Larval Production and Mortality of Pacific Saury, *Cololabis saira*, in the Northwestern Pacific Ocean[1]

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ABSTRACT: Because quantitative samples of saury eggs are difficult to obtain owing to their adhesive nature, reproductive level of the Pacific saury, *Cololabis saira*, has been estimated from the standing stock of the larvae and juveniles in Japan. Mortality curves were constructed and daily larval production at hatching was estimated for combined data from 1972 to 1986 and for consecutive individual years within this period. Durations of size classes were estimated from a growth curve and used to calculate fish production at age. Because number of fish captured by a net tow (area = 401.3 m^2) showed a diel cycle due to fish behaviors, such as net frame evasion and diel vertical movement, the average mortality curve for 15 years was based on data collected at night. We used an exponential decay model to describe the mortality of saury larvae and juveniles. The daily instantaneous mortality rate was 0.078, and the larval production at hatching was 1.255 larva/tow/day. Mortality curves for the individual years were based on data collected throughout the day and night after correction by size- and time-specific retention rates. Daily larval production at hatching fluctuated among individual years ranging from 0.154 to 5.176. Daily instantaneous mortality rates positively correlated with larval production at hatching, which might indicate the presence of a density-dependent process in larval mortality.

Together with the Japanese sardine, *Sardinops melanosticta*, and the mackerels, *Scomber japonicus* and *S. australasicus*, the Pacific saury, *Cololabis saira* (Brevoort), is one of the most important offshore pelagic fishes in Japan. Although total catch of the saury in Japan (210,000 t [metric tons] in 1984) was much smaller than that of the sardine (4,180,000 t) or the mackerels (810,000 t) (Statistics and Information Department, Japan 1986), more than 95% of the catch is destined for human consumption (Japan Saury Fishery Association 1985). In sharp contrast, the sardine (81%) and the mackerel (40%) catches (Fisheries Agency 1985) are procesed for animal foods.

Saury fishermen in Japan expect to have a reliable fishing forecast provided by the Tohoku Regional Fisheries Research Laboratory, Fisheries Agency of Japan, every summer before the beginning of the fishing season. The forecast includes the expected catch in the coming season and the potential fishing grounds. The expected catch depends on fish stock size, and the location and size of the fishing grounds are a function of fish migration in relation to oceanographic conditions. Fish stock size is determined by both reproductive level and mortality rates of developmental stages from postspawning through recruitment. Since the saury grows rapidly and becomes an adult within one year (Watanabe et al. 1988), larval production and mortality rate in young stages are believed to be more or less directly related to recruitment and catchable stock size. Matsumiya and Tanaka (1978) suggested from their intensive study of population dynamics of the northwestern Pacific saury that the fluctuations of population size are seriously affected by reproductive success.

An egg survey may be the best method for estimating the reproduction level of pelagic fishes. However, it is difficult to conduct a quantitative egg survey of the saury by towing plankton nets because the eggs attach by filaments to floating objects such as drifting kelp. We therefore have been conducting larval and juvenile surveys to estimate the reproductive level. We use catch/tow (number of fish/net tow) values of several size classes as abundance indices. The year-to-year changes of the indices may reflect the fluctuation of reproductive level.

The apparent number of larvae in a size class is influenced by the duration of growth through that size class. If growth is slow, the duration will be extended; conversely, if growth is fast, the duration will be short. The duration of growth through a size class thus defines the

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amount of time that larvae or juveniles are vulnerable to capture. Because the growth rate is not constant over the size range of the young fish sampled in this study, we must correct for this bias. The production of larvae by age is defined as the abundance of larvae by size divided by the duration of growth through the size class, which is expressed as catch/tow/day. This allows us to calculate instantaneous mortality rate (IMR), and thus, construct a mortality curve. We need to know age and growth rate of saury to calculate production at age and mortality rates.

In northern anchovy, *Engraulis mordax*, there have been extensive studies of eggs and larvae, and the methods to calculate the production and mortality rate were established (Zweifel and Smith 1981; Lasker 1985; Lo 1985; 1986). Ichthyoplankton survey data, embryonic incubation times, and larval growth rates are the essential parameters for this method. Further, one needs to have information on possible biases of tow data. For the Pacific saury, we have 15 years of larval net-tow data, a newly developed growth model based upon otolith growth increments (Watanabe et al. 1988), and information on bias correction of tow data for day and night differences. All these make it possible to compute fish production at different ages and mortalities. Extending the mortality curve to age 0, we can calculate larval production at hatching, which might be the best index of reproductive level so far available. In this paper we selected the exponential decay mortality curve and used it to calculate the larval production at hatching and the daily IMR of Pacific saury in the northwestern Pacific Ocean for 1972-86.

METHODS

Data Source

The Pacific saury spawns nearly all year round in the entire northwestern Pacific Ocean. The sampling areas and seasons were somewhat different from year-to-year, but our data set of 15 years (1972-86) included around-the-clock samples taken all year from a large area of the northwestern Pacific, lat. 29-45°N, long. 129-174°E (Fig. 1).

Saury larvae and juveniles were collected by a surface ring net that was towed for 5 minutes at 2 knots. The mouth diameter was 1.3 m, and therefore the surface area covered by one tow was 401.3 m². A mesh size of the 3.0 m forward part of the net was 2.0 mm, and the 1.5 m rear part was 0.33 mm. Samples were washed down after the 5 min tow and preserved in 10% unbuffered formalin. Larvae and juveniles of saury were measured to the nearest 0.1 mm knob length (KnL), the distance from the tip of the lower jaw to the posterior end of a muscular knob at the base of the caudal peduncle. They were then grouped into 11 size classes from 7.5 mm (including 5.0–9.9 mm) up to 57.5 mm (55.0–59.9 mm). The midpoint and both limits of each class were then converted into the capture size before preservation, using a shrinkage factor by formalin preservation (0.97) reported by Theilacker (1980) for northern anchovy. The midpoint of each size class was used to represent the class, though it is not a mean age of the class. The capture size was converted to age, and duration of each size class was obtained using the growth model developed by Watanabe et al. (1988). The growth equation from hatching to a 100 mm juvenule is

$$KnL = 5.90 \exp((0.0865/0.0293)$$

$$\times (1 - \exp(-0.0293\, t)))$$

where KnL is the fish knob length in mm after capture (before preservation) and t is the age in days from hatching.

Bias Corrections

An ichthyoplankton survey is essential for most pelagic fish research (Smith and Richardson 1977), but it is not bias free. The most common biases in catch of fish eggs and larvae are extrusion of eggs and larvae through net mesh and evasion of a net frame by fish. For the Pacific saury, the mesh size of the anterior part of the net, 2.0 mm, might be large enough to lose larvae by extrusion. Vulnerability of the fish to a net tow varies throughout a day due to changes in evasion abilities. Availability of the fish to a tow changes as well due to diel vertical movement. These factors result in differences in numbers of fish captured by net tows during the day and night. For the analysis, we defined 10 diel time periods based upon angles between the center of the sun and the celestial horizon. We used four periods in the morning—DAWN (DWN), MORNING TWILIGHT (MTW), SUNRISE (SRS), and MORNING (MRN)—and another four periods in the evening—AFTERNOON (AFT), SUNSET (SST), EVENING TWILIGHT (ETW), and DUSK (DSK). Time dura-
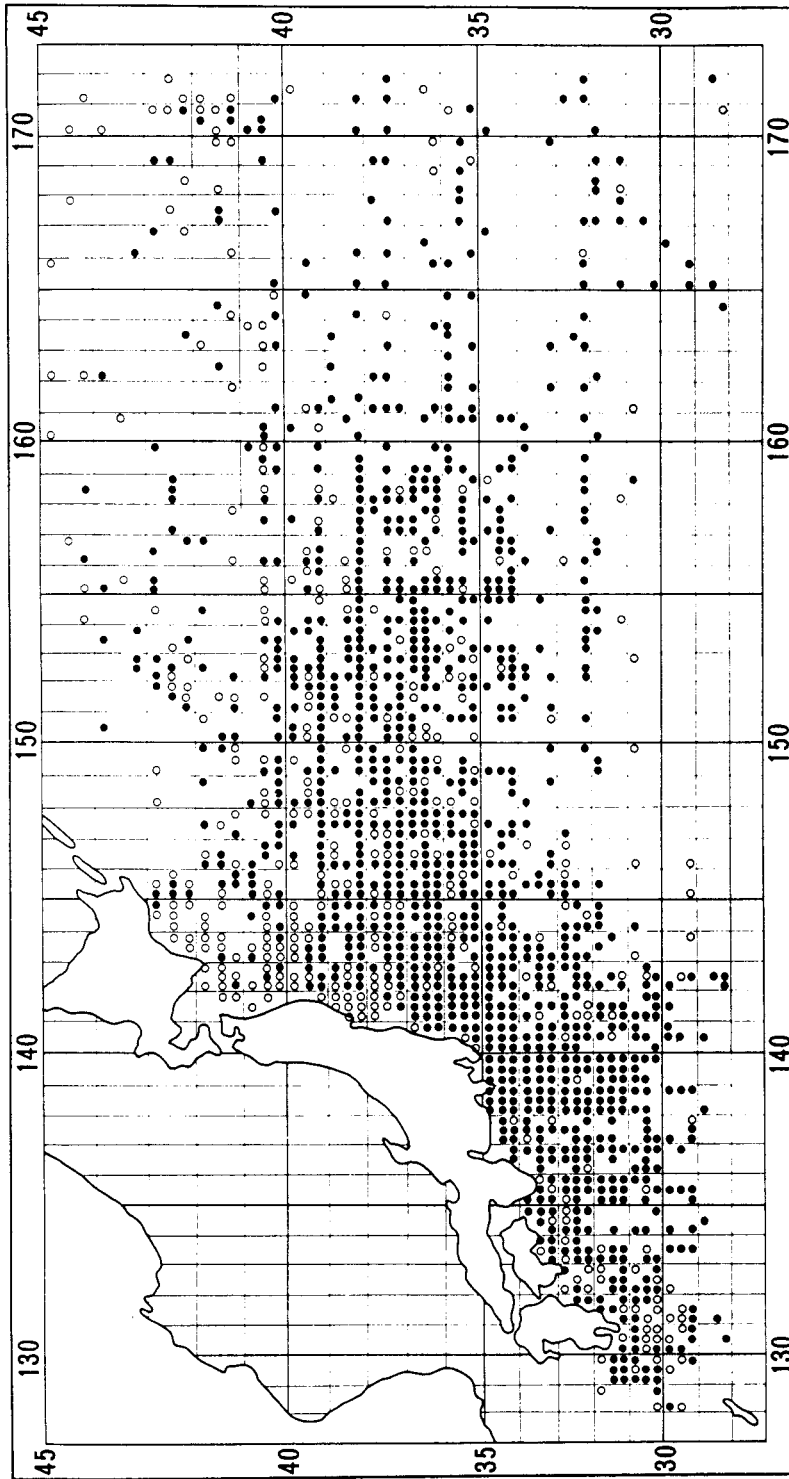
FIGURE 1.—Composite survey area of Pacific saury larvae and juveniles in the northwestern Pacific Ocean, 1972–86. Solid (open) circles represent areas where a positive tow has ever (never) been recorded in the period.

tion between the end of MRN and the beginning of AFT was named DAYTIME (DAY), and the time duration between the end of DSK and the beginning of DWN was named NIGHTTIME (NIT). We examined the data collection of 15 years (1972–86) and estimated size- and time-specific retention rates. Changes of these values are due to the fish behaviors such as net frame evasion and vertical migration. The rates were calculated by taking ratios of catch/tow in each time category and that of the NIT (Table 1). Extrusion of larvae was examined as well, comparing observed numbers of fish with predicted numbers calculated from a mortality curve (see results section for detail).

To reduce the seasonal effect of larval production and mortality, we also considered the bias on average catch/tow within a year from unproportional sampling efforts among months. Net tows were concentrated between February and May; the percentage of juvenile fish in the total catch was low in winter and increased in spring and early summer (Fig. 2). Thus, we divided 12 months of the year into 4 seasons based upon the abundance of saury larvae and juveniles: Jan-
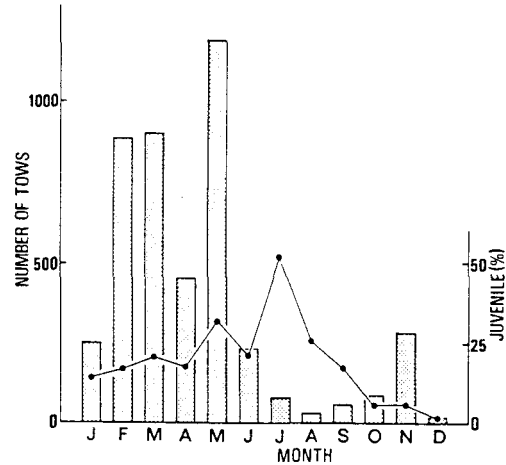

FIGURE 2.—Number of tows (columns) and percentage of juvenile Pacific sauries (dots) in total fish captured by months.

uary to March as the main spawning season, April to June as the late spawning season, July and August as the off spawning season, and Sep-

TABLE 1.—Annual average of Pacific saury catch/tow (c/t) and size- and time-specific correction factors (CF) of size classes in 10 time categories.

Time category (# tows)	Size class (mm):	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5
SRS	c/t	1.115	1.495	0.330	0.065	0.260	0.021	0.011	0.005	0.026	0.021	0.058
(92)	CF	0.864	0.724	0.220	0.072	0.475	0.064	0.050	0.029	0.215	0.158	0.450
MRN	c/t	1.588	2.281	0.521	0.352	0.154	0.043	0.039	0.028	0.019	0.003	0.000
(165)	CF	1.231	1.104	0.348	0.390	0.282	0.131	0.176	0.165	0.157	0.023	—
DAY	c/t	1.400	1.134	0.509	0.209	0.098	0.042	0.034	0.008	0.002	0.002	0.016
(1,517)	CF	1.085	0.549	0.343	0.232	0.179	0.128	0.154	0.047	0.017	0.015	0.124
AFT	c/t	2.090	2.004	1.022	0.403	0.176	0.039	0.018	0	0	0	0.003
(199)	CF	1.620	0.970	0.682	0.447	0.322	0.119	0.081	—	—	—	0.023
SST	c/t	1.486	1.175	0.937	0.501	0.524	0.189	0.006	0	0	0	0
(97)	CF	1.152	0.569	0.626	0.555	0.958	0.578	0.027	—	—	—	—
ETW	c/t	0.422	0.782	0.393	0.218	0.133	0.079	0.070	0.031	0.017	0.014	0.007
(132)	CF	0.327	0.379	0.262	0.242	0.243	0.242	0.317	0.182	0.140	0.105	0.054
DSK	c/t	1.425	1.700	1.354	0.867	0.641	0.268	0.340	0.192	0.121	0.084	
(218)	CF	1.105	0.823	0.904	0.961	1.172	0.820	1.538	2.518	1.582	0.910	0.651
NIT	c/t	1.290	2.066	1.498	0.902	0.547	0.327	0.221	0.170	0.121	0.133	0.129
(1,805)	CF	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
DWN	c/t	0.803	1.465	1.285	0.750	0.499	0.313	0.205	0.152	0.082	0.088	0.053
(203)	CF	0.622	0.709	0.858	0.831	0.912	0.957	0.928	0.894	0.678	0.662	0.411
MTW	c/t	0.568	0.610	0.434	0.250	0.158	0.053	0.026	0.046	0.020	0.092	0.020
(80)	CF	0.440	0.295	0.290	0.277	0.289	0.162	0.118	0.271	0.165	0.692	0.155

[1]SRS = SUNRISE; MRN = MORNING; DAY = DAYTIME; AFT = AFTERNOON; SST = SUNSET; ETW = EVENING TWILIGHT; DSK = DUSK; NIT = NIGHTTIME; DWN = DAWN; MTW = MORNING TWILIGHT.

tember to December as the early spawning season (Fig. 3). We calculated catch/tow values of 4 seasons separately in every size- and time-group by summing up the number of fish and net tows of 15 years and then taking average catch/tow values of 4 seasons. These values, average catch/tow values of the year, were used for calculation of the size- and time-specific retention rates mentioned above.

Mortality Models and Computations

The mortality model of the young saury from hatching (age 0) to 52 days old (57.5 mm preserved KnL) was based on the data of catch/tow/day (daily production) at ages. Two types of mortality curves were fitted to both the combined data collected in the NIT period for 1972–86 and the data set from 14 individual spawning years. One mortality curve is based on an age-dependent instantaneous mortality rate (IMR), $Z_1(t) = \beta/t$, and the other based on the age-independent constant IMR, $Z_2(t) = \alpha$, where t is the fish age in days and α and β are coefficients of IMR. The age-dependent IMR was considered because of the possibility that early larvae may suffer higher mortality than the older ones, as in the case of northern anchovy larvae along the California coast (Lo 1985, 1986). We constructed both mortality curves for saury larvae and juve-
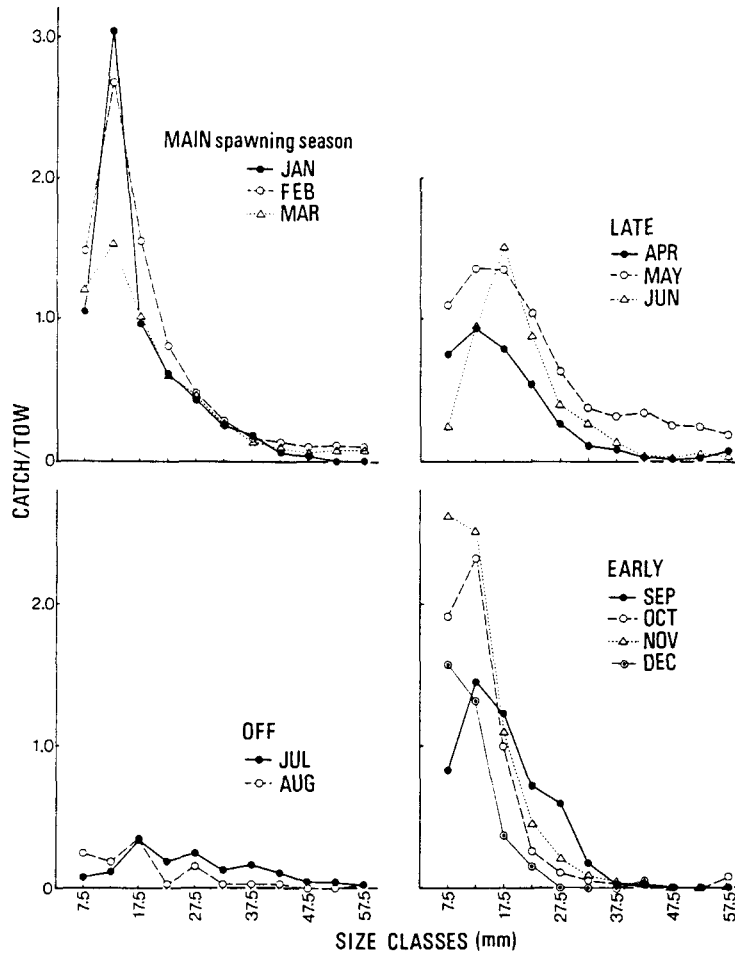

FIGURE 3.—Division of the year into four spawning seasons based on the number of Pacific sauries captured by a net tow (catch/tow) by months.

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niles. The mortality curves based on $Z_2(t)$ fitted the larval and juvenile data better than $Z_1(t)$, and therefore, we chose $Z_2(t)$ to describe the fate of young sauries. The mortality curve with a constant IMR takes the form of the exponential mortality curve,

$$P_t = P_0 \exp(-\alpha t)$$

where P_t is the daily fish production at age t, t is the age in days from hatching, P_0 is the daily larval production at hatching, and α is the daily IMR.

For the computation of larval production and mortality rate averages of 15 years, we used the data of the NIT category. For the computations of individual years, however, the number of NIT samples were not sufficient; therefore, we had to use the data from all the time periods. The data sets of individual years were classified into 10 time periods of 11 size classes and were corrected by dividing numbers of fish by their specific retention rates (Table 1). The corrected numbers of fish were summed up in each size class and divided by the total number of tows of the year to calculate catch/tow values as the abundance index of each size class.

We used the catch data of the early, main, late, and off spawning seasons (from September to August of the following year) as a unit of a spawning year instead of the calendar year. According to the recent growth model by Watanabe et al. (1988), the saury becomes adult within a year, so, we supposed that the larvae produced in a spawning year constitute the major part of the year class of the current year.

The catch/tow value of each size class was further divided by the duration of the corresponding size class. This provided the production rate (catch/tow/day), which was used for the computation of larval production at hatching and mortality. The parameters, larval production at hatching (P_0) and daily IMR, are estimated by using a nonlinear program (Par (Dixon et al. 1985)).

RESULTS

The Overall Mortality Curve for 1972–86

To understand the fate of young sauries from 1972 to 1986, the average catch/tow/day from the NIT samples (Table 2) was used to estimate the larval production at hatching and the IMR. All the fish were first grouped into 11 size classes, ranging from 7.5 mm (5.0–9.9 mm) to 57.5 mm (55.0–59.9 mm), and the midpoint of each size classes was converted to age. The data from the first two size classes (7.5 mm and 12.5 mm) were excluded from the analysis because the catch/tow/day in these two size classes was lower than the next older larvae. The downward bias could be due to extrusion of the larvae through the mesh. The estimates of the larval production at hatching (P_0) and daily IMR were 1.255 larvae/tow/day (SE = 0.111) and 0.078 (SE = 0.004), respectively (Fig. 4). The total daily mortality rate $((P_{t-1} - P_t)/P_{t-1} = 1 - (\exp(-\alpha)))$ was 7.5% from the newly hatched larvae to the 52 d old juvenile.

TABLE 2.—Daily production (catch/tow/day) at age (day) of Pacific saury from NIGHTTIME samples, 1972–86.

Midpoint size (mm)	pr[1] cp[2]	7.5 7.7	12.5 12.9	17.5 18.0	22.5 23.2	27.5 28.4	32.5 33.5	37.5 38.7	42.5 43.8	47.5 49.0	52.5 54.1	57.5 59.3
Age (day)			3.2	10.5	16.2	21.3	25.9	30.3	34.5	38.8	43.1	47.4	52.0
Size range (mm)	pr cp	5.0– 5.2–	10.0– 10.3–	15.0– 15.5–	20.0– 20.6–	25.0– 25.8–	30.0– 30.9–	35.0– 36.1–	40.0– 41.2–	45.0– 46.4–	50.0– 51.5–	55.0– 56.7– 61.8
Stage duration (day)			7.1	6.4	5.3	4.9	4.4	4.3	4.2	4.3	4.3	4.4	4.7
# fish observed			2,030	3,982	3,352	2,148	1,333	821	536	406	330	375	351
Catch/tow			1.125	2.206	1.857	1.190	0.739	0.455	0.297	0.225	0.183	0.208	0.194
Daily fish production			[3]0.158	[3]0.345	0.350	0.243	0.168	0.106	0.071	0.052	0.043	0.047	0.041

[1]Fish knob length after preservation.
[2]Fish knob length after capture (before preservation).
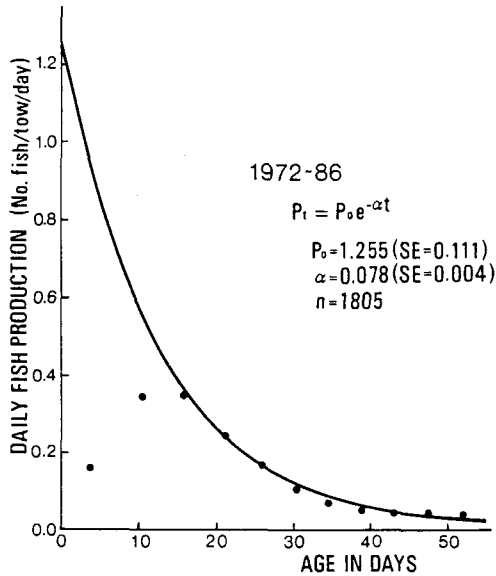[3]Not used for the computation.

FIGURE 4.—Mortality curve of young Pacific saury calculated from fish production at ages calculated from the NIT data of 15 years (1972–86). Data points of the smallest two size classes were not used for the computation. P_0 is the larval production at hatching, α is the daily IMR, and n is the number of tow samples.

Mortality Curves for Individual Spawning Years

To assess the mortality of young saury for individual spawning years, we used all the tow data collected around the clock, after the correction of catch data by the size- and time-specific retention rates (Table 1). The correction procedures are the same for all the spawning years. To illustrate the data assemblage and computation, the 1979 catch data set for 11 size classes was given (Table 3). Again, the data points of the first two size classes were not used in the estimation procedure because of the apparent downward bias. The parameter estimates and the mortality curves are summarized in Table 4, and the mortality curves are presented in Figure 5.

The larval production at hatching (P_0) fluctuated by more than 30-fold from the maximum 5.176 larvae/tow/day in 1978 to the minimum 0.154 in 1985 spawning year. Daily IMR has also ranged from 0.115 down to 0.041, with daily mortality rates of 10.9% and 4.0%, respectively.

Year-to-year fluctuations of these two parameters $(P_0$ and IMR) and the total catch of saury in Japan (Statistics and Information Department, Japan 1987) are presented in Figure 6. The total catch of saury can be an index of the stock size, though possibly including effects of economic factors such as fish price. The fishing season of saury opens in the first half of August and closes in the middle of December. Since the saury becomes adult in 9–10 months and 2 yr old fish were not found in the northwestern Pacific

TABLE 3.—Daily production (catch/tow/day) at age (day) of Pacific saury in 1979 spawning year (September 1978–August 1979).

Midpoint size (mm)	pr[1]	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5
	cp[2]	7.7	12.9	18.0	23.2	28.4	33.5	38.7	43.8	49.0	54.1	59.3
Age (day)		3.2	10.5	16.2	21.3	25.9	30.3	34.5	38.8	43.1	47.4	52.0
Size range (mm)	pr	5.0–	10.0–	15.0–	20.0–	25.0–	30.0–	35.0–	40.0–	45.0–	50.0–	55.0–
	cp	5.2–	10.3–	15.5–	20.6–	25.8–	30.9–	36.1–	41.2–	46.4–	51.5–	56.7–61.8
Stage duration (day)		7.1	6.4	5.3	4.9	4.4	4.3	4.2	4.3	4.3	4.4	4.7
# fish observed		607	1,267	738	420	194	68	61	32	16	13	9
# fish corrected		674	1,470	939	625	245	98	90	62	22	14	10
Catch/tow		1.685	3.676	2.349	1.562	0.613	0.244	0.226	0.155	0.054	0.036	0.026
Daily fish production		[3]0.236	[3]0.574	0.443	0.319	0.139	0.057	0.054	0.036	0.013	0.008	0.006

[1]Fish knob length after preservation.
[2]Fish knob length after capture (before preservation).
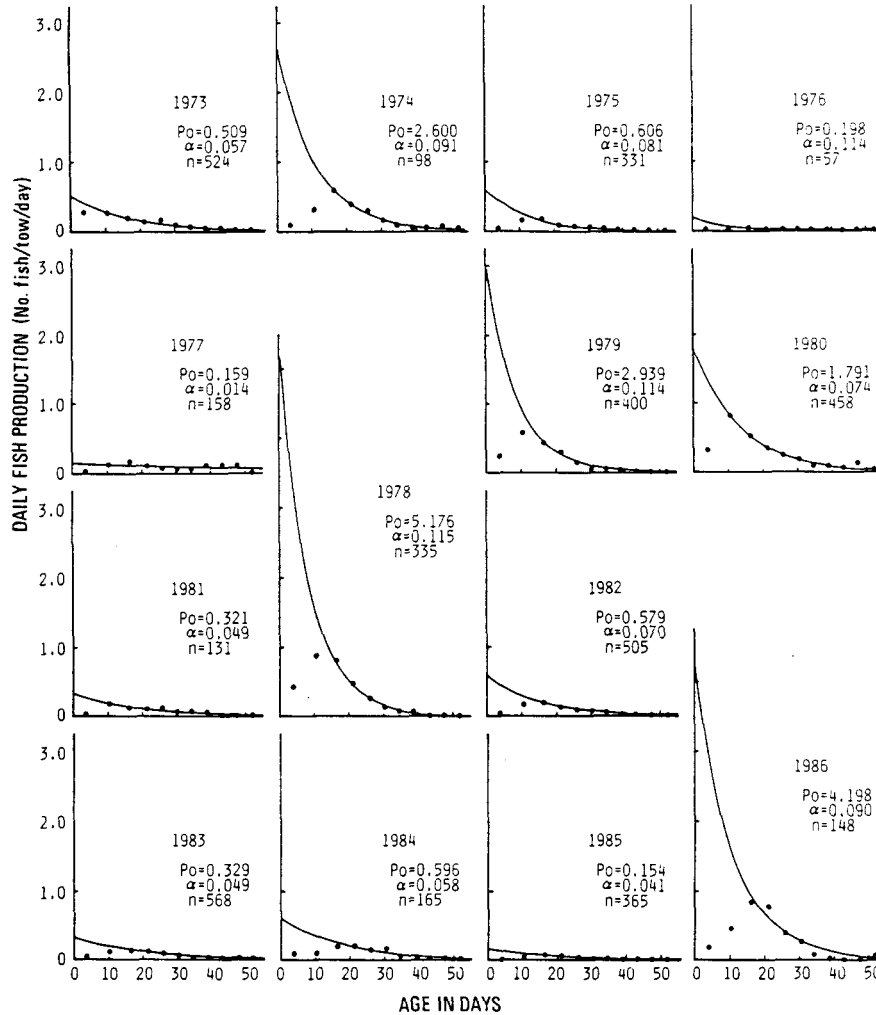[3]Not used for the computation.

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FIGURE 5.—Mortality curves of individual spawning years. P_0 is the Pacific saury larval production at hatching, α is the daily IMR, and n is the number of tow samples.

(Watanabe et al. 1988), the total catch in a fishing season must come from larvae produced in the spawning period of the same year. For example, the 1973 catch is related to larval production at hatching and daily IMR of the 1973 spawning year (from September 1972 to August 1973).

Larval production at hatching and the daily IMR have fluctuated somewhat concordantly from 1973 to 1986. The Spearman's Rho is 0.704 ($n = 14$, $P < 0.05$), indicating a positive correlation between P_0 and IMR among years. The

exception to this trend was 1976. The production value of 1976 was one of the lowest in 14 years whereas the daily IMR was very high, probably resulting in a minimum catch of <100,000 t in 1976.

Mesh Retention of Larvae

The low values of larval production for the first two size classes precluded their use in the estimation of larval mortality. Since the mesh size of the anterior 3.0 m of the net is 2.0 mm, we

TABLE 4.—Daily larval production at hatching (P_0) and daily instantaneous mortality rates (IMR) of individual spawning years with standard error in parentheses.

Spawning year	P_0 (larva/tow/day)	IMR	Mean square error ($\times 10^{-4}$)
1973	0.509 (0.100)	0.057 (0.008)	4.05
1974	2.600 (0.410)	0.091 (0.007)	10.20
1975	0.606 (0.112)	0.081 (0.009)	1.37
1976	0.198 (0.080)	0.114 (0.022)	0.13
1977	0.158 (0.067)	0.014 (0.013)	19.00
1978	5.176 (0.433)	0.115 (0.004)	3.33
1979	2.939 (0.653)	0.114 (0.012)	8.02
1980	1.791 (0.284)	0.074 (0.007)	12.50
1981	0.321 (0.100)	0.049 (0.012)	6.00
1982	0.579 (0.084)	0.070 (0.006)	1.36
1983	0.329 (0.055)	0.049 (0.007)	1.83
1984	0.596 (0.213)	0.058 (0.015)	17.10
1985	0.154 (0.037)	0.041 (0.009)	1.30
1986	4.198 (1.325)	0.090 (0.015)	104.00

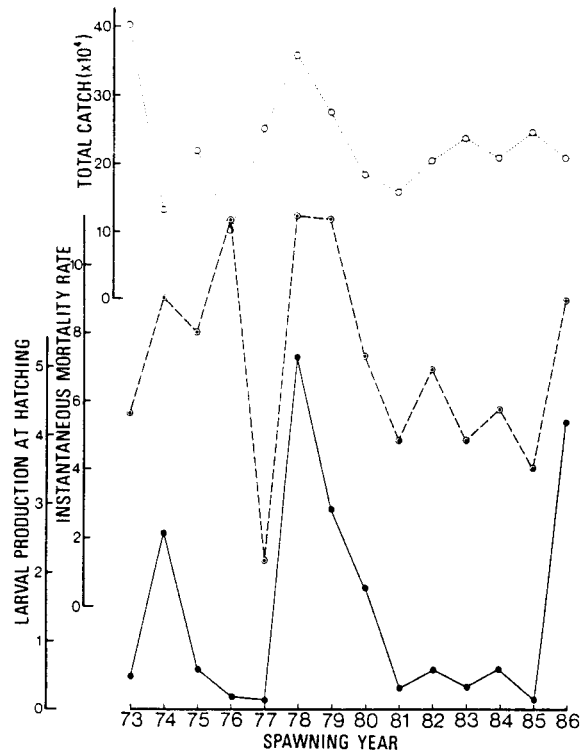FIGURE 6.—Year-to-year fluctuations of daily Pacific Saury larval production at hatching in number of larvae per tow (———●———), daily IMR (-----⊙-----), and the annual total catch in metric tons (-----○-----) of the saury.

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think that the downward bias is due to extrusion through the mesh. The mesh retention rate of larvae in the first two size classes could be estimated from the ratio of the observed catch/tow/day and the predicted larval production computed from the overall average mortality curve of 15 years. The estimate of mesh retention rate for larvae of 7.5 mm (3.2 days old) is,

Observed: 0.158 (larvae/tow/day)
Predicted: 0.978 (larvae/tow/day) = 1.255
    exp(−0.078 × 3.2)
Retention rate: 0.16 = 0.158/0.978

and for larvae of 12.5 mm (10.5 days old) is,

Observed: 0.345 (larvae/tow/day)
Predicted: 0.553 (larvae/tow/day) = 1.255
    exp(−0.078 × 10.5)
Retention rate: 0.62 = 0.345/0.553.

DISCUSSION

Production and mortality rates of fish larvae and juveniles cannot be obtained without good growth models, which are indispensable in calculating stage durations. A new growth model based on growth increments of otoliths has recently been established (Watanabe et al. 1988) enabling calculation of mortality rates. The current results are virtually the first attempt to calculate larval production at hatching. These should provide the best index of reproductive level ever obtained.

Sablin (1978) first calculated mortality rate of juvenile saury for 8 individual years (1968–75), using catch/tow values of two size groups, 26–30 mm and 46–50 mm, and 20 mm/mo as a growth rate of this size range. The average monthly IMR estimated by Sablin was 1.15 with a range from 0.76 to 1.62. He obtained the IMR from 2 size groups for individual years, whereas we used catch data from 9 size classes in computing the IMR. We believe the estimates of IMR reported here are an improvement over those of Sablin.

Monthly mortality rates using the Sablin IMRs (1978) ranged from 53.2% to 80.2% with an average of 68.3%. These values were much lower than the monthly rates calculated from the daily IMRs in this paper, 70.8–96.8% with an average 90.4%. The discrepancy between the two seems to derive from the difference in growth rates used for the computations (Fig. 7). Sablin used a rate of 20 mm/mo (0.67 mm/d) for the size range

from 26–30 mm to 46–50 mm. We used the growth model by Watanabe et al. (1988), which shows that sauries grow from 27.5 mm to 47.5 mm in 17.2 days (1.16 mm/d). This was 1.7 times faster than growth rate of Sablin. We recalculated monthly mortality rates using the Sablin IMRs and the Watanabe et al. growth rate of 1.16 mm/d producing estimates close to ours, 73.4–94.1% with an average of 86.5%.

The absolute value of total annual production of newly hatched larvae of the Pacific saury can be calculated from our results using the assumptions that 1) all fish in a vertical water column are in the upper one meter, and 2) those in a volume of water strained are captured by the net during the NIT period. The values of larval production at age 0 are on daily basis over the area covered by a net tow. Thus, the annual total production of the hatched larvae can be computed as below:

Annual Total Production of Hatched Larvae =
$$P_0 \cdot 365 \cdot A/401.3$$

where P_0 is larval production at hatching, A is total spawning area in m^2, and 401.3 is surface area in m^2 covered by one net tow. However, the distribution of saury larvae and juveniles in the northwestern Pacific extends far to the east of Japan, and we cannot delimit the total spawning area. Thus, calculation of the absolute larval production of saury at hatching for the entire area is not practical. However, the calculation of abso-
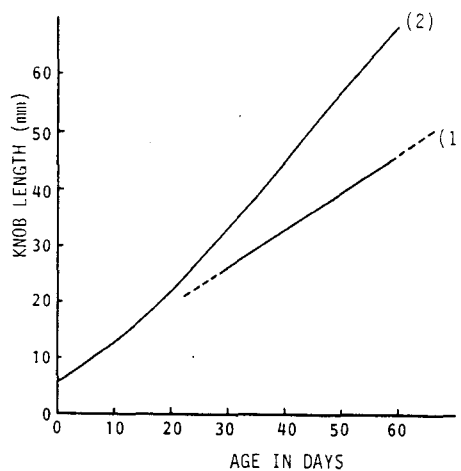

FIGURE 7.—Growth curves used by Sablin (1973) (1) and by us (2) for Pacific saury.

lute larval production in a limited area, which can be covered with a high precision, is possible and will be useful.

The assumption that all the fish in a volume of water strained by the net tow are captured in the NIT period is not realistic for a variety of reasons. The larval net used in this study has bridles in front of the mouth, and to some extent evasion can be expected due to turbulence in front of the net. Visual evasion is possible even in the NIT period because natural waters are not totally dark due to moonlight and a variety of bioluminescent organisms.

Vertical distribution pattern of young sauries has been investigated by towing nets on horizontal strata at several depths (Okiyama 1965; Parin 1967). However, the fraction of the young saury population in the upper one meter available to our net is not known.

The volume of water filtered by a tow may be different among tows depending on wave conditions, mesh clogging, etc. The standardization of catch data by a volume of water filtered must also be done to improve the accuracy of estimates. In our study, we did not have a flow meter with our net. Biases, resulted from these problems, must be resolved before absolute larval production can be obtained.

Unaccounted variances due to the retention correction factor and the duration computed from growth curve could lead to underestimation of the variance of parameter estimates in the mortality curve. On the other hand, the standard error of both P_0 and IMR in the current paper may be higher than the estimates from a regression where each daily fish production estimate is weighted by the inverse of its variance. The effect of the unaccounted variance caused by the retention correction factor could be small because the retention rates were computed from a large number of tows, reducing the standard error of estimated retention to insignificant levels. The variance of duration is unknown. Theoretically it could be estimated from the growth curve, but we did not compute it. A simulation study on evaluating the precision and bias of mortality estimates for northern anchovy (N.C.H.L., unpubl. data) indicated that the variation contributed from bias correction factors is minimal.

We employed an age-independent mortality model in this paper. This does not necessarily mean that the mortality of saury larvae is age-independent. Because of biased catch data due to mesh extrusion in the smallest two size classes,

we could not use these two values. This might have had some effect on choosing a mortality model. For further studies we have devised a cylinder-conical larval net for saury that is constructed with one type of mesh (0.53 mm). The body depth at the pectoral fins in early post-yolk-sac larvae is 0.6–0.7 mm, so the new net is expected to retain larvae of the smallest size classes. Thus, the net will enable us to get an unbiased sample of early larvae, and the use of a data set of all size classes including 7.5 and 12.5 mm classes might cause a shift of the mortality model from age-independent to age-dependent type.

Because mortality is a necessary piece of information for computing mean age for each size group, we used the ages corresponding to the midpoints of the size classes for the mortality computation instead of mean ages. It is acceptable to use the midpoint to convert size to age when the mortality information is unavailable, when mortality is low, or when the size interval is small. Bias resulted from the use of the midpoint was large for the first size class: 2.4 days with mortality correction assuming the IMR = 0.08 and 3.2 days using the midpoint 7.7 mm. However, the first two size classes were not included in the mortality computation, so bias caused by using the midpoints was minimal.

The high production values in large juvenile classes (Table 2, Figs. 4, 5) may be due to an underestimation of the durations of these size classes. Year-to-year variations of growth may be large enough to cause considerable differences in durations. The standing stock of larvae in a size class is influenced by the duration of growth through that size class. Because an accurate mortality estimate depends on accurate growth rate estimates, calculation of the growth rate every year, or at least every time the fish size composition changes, is necessary to obtain accurate mortality rates for individual years.

As shown for the northern anchovy, direct estimates of spawning biomass from an ichthyoplankton survey can be obtained (Lasker 1985). This method can be applied to other fishes that produce pelagic eggs. However, the saury produces adhesive eggs and quantitative sampling of them is difficult. Larval census is so far the best index for spawning biomass of the saury. Even if it were possible to obtain quantitative samples of eggs, uncertainties in embryonic mortality rates may rule out use of egg production. The saury has a long incubation time of about 2 weeks under 13°C (Yusa 1960), and slight differ-

ences in the daily mortality rates of embryonic stages, rather than egg production, could have profound influence on larval production at hatching. In other words, larval production at hatching may not necessarily be accurately related to egg production without knowing mortality rates of embryonic stages. Although crude estimation of spawning biomass by conventional plankton tows might be possible (Smith et al. 1970), a radical departure from the egg sampling method using information on vertical and horizontal distribution patterns of the eggs is required to devise an egg production method for the saury.

Lo (1985) calculated the time series of egg production at fertilization of the northern anchovy in 1951–82. Year-to-year difference in the egg production was more than 1,000-fold, which is much larger than the difference in saury larval production at hatching in our study, about 33-fold. She also calculated mean yolk-sac larval abundance for the years that showed a difference of more than 1,000-fold. Annual fluctuation of reproductive level in the saury seemed to be smaller than the northern anchovy. This might be related to the differences in spawning ecology of these two species. The saury is reported to be a multiple spawner that spawns in 2 mo intervals in the spawning season (Hatanaka 1955) with a batch fecundity of 500–3,000 egg/female (Hatanaka 1953). The spawning frequency is 3–5 times/yr and the annual fecundity is estimated to be 1,500–15,000. In contrast, time between spawning incidence of the northern anchovy off southern California is 6–8 days and the batch fecundity is 389 eggs/g of ovary free female body weight (Hunter and Goldberg 1980). The saury is less fecund than the northern anchovy and seems to be less variable in its annual fecundity owing to a long maturation period of ovarian eggs. Small year-to-year differences in the reproductive level in the saury might be the result of less variable spawning effort.

The correlation of the larval production at hatching and the daily IMR in the individual years may indicate that the mortality of young saury is density dependent. Watanabe (1987) showed an inverse correlation between the egg abundance and the overall survival rate of larval and juvenile Japanese sardine up to 1 yr old. He further examined correlations between the egg abundance and the biomass of larvae of the 40 mm size class, and between the biomasses of the 40 mm size class and of the 1 yr recruit size class. He found that egg abundance and survival rate up to 40 mm size class are inversely correlated,

whereas the biomass of the 40 mm and 1 yr size class are positively correlated. His conclusion was that the mortality rate of larval sardine is density dependent up to 40 mm. Thus, in some pelagic fish, mortality rates of early life stages could be density dependent.

ACKNOWLEDGMENT

LITERATURE CITED

Dixon, W. J., M. B. Brown, L. Engelman, J. W. Frane, M. A. Hill, R. I. Jennrich, and J. D. Toporek.
    1985. BMDP Statistical software. Univ. Calif. Press, Berkeley.
Fisheries Agency.
    1985. Annual report on Japan's fisheries, fiscal 1985 (summary). Minist. Agric., For. Fish., Gov. Jpn., Tokyo, 38 p.
Hatanaka, M.
    1955. Biological studies on the population of the saury, Cololabis saira (BREVOORT). Part 1 Reproduction and growth. Tohoku J. Agric. Res. 4:227–269.
Hatanaka, M., T. Watanabe, K. Sekino, M. Kosaka, and K. Kimura.
    1953. Studies on the reproduction of the saury, Cololabis saira (BREVOORT), of the Pacific coast of Japan. Tohoku J. Agric. Res. 2:293–302.
Hunter, J. R., and S. R. Goldberg.
    1980. Spawning incidence and batch fecundity in northern anchovy, Engraulis mordax. Fish. Bull., U.S. 77:641–652.
Japan Saury Fishery Association.
    1985. Sanma bouke-ami gyogyo kankei shiryo (Statistics of the saury stick-held dip net fishery). (In Jpn.) Jpn. Saury Fish. Assoc. 23:1–56.
Lasker, R.
    1985. An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, Engraulis mordax. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36, 99 p.
Lo, N. C. H.
    1985. Egg production of the central stock of northern anchovy, Engraulis mordax, 1951–82. Fish. Bull., U.S. 83:137–150.
    1986. Modeling life-stage-specific instantaneous mortality rates, an application to northern anchovy, Engraulis mordax, eggs and larvae. Fish. Bull., U.S. 84:395–408.
Matsumiya, Y., and S. Tanaka.
    1978. Dynamics of the saury population in the Pacific Ocean off northern Japan – III. Reproductive relations of large and medium sized fish. Bull. Jpn. Soc. Sci. Fish. 44:451–455.

Okiyama, M.
1965. A preliminary study on the fish eggs and larvae occurring in the Sado Strait, Japan Sea, with some remarks on the vertical distribution of some fishes. (In Jpn.) Bull. Jpn. Sea Reg. Fish. Res. Lab. 15:13–37.

Parin, N. V.
1967. Diurnal variations in the larval occurrence of some oceanic fishes near the ocean surface. Oceanology 7:115–121.

Sablin, V. V.
1978. Smertnost' sajry Cololabis saira (Brevoort) na rannikh stadiyakh zhizni (The mortality of the saury Cololabis saira (Brevoort) at early life stages). (In Russ.) Izv. TINRO 102:72–75.

Smith, P. E., E. H. Ahlstrom, and H. D. Casey.
1970. The saury as a latent resource of the California Current. Calif. Mar. Res. Comm., CalCOFI Rep. 14:88–130.

Smith, P. E., and S. L. Richardson,
1977. Standard techniques for pelagic fish egg and larva surveys. FAO Fish. Tech. Pap. 175, 100 p.

Statistics and Information Department, Japan.
1986. Showa 60 nen gyogyo to shokugyo seisan tokei nenpo (Annual report of fisheries and aquaculture statistics, 1985). (In Jpn.) Minist. Agric., For. Fish., Agric. Stat. Assoc., Tokyo, 288 p.

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

Watanabe, T.
1987. Appearance of the dominant 1980 year-class of Japanese sardine. (In Jpn.) Bull. Jpn. Soc. Fish. Oceanogr. 51:34–38.

Watanabe, Y., J. L. Butler, and T. Mori.
1988. Growth of saury, Cololabis saira, in the northeastern and northwestern Pacific Ocean. Fish. Bull., U.S. 86:489–498.

Yusa, T.
1960. Embryonic development of the saury Cololabis saira (BREVOORT). Bull. Tohoku Reg. Fish. Res. Lab. 17:1–14.

Zweifel, J. R., and P. E. Smith.
1981. Estimates of abundance and mortality of larval anchovy (1951–1975). Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:248–259.