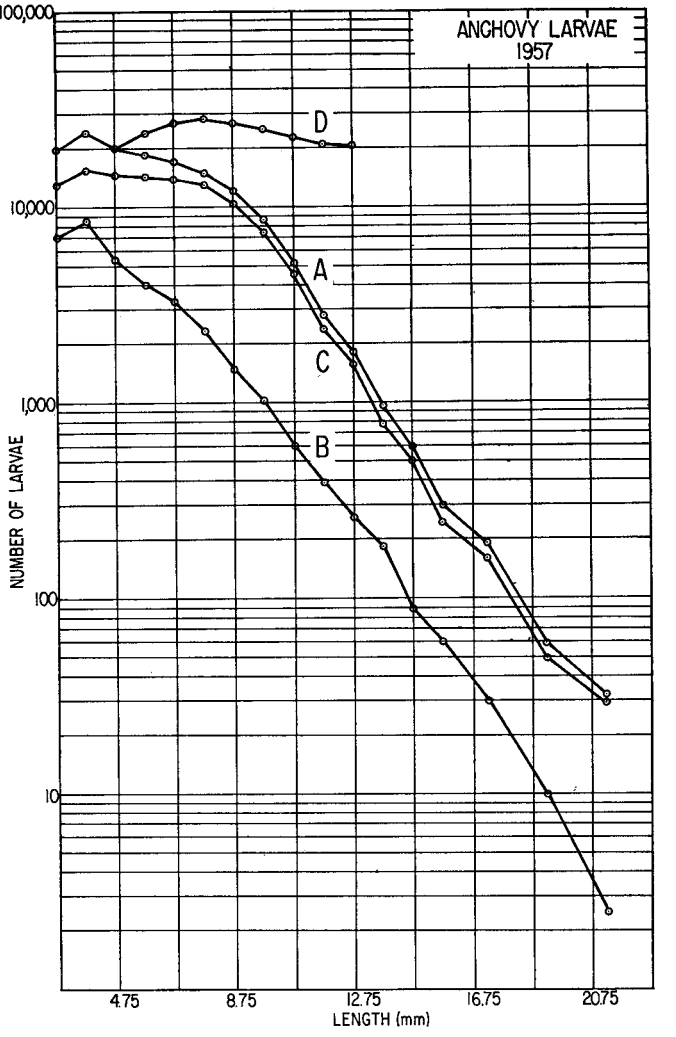

ANCHOVY LARVAE
1957
100,000
10,000
1,000
100
10
NUMBER OF LARVAE
D
A
C
B
4.75
8.75
12.75
16.75
20.75
LENGTH (mm)

FIG. 48

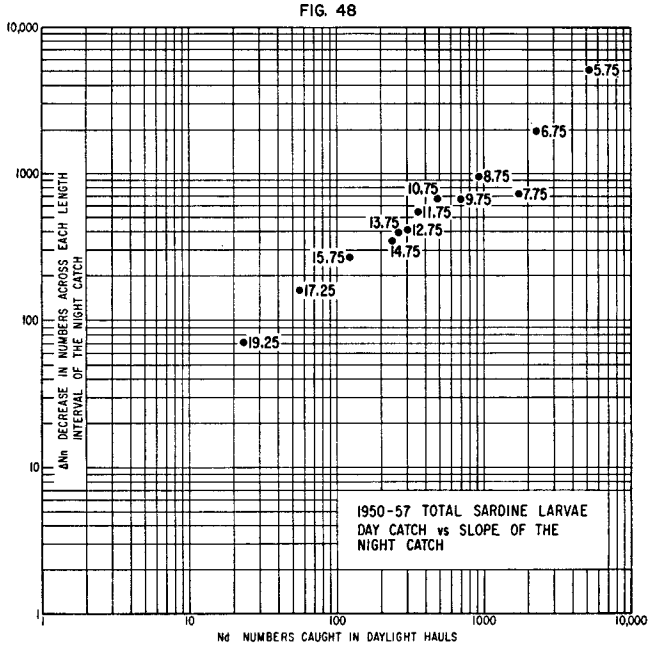


FIG. 49

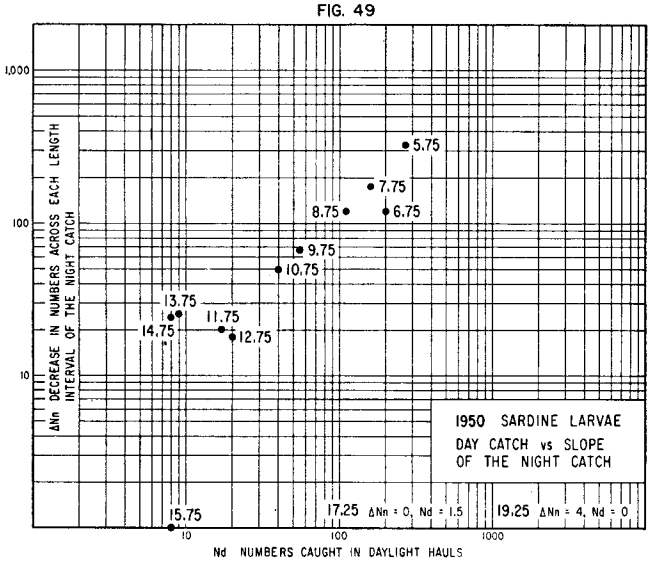


FIG. 50

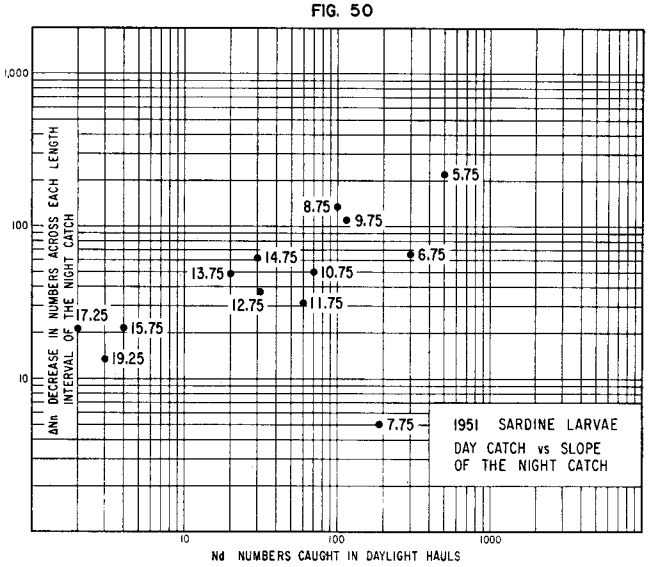


FIG. 51

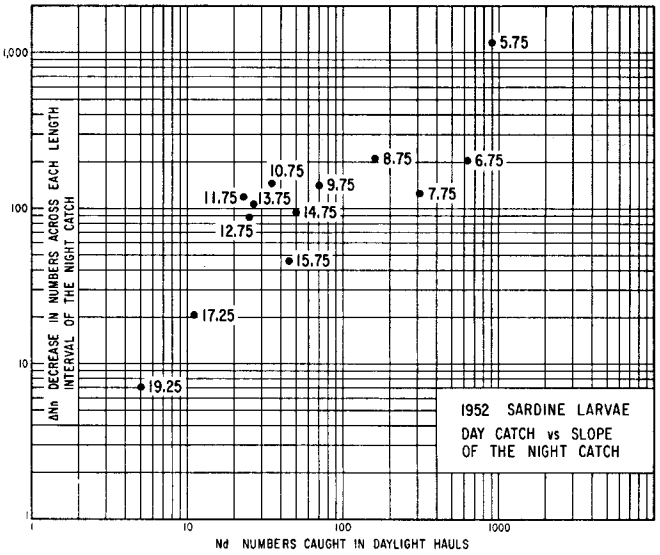


FIG. 52

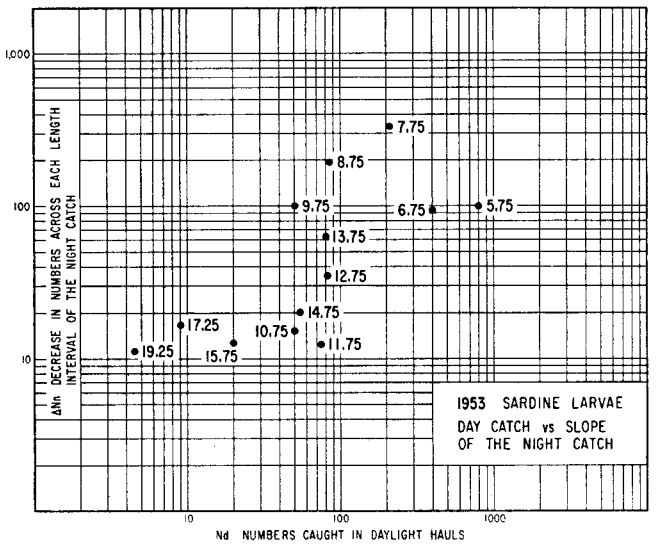


FIG. 53

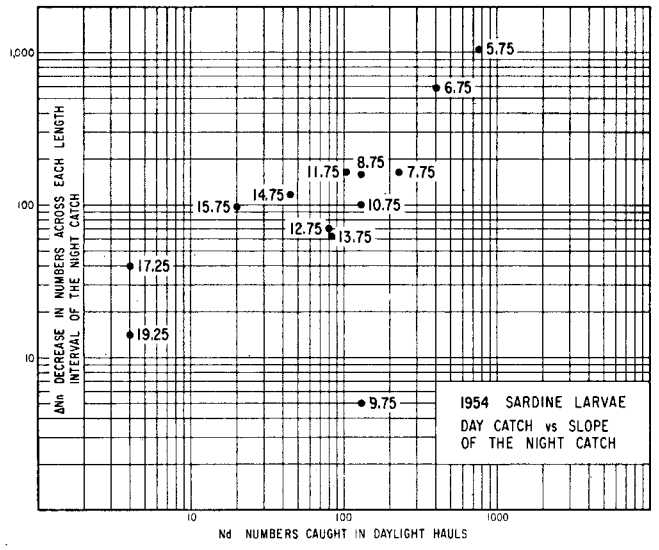


FIG. 54

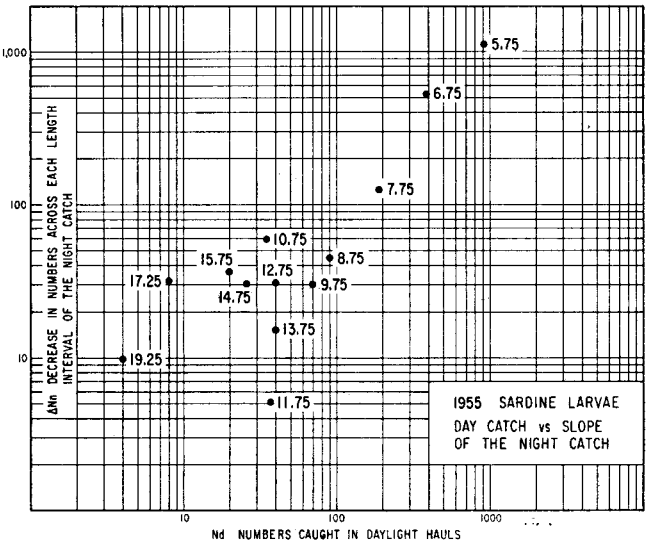


FIG. 55

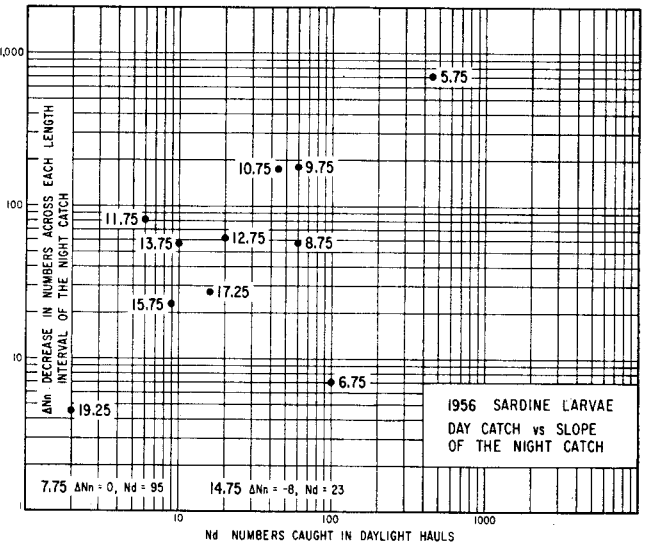
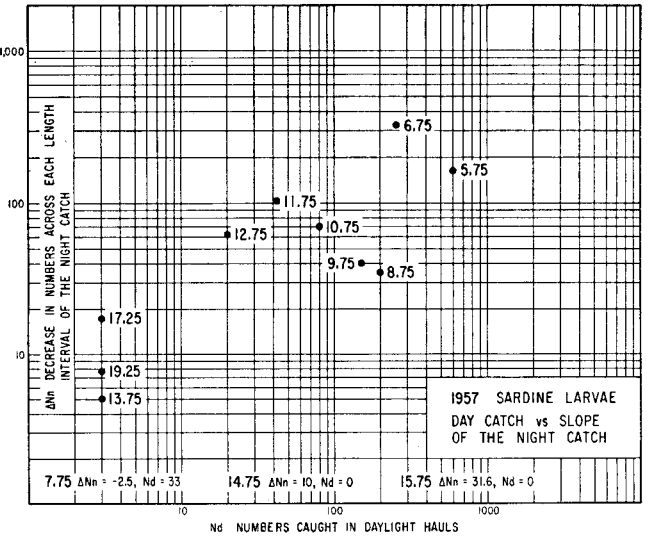


FIG. 56



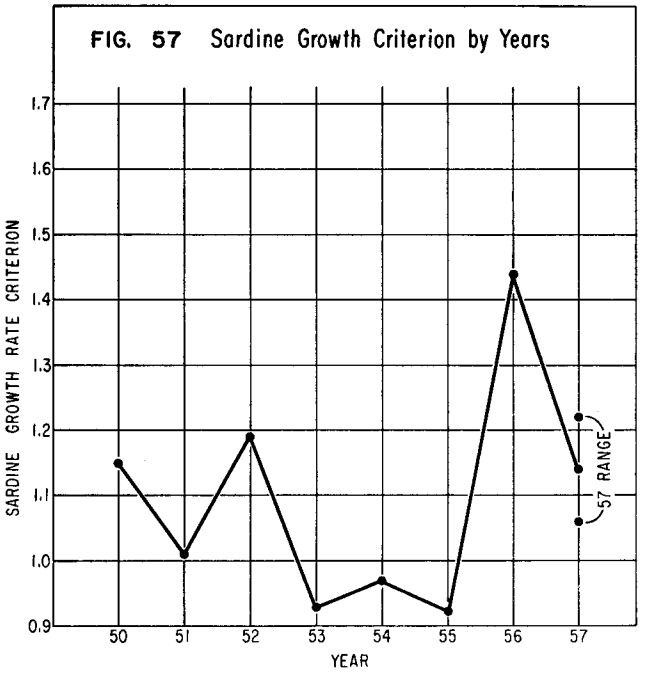


FIG. 57 Sardine Growth Criterion by Years

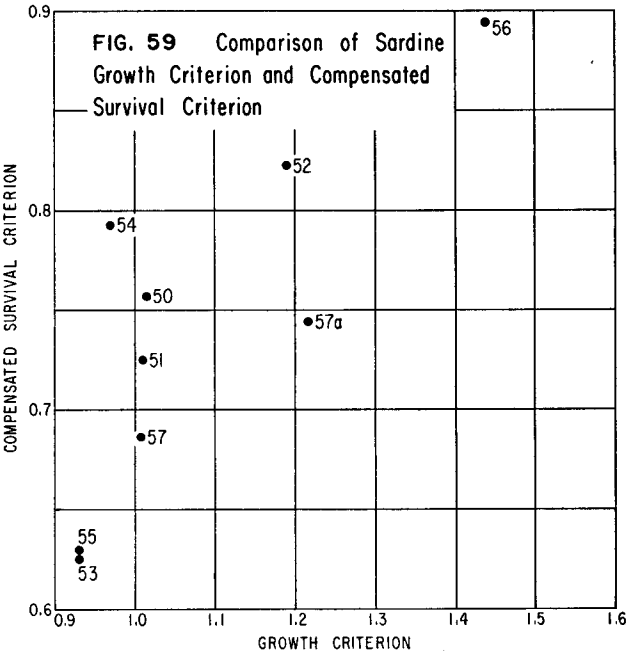


FIG. 59 Comparison of Sardine Growth Criterion and Compensated Survival Criterion

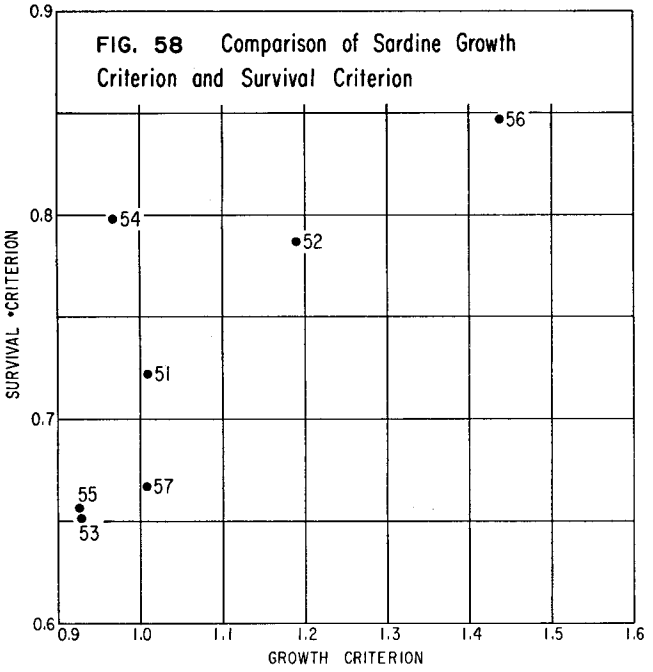


FIG. 58 Comparison of Sardine Growth Criterion and Survival Criterion

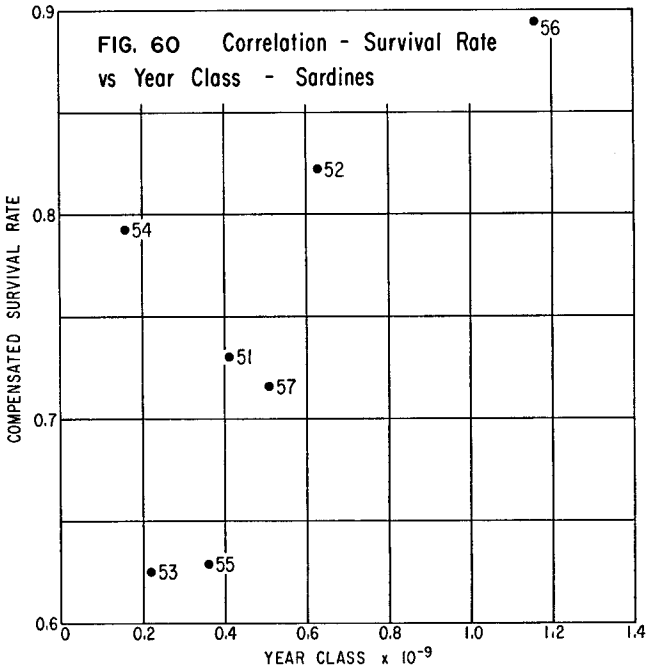


FIG. 60 Correlation - Survival Rate vs Year Class - Sardines

FIG. 61 Correlation - Sardine Relative Growth Rate vs Year Class

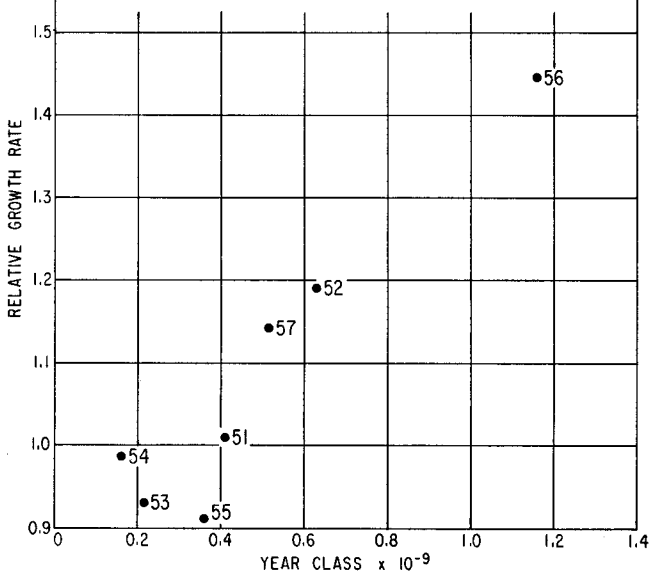


FIG. 62 Sardine Survival vs Year Class

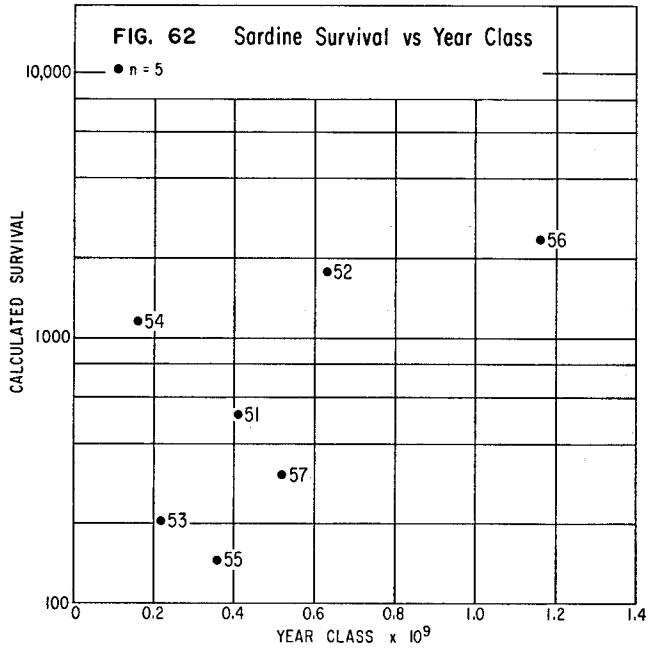


FIG. 63 Comparison "Survival" of Sardines and Anchovy "Condition"

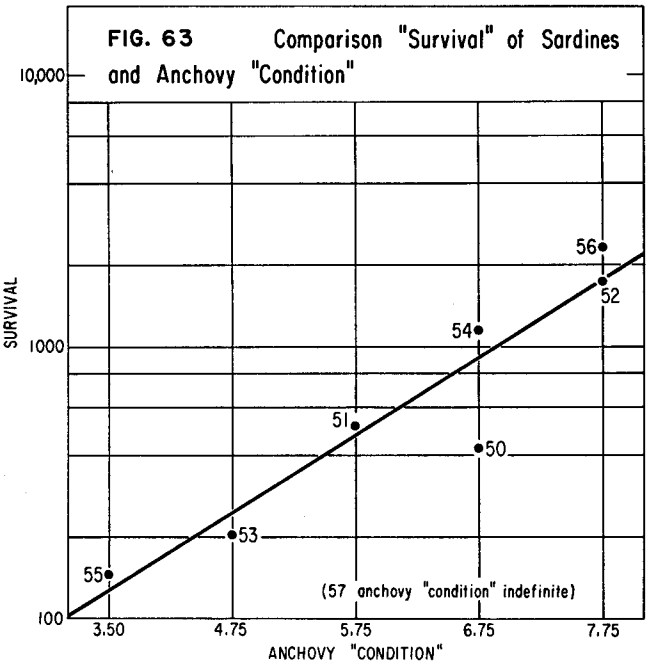
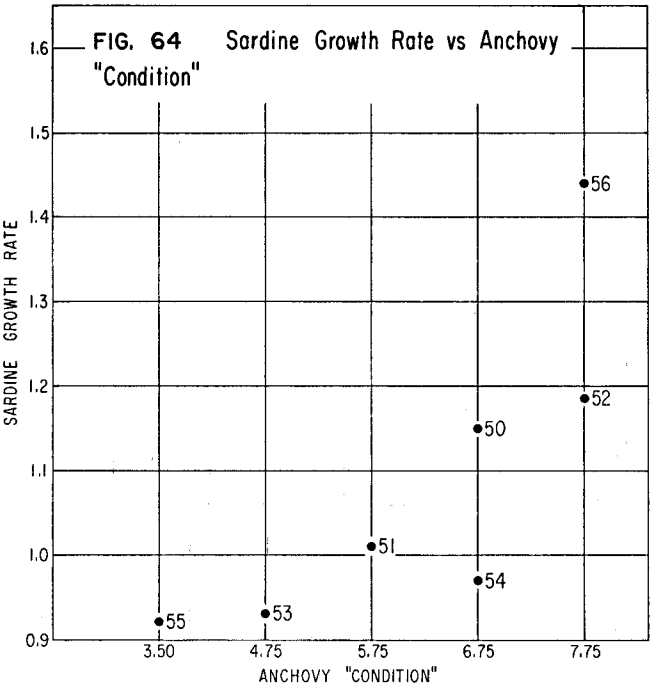


FIG. 64 Sardine Growth Rate vs Anchovy "Condition"



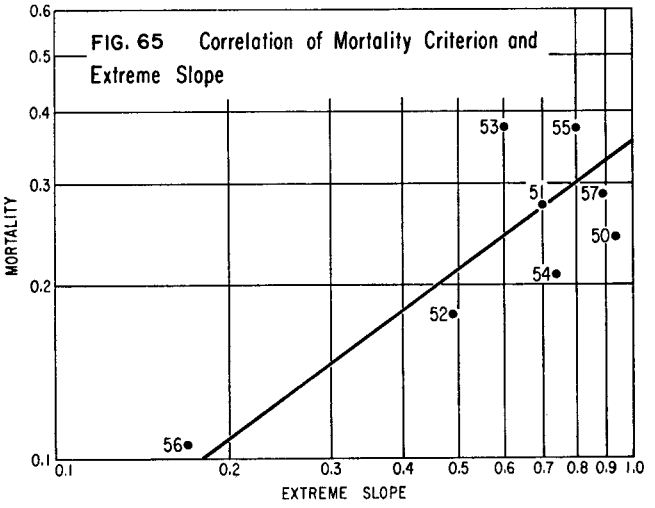


FIG. 65 Correlation of Mortality Criterion and Extreme Slope

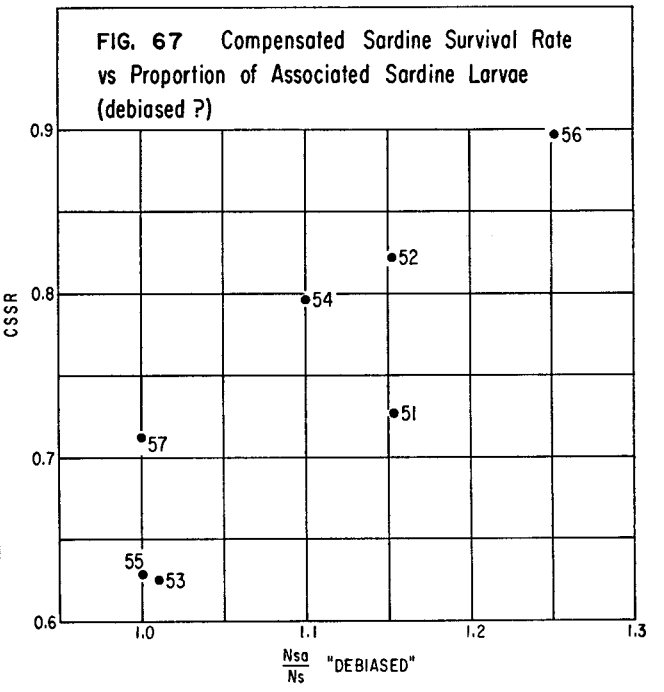


FIG. 67 Compensated Sardine Survival Rate vs Proportion of Associated Sardine Larvae (debiased ?)

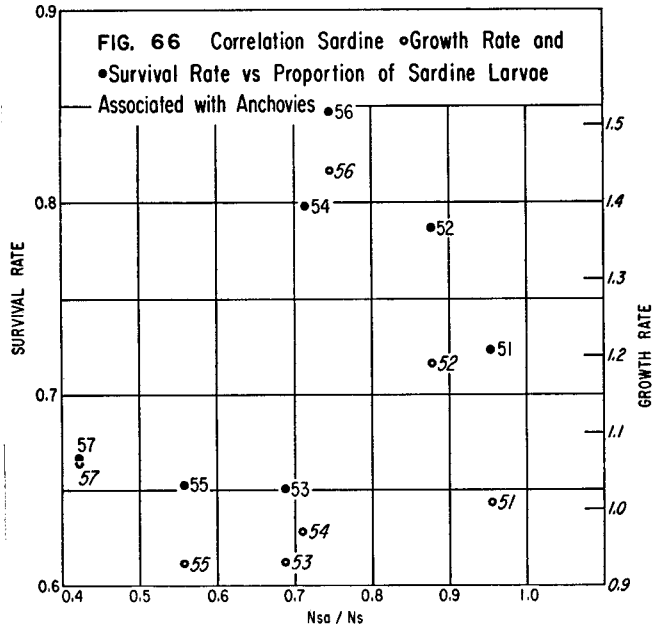


FIG. 66 Correlation Sardine ∘Growth Rate and •Survival Rate vs Proportion of Sardine Larvae Associated with Anchovies

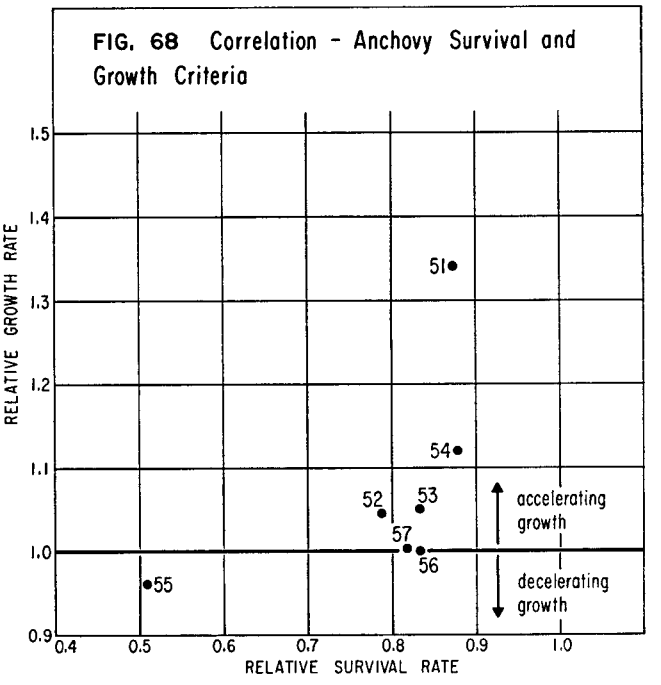


FIG. 68 Correlation - Anchovy Survival and Growth Criteria

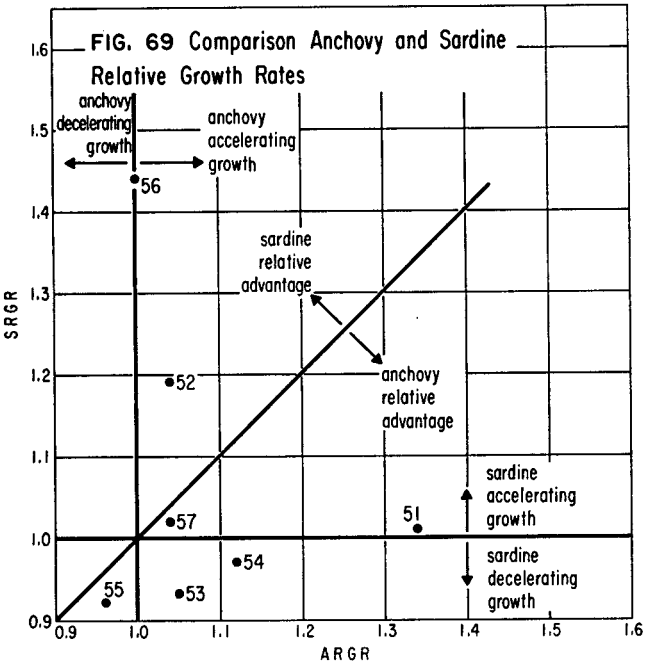
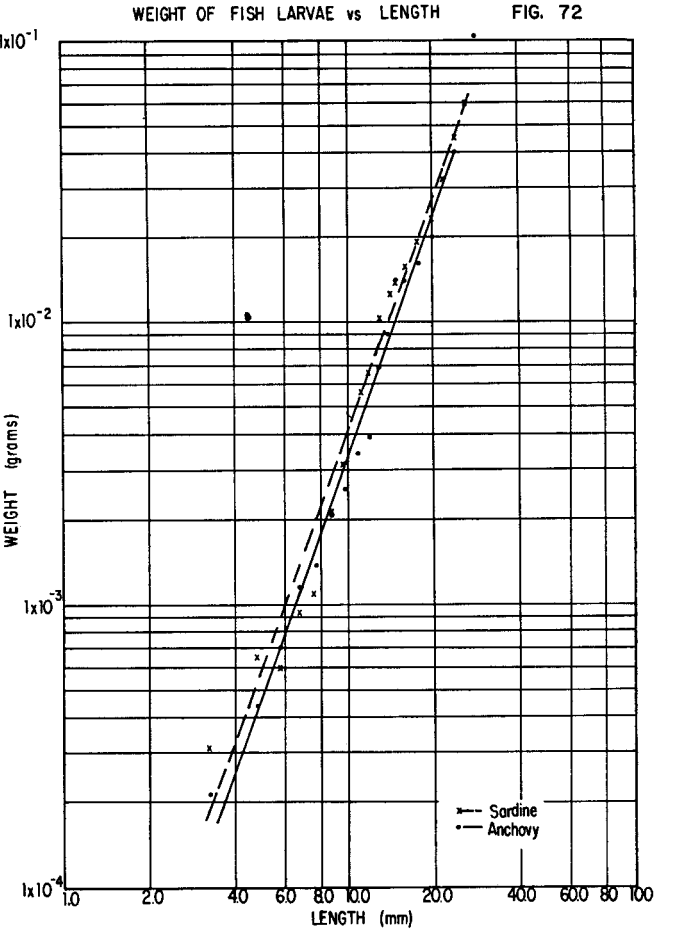


FIG. 69 Comparison Anchovy and Sardine
Relative Growth Rates
anchovy decelerating growth
anchovy accelerating growth
sardine relative advantage
anchovy relative advantage
sardine accelerating growth
sardine decelerating growth
SRGR
ARGR
56
52
57
54
55
53
51


WEIGHT OF FISH LARVAE vs LENGTH
FIG. 72
WEIGHT (grams)
LENGTH (mm)
Sardine
Anchovy

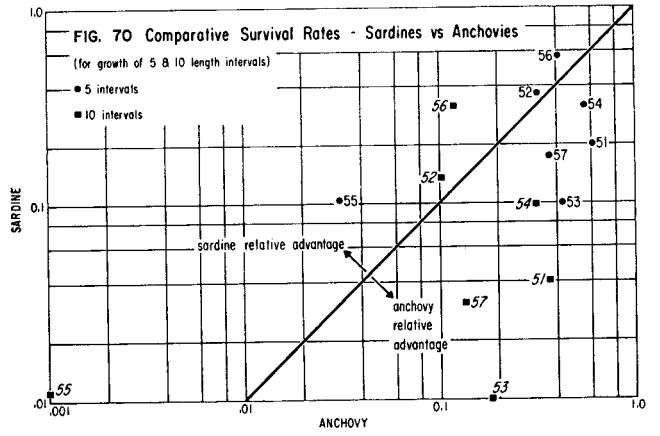


FIG. 70 Comparative Survival Rates - Sardines vs Anchovies
(for growth of 5 & 10 length intervals)
5 intervals
10 intervals
sardine relative advantage
anchovy relative advantage
SARDINE
ANCHOVY

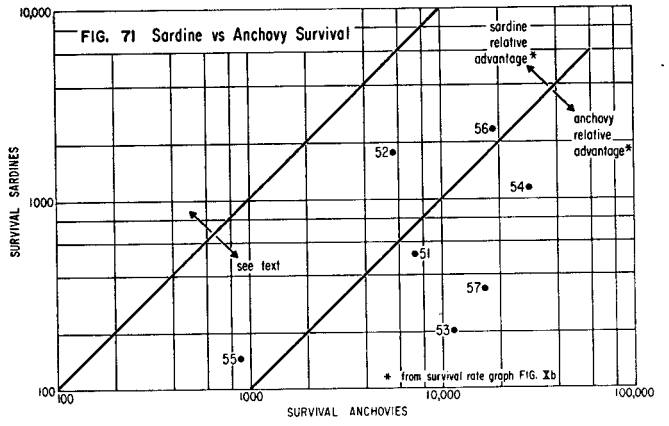


FIG. 71 Sardine vs Anchovy Survival
sardine relative advantage*
anchovy relative advantage*
see text
* from survival rate graph FIG. 3b
SURVIVAL SARDINES
SURVIVAL ANCHOVIES

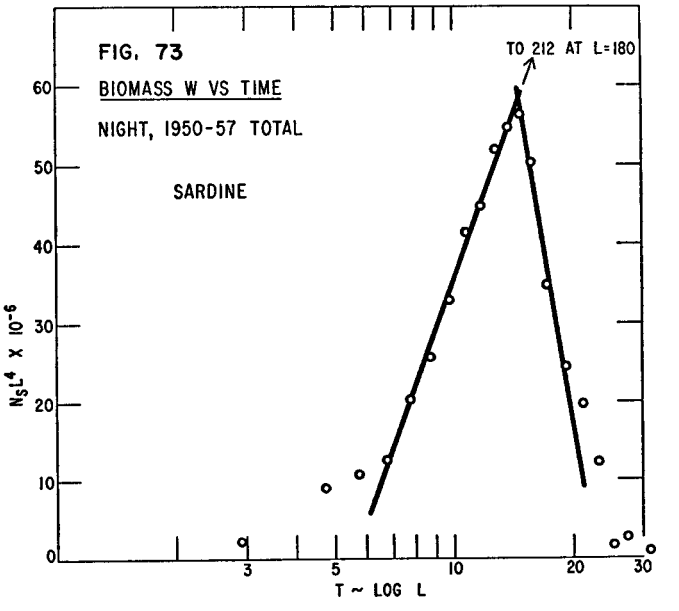


FIG. 73
BIOMASS W VS TIME
NIGHT, 1950-57 TOTAL
SARDINE
TO 212 AT L=180
T ~ LOG L

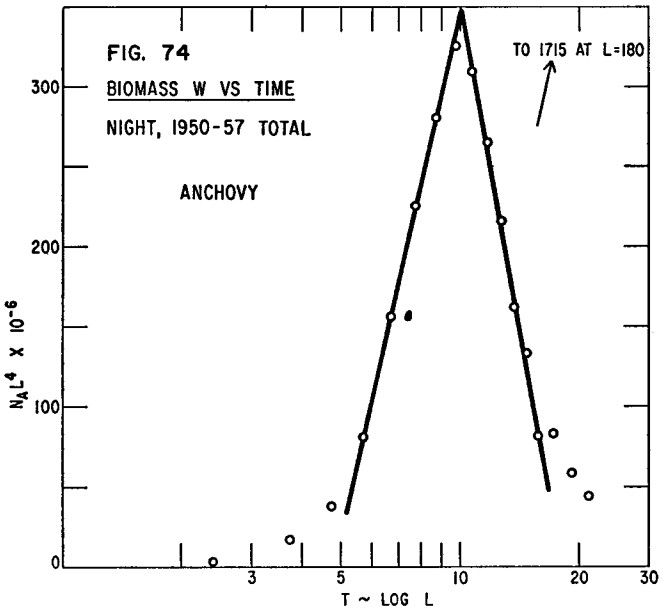


FIG. 74
BIOMASS W VS TIME
NIGHT, 1950-57 TOTAL
ANCHOVY
TO 1715 AT L=180
$N_A L^4 \times 10^{-6}$
300
200
100
0
3
5
10
20
30
T ~ LOG L

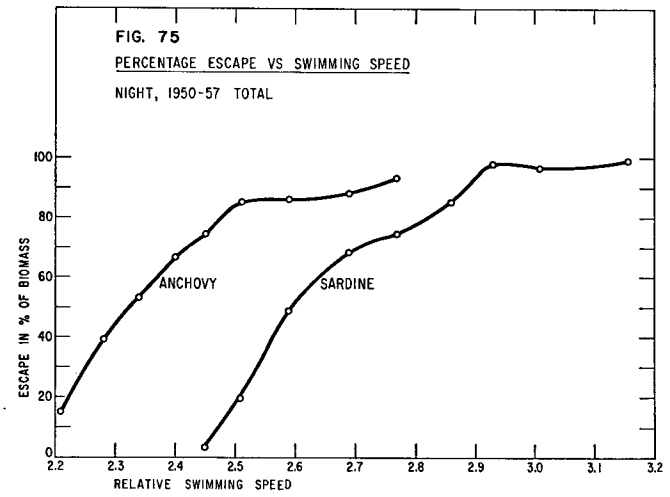


FIG. 75
PERCENTAGE ESCAPE VS SWIMMING SPEED
NIGHT, 1950-57 TOTAL
ESCAPE IN % OF BIOMASS
100
80
60
40
20
0
ANCHOVY
SARDINE
2.2
2.3
2.4
2.5
2.6
2.7
2.8
2.9
3.0
3.1
3.2
RELATIVE SWIMMING SPEED