# DEPENDENCE OF CATCH RATES ON SIZE OF FISH LARVAE 

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## INTRODUCTION

Numerous authors have used data obtained from systematic collections of fish larvae to estimate absolute or relative abundances of fish. Often a density measure of the number of larvae summed over size is used: Ahlstrom (1961) compared the relative abundances of rockfish larvae collected off the coasts of California and Baja California; Ahlstrom (1966) presented an extensive set of data collected in the same area and examined the abundance of Pacific sardine and northern anchovy over a period of 15 years; Ahlstrom (1968) employed the same data to estimate the spawning stocks of Pacific sardine and northern anchovy. Einarsson (1961) compared catches of Sebastes larvae from waters off the coast of Iceland over a period of several years; Hansen (1968) estimated year class strengths of cod from larvae data; Raitt (1964) used data obtained from a survey of Sebastes larvae off the coast of Scotland to estimate the number of adult females; Smidt (1963) compared yearly catches of larvae of Greenland halibut and halibut.
Although the use of fish larvae summed over size appears to be widespread, possible sources of error, such as avoidance, differential retention by size, behavior, and variable growth and mortality rates need to be evaluated.
Several studies, Ahlstrom (1954), Ahlstrom (1965), Clutter and Anraku (1968), Farris (1961), Isaacs (1965) and Vannucci (1968), have examined these sources of error, but much work is needed before these sources of errors can be eliminated.

Catch curves of larvae of four species of fish, Pacific hake (Merluccius productus), Pacific sardine (Sardinops caeruleus), northern anchovy (Engraulis mordax), and jack mackerel (Trachurus symmetricus) are examined in this paper. A simple mathematical expression is derived to describe portions of the catch curve. Variability among years, areas, and species is examined and discussed with respect to the sources of error previously mentioned. The effect of variability in the catch curves on catches of fish larvae summed over size is shown.
The data were obtained from California Coopera-
tive Oceanic Fisheries Investigations surveys of the coastal waters of California and Baja California. These surveys used cylindrical-conical plankton nets constructed of \# 30 xxx grit gauze (mesh size 0.5504 mm ) with a mouth diameter of 1 m . Oblique hauls to a depth of 140 m , depth permitting, sampled the water column. Each haul sampled about $500 \mathrm{~m}^{3}$ of water. Counts of fish larvae were standardized to numbers per $10 \mathrm{~m}^{2}$ of surface area. Ahlstrom (1966) described procedures of sampling in greater detail.

This study utilizes data from about 12000 samples. Only data taken during the months of January through July were used. Sampling was not adequate for other months, and previous studies showed that the preponderance of larvae of the species of concern is taken during the January-through-July period. Differences in effort per month were adjusted by the use of a weighting factor proportional to the inverse of the effort per month. No attempt was made to adjust for differences in effort per area. Catch curves of jack mackerel and Pacific hake larvae were derived from data obtained during 1966. The study of Pacific sardine and northern anchovy utilizes data from 19511960. Pacific hake larvae have only been measured in recent years. Although jack mackerel larvae have been measured since 1951, the data are not readily available. Samples were not taken during the month of March in 1966.

## CATCH CURVES

pacific hake
Figure 170 illustrates day and night catch curves of Pacific hake larvae collected during 1966. These curves have most of the characteristics of catch curves I have examined for fish larvae. A mode occurs at 2.5 mm for the night catches and at 3 mm for the day catches. A portion of Pacific hake larvae at smaller sizes probably passes through the mesh of the collecting gear causing the modes. The curves then decline in an approximately exponential fashion. There is a slight tendency for the rate of decline to decrease with increasing size. The ratio of night to day catches tends
to increase with size. The phenomenon has been attributed to net avoidance by several authors. Insignificant numbers of Pacific hake larvae were captured at sizes greater than 14 mm . Finally there is an indication that catches are higher at whole mm sizes than at the preceding half mm sizes. This may be due to a bias towards measuring individuals as whole units rather than half units.

Since the decline in catch, as size increases, is nearly exponential, I chose to use an exponential equation to describe mathematically the catch curves between the modal size and largest size of significant catches. The catch equation is given by

$$
\begin{equation*}
\mathcal{N}_{s d}=\mathcal{N}_{s_{0} d} A \exp \left[-B\left(s-s_{0}\right)\right] E_{s d} \tag{1}
\end{equation*}
$$

where $\quad \mathcal{N}_{s d}=$ number of larvae of size $s$ caught during time $d$
$s \quad=s_{0}, \ldots \ldots, s_{t}$
$s_{0}=$ modal size
$s_{t}=$ largest size of significant catches
$d=$ time of day; i.e., day ( 3 ) or night (1)
$A=$ constant
$B=$ instantaneous rate of decline in catch with size
$E_{s d}=$ error term assumed to be independent of $s$ and $d$ and to have a log-normal distribution.

The parameters in equation (1) change for night and day because of the differences between night and day catch rates. An equation was derived to describe simultaneously the night and day catch curves. The ratio between day and night catches tends to increase in a linear fashion. However, it is simpler to estimate parameters of a model that assumes that the night to day ratio increases in an exponential fashion because the change of catch rate with size is exponential. I believe that the increased simplicity justifies the decrease in precision. The new equation is:
$\mathcal{N}_{s a}=\mathcal{N}_{s 0 d} A \exp \left[-B\left(s-s_{0}\right)\right] \exp \left[C d\left(s-s_{0}\right)\right] E_{s a}$
where $C=$ instantaneous rate of increase of the night to day ratio with size.

The parameters $A, B$, and $C$ were estimated by the technique of multiple linear regression after transforming the equation to

$$
\begin{gather*}
\log _{e}\left(\mathcal{N}_{s d} / \mathcal{N}_{s 0 d}\right)=\log _{\mathrm{e}}(A)-B\left(s-s_{0}\right)  \tag{3}\\
+C d\left(s-s_{0}\right)+\log _{\mathrm{e}}\left(E_{s d}\right)
\end{gather*}
$$

The results are shown in Table 94. For the Pacific hake, approximately $92 \%\left(R^{2}\right)$ of the variance is ex-


Figure 170. Catch curve of Pacific hake catches, 1966. Solid line indicates night catches. Dashed line indicates day catches.
plained by the model. The estimated value of $B$ is $0 \cdot 48$. This means that the catch rate at night of Pacific hake declines about $38 \%$ per mm of growth.

## JAGK MAGKEREL

The day and night catch curves of jack mackerel larvae captured during 1966 are shown in Figure 171. The modal size occurs at 3 mm in both curves. The two curves are nearly identical until catches become insignificant at 8.5 mm . There is a tendency for the night to day catch ratio to decrease at the larger sizes. Estimates of the parameters of equation (2) are given in Table 95. The model explains about $98 \%$ of the variance. Although the estimated value of $C$ is significant ( $P=0.05$ ), it is negative and low. It may be prudent to agree with the conclusion of Farris (1961) that there is not a significant relationship between the day to night ratio of jack mackerel larvae catches and size. If $C$ is not included in the equation, the estimate of $A$ remains the same and the estimate of $B$ changes slightly to $1 \cdot 12$. In either case the catch rate during the day of jack mackerel larvae decreases about $67 \%$

Table 94. Estimates of parameters of equation (2)

| Species | Years | A | $B$ | C | $S_{0}$ | $R$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Pacific hake | 1966 | $0 \cdot 50$ | $0 \cdot 48$ | 0.21 | 3.00 | 0.96 |
| Jack mackerel. | 1966 | $1 \cdot 13$ | $1 \cdot 18$ | $-0.11$ | $3 \cdot 00$ | 0.99 |
| Pacific sardine | 1951 | $0 \cdot 68$ | $0 \cdot 15$ | 0.24 | 4.75 | 0.97 |
| ", " | 1952 | 0.53 | 0.21 | $0 \cdot 24$ | 4.75 | 0.92 |
| ", " | 1953 | $0 \cdot 41$ | $0 \cdot 15$ | 0.23 | 4.75 | $0 \cdot 86$ |
| " | 1954 | $0 \cdot 47$ | $0 \cdot 19$ | $0 \cdot 24$ | 4.75 | 0.94 |
| " | 1955 | $0 \cdot 46$ | 0.26 | $0 \cdot 12$ | $4 \cdot 75$ | 0.95 |
| " " | 1956 | $0 \cdot 48$ | $0 \cdot 15$ | $0 \cdot 17$ | 4.75 | $0 \cdot 86$ |
| ", " | 1957 | 1.07 | 0.23 | $0 \cdot 28$ | $4 \cdot 75$ | 0.92 |
| ", " | 1958 | 0.94 | 0.33 | $0 \cdot 17$ | 4.75 | 0.94 |
| " | 1959 | $0 \cdot 41$ | 0.23 | 0.21 | 4.75 | $0 \cdot 88$ |
| " " | 1960 | $0 \cdot 63$ | $0 \cdot 21$ | $0 \cdot 41$ | $4 \cdot 75$ | 0.95 |
| " " | 1951-60 | 0.52 | $0 \cdot 22$ | $0 \cdot 20$ | $4 \cdot 75$ | $0 \cdot 96$ |
| North. anchovy | 1951 | 1.03 | $0 \cdot 46$ | $0 \cdot 00$ | 6.75 | 0.99 |
| ", " | 1952 | $1 \cdot 19$ | $0 \cdot 43$ | $0 \cdot 19$ | 6.75 | 0.99 |
| ", " | 1953 | 1.27 | 0.41 | $0 \cdot 16$ | 6.75 | 0.97 |
| " | 1954 | $1 \cdot 12$ | $0 \cdot 40$ | $0 \cdot 17$ | 6.75 | 1.00 |
| " " | 1955 | $1 \cdot 32$ | $0 \cdot 42$ | $0 \cdot 13$ | 6.75 | 0.99 |
| " | 1956 | $1 \cdot 42$ | 0.37 | $0 \cdot 26$ | 6.75 | 0.98 |
| " " | 1957 | 1.23 | 0.41 | 0.08 | 6.75 | 0.98 |
| " " | 1958 | $1 \cdot 20$ | 0.41 | $0 \cdot 17$ | 6.75 | 1.00 |
| ", " | 1959 | $1 \cdot 12$ | 0.32 | 0.22 | 6.75 | 0.99 |
| " " | 1960 | $1 \cdot 13$ | 0.39 | $0 \cdot 26$ | 6.75 | 1.00 |
| " " | 1951-60 | $1 \cdot 28$ | $0 \cdot 42$ | $0 \cdot 16$ | 6.75 | 1.00 |
| Northern anchovy (separated by subpopulations) |  |  |  |  |  |  |
| northern | 1951-60 | $1 \cdot 22$ | $0 \cdot 38$ | $0 \cdot 14$ | 6.75 | 1.00 |
| southern | 1951-60 | $1 \cdot 43$ | $0 \cdot 46$ | $0 \cdot 23$ | 6.75 | 0.99 |



Figure 171. Catch curve of jack mackerel larvae, 1966. Solid line indicates night catches. Dashed line indicates day catches.


Figure 172. Catch curve of Pacific sardine Iarvae 1951-60. Solid line indicates night catches. Dashed line indicates day catches.
per mm of growth. Ahlstrom (pers. comm.) has estimates of catch by size of jack mackerel larvae from 1952, 1953, and 1954. Differences in effort by month and area were adjusted. These data indicate that $B$ should be about $0 \cdot 85$. In this case the catch rate decline is about $57 \%$ per mm of growth.

## pacific sardine

For Pacific sardine larvae collected during 19511960 (Fig. 172), modal size is at 3 mm for day catches and 4.75 mm for night catches. The size increment is increased at 17.25 mm because of a scarcity of larvae beyond this size. There is a slight increase in catch rate at 17.25 mm over the preceding size because of the change in increment. This artefact could be partially corrected by dividing the catch rate of larvae greater than 15.75 mm by two. However, the average size of larvae captured in the intervals of concern is not evident a priori because of the exponential decline in catch rate. Thus, Pacific sardine larvae, and northern anchovy larvae, larger than 15.75 mm are not included in the analysis. There is a tendency for the slopes to be greater between 4.75 mm and 6.75 mm than between 6.75 mm and 15.75 mm . This tendency


Figure 173. Estimates of $B$ for Pacific sardine and average temperature at 10 m .


Figure 174. Estimates of $C$ for Pacific sardine and average temperature at 10 m .
appears in most of the years that were examined. However, for the sake of simplicity the slopes are assumed to be constant between 4.75 mm and 15.75 mm . The concavity between 4.75 mm and 15.75 mm of the day curve (Fig. 172) did not appear in a consistent fashion during the years studied and is assumed to be unimportant.

Estimates of the parameters of equation (2) are given in Table 94 for each year and for all of the years combined. The estimate of $B$, for all years combined, is 0.22 and the range $0.15-0.33$. This indicates that the catch rate of Pacific sardine at night declines about $20 \%$ per mm of growth. The model explains about $92 \%$ of the variance of the combined data.

It is plausible that $B$ and $C$ are related to temperature for several reasons including temperaturespecific growth and predation rates. Average temperatures at 10 m were calculated for each year by weighting observed temperatures by catches of larvae. Temperatures at 10 m depth are used because data of


Figure 175. Percentage of number of Pacific sardine larvae 4.75 mm long captured at indicated size as predicted by equation (4) at temperatures of $15.5^{\circ} \mathrm{C}$ (solid line) and $18^{\circ} \mathrm{C}$ (dashed line). Open circles indicate day catches. Closed circles indicate night catches.

Ahlstrom (1959) indicate that this is the average depth of Pacific sardine larvae. The temperatures are shown in Table 95.

Plots (Fig. 173, 174) of $B$ and $C$ against temperature indicate a linear relationship. Thus, equation (2) was modified by replacing the parameters $B$ and $C$ with linear relations reflecting their dependence on temperature. The parameters of the modified equation were then estimated by multiple linear regression. The results are significantly better ( $P=0.01$ ) than the results from using equation (2). About $80 \%$ of the variance in the dependent variable is explained by the model. Figure 175 illustrates catches of Pacific sardine larvae predicted by the model at temperatures of $15.5^{\circ} \mathrm{C}$ and $18.0^{\circ} \mathrm{C}$, the extremes encountered in the study. Temperature appears to have less effect on catch rate than light.

Table 95. Average temperatures at 10 m weighted by number of Pacific sardine larvae captured

| Year | Average temperature $\left({ }^{\circ} \mathrm{C}\right)$ |
| :---: | :---: |
| $1951 \ldots \ldots \ldots$ | $15 \cdot 48$ |
| $1952 \ldots \ldots \ldots$ | 16.93 |
| $1953 \ldots \ldots \ldots$ | 16.30 |
| $1954 \ldots \ldots \ldots$ | 16.00 |
| $1955 \ldots \ldots \ldots$ | 15.50 |
| $1956 \ldots \ldots$ | 15.74 |
| $1957 \ldots \ldots$ | 17.21 |
| $1958 \ldots \ldots$ | 18.09 |
| $1959 \ldots \ldots$ | 16.43 |
| $1960 \ldots \ldots$ | 18.09 |

## NORTHERN ANGHOVY

Catch curves of northern anchovy larvae captured during 1951-1960 (Fig. 176) show a modal size of 2.5 mm for day catches and 3.75 mm for those at night. Catches at night remain fairly constant until the size of 6.75 mm . Thus anchovy larvae less than 6.75 mm are not included in the analysis. Both curves decline in a nearly exponential fashion between


Figure 176. Catch curve of northern anchovy larvae, 1951-60. Solid line indicates night catches. Dashed line indicates day catches.
6.75 mm and 15.75 mm . However, there is a slight tendency for the rate of decline to increase with size.

The estimate of $B$ for all years combined is 0.39 . This means that the catch rate during the day declined about $32 \%$ per mm of growth. About $99 \%$ of the variance is explained by the model. As in the case of the sardine larvae there are considerable differences among the estimates of $B(0.32-0.46)$ and $C(0.0-$ 0.26 ) during the years studied. The parameters of the modified version of equation (2) were estimated using average temperatures at 10 m . The results were not significant. The work of Ahlstrom (1959) indicated that the average depth of northern anchovy larvae is about 20 m . Unfortunately, temperatures at this depth are not available at the present.

There is strong evidence for the existence of at least two sub-populations of northern anchovies (A. M. Vrooman, pers. comm.). The sub-populations are separated in the area of Cape Colnet, Baja California. It seemed possible that the sub-populations contributed to the variability in $B$ and $C$. Therefore, I separated the catches of anchovy larvae into northern and southern sub-populations at obvious discontinuities in the distributions of the catches. These discontinuities occurred between the U.S.-Mexican border and Punta Eugenia, Baja California. Estimates of the parameters of equation (2) for the two sub-populations are shown in Table 94. The estimates of both $B$ and $C$ are higher for the southern than for the northern sub-population. About $99 \%$ of the variability is explained by the model in both cases.

## DISCUSSION

There are considerable differences among the estimates of $B$ (rate of decline) for the four species. Jack mackerel have the highest estimate, $1 \cdot 18$, while the Pacific sardine have the lowest, $0 \cdot 22$. It is interesting to note that recent work by $\mathbf{K}$. Lillelund (pers. comm.) showed that predation on newly hatched sardine larvae by Labidocera is less than that on newly hatched anchovy larvae. With the exception of jack mackerel, the estimates of $C$ (rate of increase of night to day catch ratio) are quite similar, at about $0 \cdot 2$. Farris (1961) attributed the lack of a relationship between size and the night to day ratio of catches of jack mackerel to a lack of avoidance by jack mackerel to capture. It seems unlikely that jack mackerel larvae do not avoid capture, since they are more developed structurally at small sizes than the other species studied. Also, the estimate of $B$ is highest for jack mackerel. It is more likely that mackerel larvae are able to avoid capture equally well by day and night. With this in mind it does not seem prudent to interpret the rate of decline of night catches, as a mortality
rate. Ahlstrom (pers. comm.) has examined the night to day ratios of catch rates of larvae of numerous species of fish and observed that the night to day ratio of jack mackerel appears to be unique for fish that inhabit the euphotic zone.

The growth rate may also contribute to $B$. The time spent in a size interval is dependent on growth rate. Since this rate has been shown to be related to temperature, the relation between estimates of $B$ and temperature may be partially caused by different growth rates. Unfortunately, we do not have sufficient data on growth and temperature to come to any conclusions regarding the contribution of growth to $B$. Some work has been done on Pacific sardine growth at small sizes ( $<7 \mathrm{~mm}$ ) at temperatures encountered in the present study. We also have some data on Pacific sardines at larger sizes at higher temperatures than encountered in the study. J. Zweifel- (pers. comm.) has extrapolated these data to the temperatures encountered in the study. The dependence of $B$ on temperature is shown to some extent by using these data for larvae between 5 and 11 mm .

The demonstrated differences among the catch curves can have significant effects on the catches of fish larvae, summed over size. For example, given equal numbers of newly hatched larvae, one would expect to catch fewer jack mackerel larvae than sardine larvae because of the difference in their rates of decline. Also, northern anchovy larvae appear to be fully retained at considerably larger sizes than the other species. The flat area of the catch curve of anchovy between 4.75 mm and 6.57 mm (Fig. 176) may be explained if the rate of decline cancels out the increased retention by the net. To study the effect on total catch, I set the number of larvae captured at the smallest size to one for Pacific sardine, jack mackerel, and Pacific hake, then corrected for changes in size increment of the smallest size, and used equation (2) to estimate the catches summed over size up to 15.75 mm . I also corrected for the apparently low retention rate in the case of anchovy larvae. Assuming that the ratio of night to day hauls is one, the total catches would be

$$
\begin{array}{ll}
\text { Pacific sardine . . . . . . . . . . } & 3 \cdot 4 \\
\text { Pacific hake . . . . . . . . . . } & 2 \cdot 3 \\
\text { jack mackerel. . . . . . . . . } & 1 \cdot 5 \\
\text { northern anchovy . . . . . . } & 1 \cdot 0
\end{array}
$$

The implications of these figures on estimates of spawning stock size made from total number of larvae are obvious. The problem is not as serious when relative strengths of year classes of the same species are estimated.

The results of this study suggest that there are serious sources of error in the use of total numbers of larvae for the estimate of spawning stocks. Attempts to correct for these sources of error can be made in the fashion described in the preceding paragraph. It would be preferable to determine experimentally rates of growth, retention, and avoidance. It should be possible to determine size-specific rates of retention and avoidance with the use of plankton nets of different mesh and mouth sizes.

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