

Growth and Survival of Pacific Saury *Cololabis saira* in the Kuroshio-Oyashio Transitional Waters

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(Received 20 June 2002; in revised form 27 December 2002; accepted 4 February 2003)

Growth and mortality rates of larval and early juvenile Pacific saury *Cololabis saira* were estimated for spring and autumn spawning seasons in the Kuroshio-Oyashio transitional waters and for winter spawning season in the Kuroshio waters in 9 years from 1990–1998, based on quantitative fish sampling and otolith daily ring readings. Growth and mortality rates were more variable in the Kuroshio-Oyashio transitional waters than in the Kuroshio waters. The estimated production of 40-mm preschooling juveniles was a positive function of larval production in the hatching length class (5.9–9.9 mm) in the Kuroshio waters. In the Kuroshio-Oyashio transitional waters, rather than larval production in the hatching length class, cumulative survival through the larval and early juvenile stages determined the juvenile production. Variable growth and survival rates of saury observed in the transitional waters seem to be associated with large environmental variability in the waters, including shifts of the Kuroshio and Oyashio fronts and development of streamers and eddies between the fronts.

Keywords:

· Transitional waters,
· Kuroshio waters,
· Pacific saury,
· larvae,
· juveniles,
· daily production,
· growth,
· survival.

1. Introduction

Pacific saury *Cololabis saira* has been exploited as one of the important small pelagic fishes in Japan. Total catch during the permitted fishing season from August to December increased in the 1950s after the introduction of effective fishing gear the “stick-held dip net” or “bouke-ami” in Japanese. The catch peaked at 575 thousand ton in 1958 but declined in the 1960s down to a minimum of 52 thousand ton in 1969 (Fig. 1). It recovered rapidly by 1973 and fluctuated greatly in the 1970s. The fishermen’s association started regulating fishing after the 1980s to avoid the unstable fish prices they experienced during the 1970s. The catches in the 1980s and 1990s were stabilized, but the population was considered to have fluctuated greatly in these years. The potential catch in 1993 was estimated at 370 thousand ton instead of actual catch of 273 thousand ton, if it were not for the efforts regulation (Fisheries Agency, 1997).

The distribution range of Pacific saury extends over the entire North Pacific from coast to coast to the north of 25°N (Hubbs and Wisner, 1980). Not only adults but larvae and juveniles of this species are distributed continuously from the inshore waters of Japan to as far offshore as 175°E in the western and central North Pacific (Watanabe and Lo, 1989). The saury is an oceanic spawner compared with other small pelagic fish species such as Japanese sardine *Sardinops melanostictus*, Japanese anchovy *Engraulis japonicus*, and mackerels *Scomber japonicus* and *S. australasicus* which spawn in coastal and nearshore waters around Japan (Zenitani *et al.*, 1995).

The saury migrates north into the subarctic Oyashio waters around the Kurile Islands in summer for feeding on abundant calanoid copepods (Odate, S., 1977). They start southward migration at the end of summer (Fukushima, 1979). The spawning season of saury starts in September in the transitional waters between the Kuroshio Extension and the subarctic Oyashio front off northern Japan (Watanabe *et al.*, 1997). Active spawning is observed in October and November but tends to decline in December in the transitional waters. They shift

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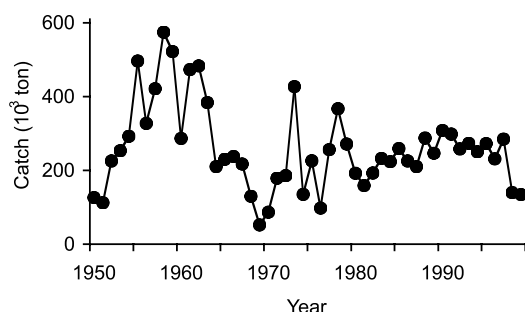


Fig. 1. Total catch of the saury in 50 years from 1950–1999. Fishing effort was regulated by the fishermen association in the 1980s and 1990s in order to avoid the unstable fish prices they had experienced in the 1970s.

the spawning grounds from the transitional waters to the warm Kuroshio waters off southern Japan in winter. Spawning activity in the Kuroshio waters is high in February and March (Watanabe and Lo, 1989). The spawning grounds return to the transitional waters again in spring with moderate activity in May. Spawning activity in July and August is usually low in the Pacific waters, but is high in spring and summer months in the Sea of Japan (Fukataki, 1959). Spawning of this species thus extends all year round in the waters around Japan.

Among the seasonally and spatially wide ranges of spawning activities, vital parameters in early life stages, such as growth rates and instantaneous mortality rates, may be different depending on the spatially and temporally different environmental conditions (Watanabe *et al.*, 1997). Daily growth rates can be estimated based on age determination by reading otolith daily rings (Watanabe *et al.*, 1988). Based on quantitative data collected from larvae and juveniles and their daily growth rates, a mortality curve in these stages can be constructed and daily larval production at hatching can be estimated (Watanabe and Lo, 1989). In this paper, we estimated parameters of larval production at hatching, age of 40 mm juveniles, and cumulative survival from hatching to 40 mm juveniles for 3 spawning seasons of 9 years from 1990–1998. We have compared interannual variability in the vital parameters in the Kuroshio-Oyashio transitional waters and Kuroshio waters in association with environmental variabilities in these spawning grounds.

2. Data Sources and Methods

2.1 SST

SST data in the western North Pacific for 8 years from 1990–1997 were obtained from the Global Sea Ice and Sea Surface Temperature Data Set (GISST version 2.3a) of the United Kingdom Meteorological Office

(UKMO) (Parker *et al.*, 1994), and were compiled in the Kuroshio-Oyashio transitional waters (33–42°N, 140–175°E) in May and November and in the Kuroshio waters (28–36°N, 129–145°E) in February. The 8 year average of SST in each 1° × 1° grid was calculated and used to draw average SST contours for the waters. SST anomalies in each grid of the 8 years from the 8 year average were calculated for February, May, and November.

2.2 Field collections

Larvae and juveniles of saury were collected in the Kuroshio-Oyashio transitional waters mainly between 35–40°N 140–160°E in autumn (September to December), in the Kuroshio waters mainly between 29–35°N 130–143°E in winter (January to March), and in the transitional waters between 35–40°N 140–165°E in spring (April to June). We used a cylindrical-conical net with 1.3-m mouth diameter and 0.45-mm mesh aperture. The side length of the cylinder section was 2.5 m and that of the conical section 3.0 m. The net is towed on the sea surface for 10 minutes at 2 knot to collect saury larvae and juveniles inhabiting the epi-pelagic stratum (Okiyama, 1965; Odate and Hayashi, 1977). Sea surface area covered by a tow was 803 m². Fish abundance was expressed in number per unit of sea surface area (km²).

Net tow samples were preserved in 5% seawater formalin for body length measurements or in 80% ethanol for both body length measurements and otolith readings. For each of the 27 spawning seasons in the 9 years from 1990–1998, a total of 58–391 tow samples were collected and 906–9500 saury larvae and juveniles were sorted out from the samples and measured for body length (L, the distance from the tip of lower jaw to the posterior end of a muscular knob at the base of the caudal peduncle) to the nearest 0.1 mm.

Teleost fishes have 3 pairs of otoliths in the inner year, sagitta, asteriscus, and lapillus, which are composed of calcium carbonate crystal (calcite) and organic matrix. The sagitta is largest among the 3 otoliths and grows by adding one crystal layer of 2–7 μm in thickness every day after 4 days before hatching in the Pacific saury (Watanabe and Kuji, 1991). We can estimate the daily age of individual saury by counting the number of daily growth rings in a sagittal otolith under a light microscope (Fig. 2).

2.3 Corrections for body shrinkage and catch efficiency

The body length of larval and juvenile sauries had shrunk due to preservation in 5% formalin. We corrected body length by multiplying by a factor of 1.12 for fish smaller than 9.9 mm and 1.01 for those larger than 10.0 mm (Oozeki *et al.*, 1991). For fish preserved in 80% ethanol we used a correction factor of 1.08 for fish smaller than 9.9 mm and 0.98 for those larger than 10.0 mm

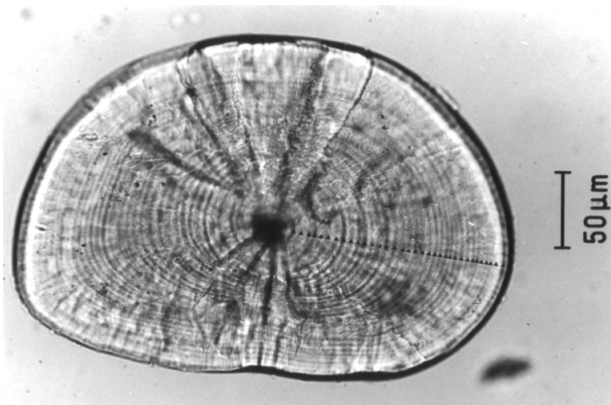


Fig. 2. Sagittal otolith of 32.7 mm juvenile saury with 34 daily growth rings. As a saury larva has 5 rings at hatching, this specimen was estimated to be 29 days old.

(Oozeki *et al.*, 1991).

Larvae (5.9–24.9 mm L) and juveniles (25.0–44.9 mm L) in a tow sample were classified into 8 L-classes of 5-mm intervals, 5.9–9.9, 10.0–14.9, ..., 40.0–44.9 mm in corrected L. Since the saury starts schooling behavior at about 50 mm L (Watanabe and Kuji, 1991), juveniles larger than 45.0 mm L were not included in the size frequency analyses due to low catch efficiency by the net used.

Catch efficiencies are different depending on the time of day and fish length. Therefore, numbers of fish per net tow in the 8 L-classes were corrected for diurnal differences in catch efficiency by the net used, using the matrix of correction factors in time-of-day and fish L (Watanabe, 1990). After this procedure, we obtained a body length frequency distribution for each tow sample. Mean numbers of fish per km² sea surface area in the 8 L-classes in the autumn, winter, and spring spawning seasons were calculated from all the net tow samples in a season.

2.4 Growth curve

Sample sizes ranging from 40–339 sagittal otoliths were dissected out from ethanol preserved fish specimens, including those larger than 45.0 mm after measuring body length (L). The samples were cleaned and mounted with a clear enamel resin on a glass plate. The number of daily growth rings in each sagitta was counted using the otolith reading system (Ratok System Engineering Co. Ltd) consisting of a light microscope, a video camera and a monitor, and an image analysis system. As saury larvae have five rings in their otoliths when hatched (Watanabe and Kuji, 1991), the daily age of fish was calculated to be the total number of rings minus five. We pooled all the otolith data for each spawning season to obtain L-at-age

plots of a season. The plots of each season were regressed to the Gompertz growth model (Watanabe *et al.*, 1997).

$$L_t = L_{\infty} \cdot \exp(-\exp(-K(t - t_f))),$$

where L_t is fish L (mm) at age t and, L_{∞} is an asymptotic L, K is a non-dimensional growth coefficient, and t_f is age at the inflection point of the growth curve.

2.5 Mortality curve

Using the Gompertz growth curve for each season, we calculated mid-interval ages ($t_{7.9}$, $t_{12.5}$, $t_{17.5}$, ..., $t_{37.5}$) and durations ($t_{10.0}-t_{5.9}$, $t_{15.0}-t_{10.0}$, $t_{20.0}-t_{15.0}$, ..., $t_{45.0}-t_{40.0}$) in days of the 8 L-classes of 5 mm intervals. The L range of the smallest L-class was fixed at 5.9–9.9 mm and the mid-L at 7.9 mm. Daily fish production per km² of sea surface area was calculated by dividing the mean number of fish (km⁻²) in each of 8 L-classes by duration in days of the corresponding L-class. Production in the smallest L-class (5.9–9.9 mm) was termed larval production in the hatching L-class ($P_{t_{7.9}}$), which can be used as a parameter of spawning activity of the adult population in a season. Estimates of daily production of the 8 L-classes including the hatching L-class were then plotted against the mid-ages of the L-classes, and the plots were fitted to an exponential decay model (Watanabe and Lo, 1989).

$$P_t = P_0 \cdot \exp(-Z \cdot t),$$

where P_t is a daily fish production (km⁻²day⁻¹) at age t , P_0 is a daily larval production (km⁻²day⁻¹) at age 0, and Z is a daily instantaneous mortality rate.

The age of preschooling juveniles at 40 mm L (t_{40}) of each season was calculated from the Gompertz growth curve of the season. The daily production of 40 mm juveniles, $P_{t_{40}}$ (fish km⁻²day⁻¹), was calculated as,

$$P_{t_{40}} = P_0 \cdot \exp(-Z \cdot t_{40}).$$

3. Results

3.1 Location of spawning grounds

Saury larvae were distributed continuously in the inshore and offshore waters off northern Japan in the Kuroshio-Oyashio transitional waters in the autumn spawning season from September to December. In 1995, for example, the geographical range of positive net tows of larval collection extended from 35–42°N and 140–157°E (Fig. 3).

Larval distribution was minimal in the transitional water in winter. The distribution range shifted to the southern waters around the Kuroshio Current off southern Japan (Fig. 3). The axis of the Kuroshio shifted latitudinally in the years studied (Maritime Safety Agency, 1990–

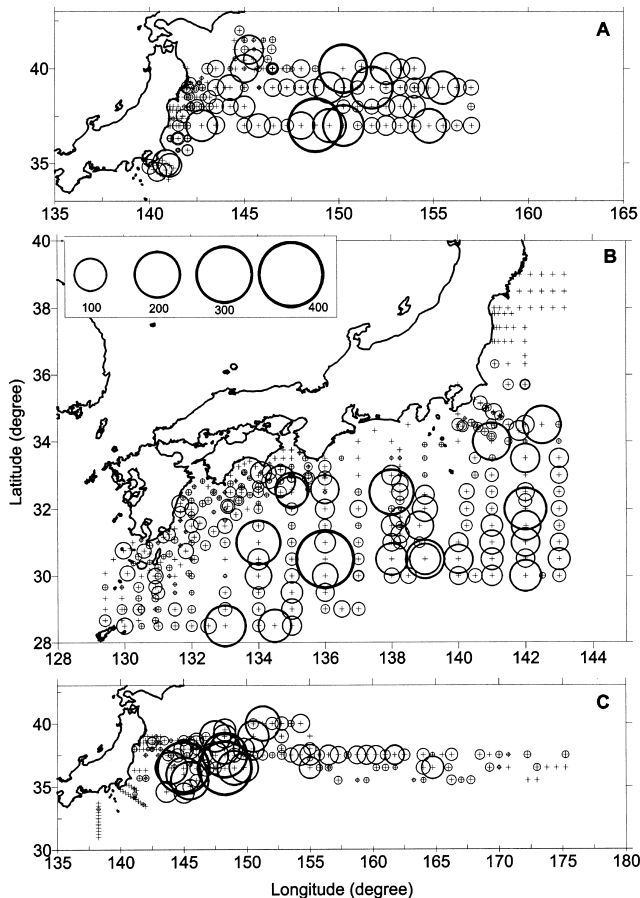


Fig. 3. Distribution of saury larvae in the transitional waters in autumn 1995 (top), in the Kuroshio waters in winter 1996 (middle), and in the transitional waters in spring 1996 (bottom).

1998), but the geographical range of positive net tows of larval collection did not change substantially, being distributed from 28–35°N and 130–143°E in these years.

In spring 1996, high larval distributions were observed in the Kuroshio-Oyashio transitional waters (Fig. 3). Only a small number of larvae were collected in the Kuroshio waters. The geographical range of positive net tows of larval collection extended from the inshore waters of northern Japan to as far offshore as 175°E near to the Emperor Sea Mounts. The latitudinal range of the distribution expanded from 34–40°N.

Our survey area did not cover the entire distribution range of saury larvae. Therefore it was not possible to delimit geographical ranges of spawning activity of the saury by seasons. However, the survey in each spawning season covered a substantial proportion of the larval distribution range and we believe that we obtained representative fish samples with which we were able to estimate vital parameters of larval and juvenile growth and survival in this study.

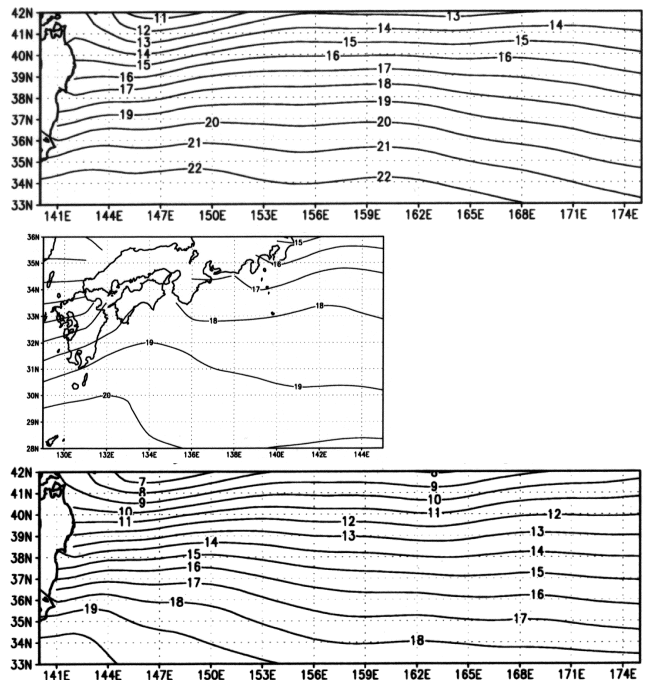


Fig. 4. Average SST from 1990–1997 in November in the transitional waters (top), in February in the Kuroshio waters (middle), and in May in the transitional waters (bottom). Data from GISST of UKMO were averaged for each month.

3.2 SST

Contours of the 8 year average SST ran perpendicular to the coastline of northern Japan in autumn. The SST gradient in the spawning grounds of the saury was steep in the transitional waters in November 1995, for example, ranging from 13–21°C (Fig. 4). A positive SST anomaly (+0.8°C) was located around 38°N 151°E in this month, and the three centers of negative SST anomaly (−0.3, −0.3, −0.6°C) were located in its inshore and off-shore areas (Fig. 5).

The SST gradient was not as steep in the Kuroshio waters in winter as that in the transitional waters. There were four contours in the spawning grounds from 17–20°C in an example of February 1996 (Fig. 4). The SST anomaly was negative in the eastern part of the spawning grounds in this month, ranged from ± 0 in the western part to −0.6°C in the eastern range (Fig. 5).

In the spawning grounds in the transitional waters in spring, the SST distribution was basically the same as that in autumn. SST contours ran perpendicular to the coastline of northern Japan, ranging from 10–18°C in May 1997 (Fig. 4). The SST anomaly was even stronger in May 1997 than in November 1995 (Fig. 5). Strong negative anomaly centers (−0.8, −0.9°C) were located in the northern part of the spawning grounds in May 1997, and the southern part exhibited a strong positive anomaly (+1.0°C).

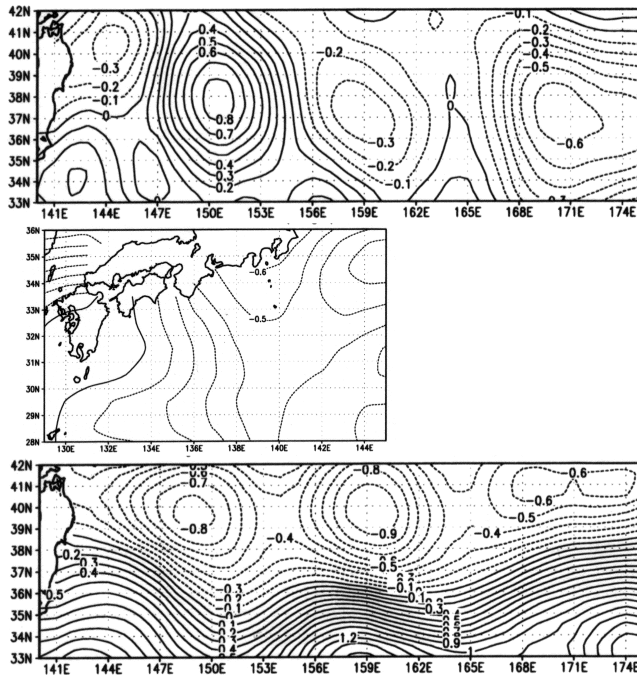


Fig. 5. SST anomalies in November 1995 (top), February 1996 (middle), and May 1997 (bottom) from the 8 years average in $1^\circ \times 1^\circ$ grids of respective months.

3.3 Vital parameters

The growth curve of saury larvae and juveniles in the Kuroshio waters in winter 1994, for example, was calculated as

$$L_t = 81.9 \cdot \exp(-\exp(-0.0313(t - 36.2))).$$

In this growth curve the growth rate accelerates up to the inflection point of 36.2 days and decelerates after this point. The age of 40 mm juveniles calculated from this growth equation was 46.8 days after hatching (Fig. 6).

The mortality curve of saury larvae and juveniles in winter 1994 (Fig. 6) was expressed as

$$P_t = 4308 \cdot \exp(-0.086t).$$

Larval production in the hatching L-class (5.9–9.9 mm L, mid-size = 7.9 mm L, mid-age ($t_{7.9}$) = 9.8 days) estimated from this mortality curve was $1854.6 \text{ fish km}^{-2}\text{day}^{-1}$. Cumulative survival from the hatching L-class up to 40 mm juvenile ($P_{t_{40}}/P_{t_{7.9}}$) was estimated to be 4.15%, and 40 mm juvenile production was estimated to be $77.0 \text{ fish km}^{-2}\text{day}^{-1}$.

Estimated growth and survival parameters in the transitional waters in autumn spawning season for the 9 years from 1990–1998 are summarized in Table 1. Larval production in the hatching L-class was large (2566.3 ± 1655.4

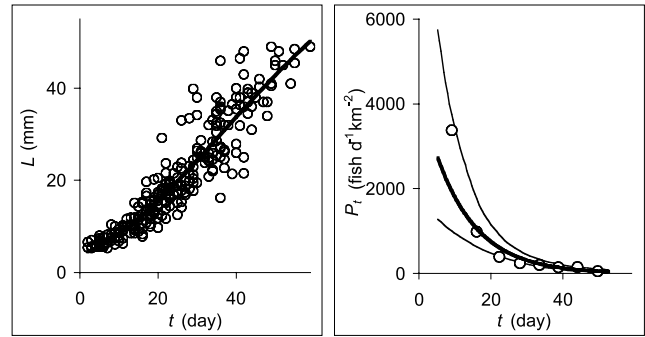


Fig. 6. Examples of Gompertz growth curve (left) and exponential mortality curve (right) of larval and juvenile saury of 1994 winter-spawned cohort in the Kuroshio waters. Circles in the growth curve panel represent body length at age of individual larvae and juveniles. Circles in the mortality panel show fish productions of 8 body length classes regressed to the exponential curve and thin lines indicate 95% confidence limits of the curve.

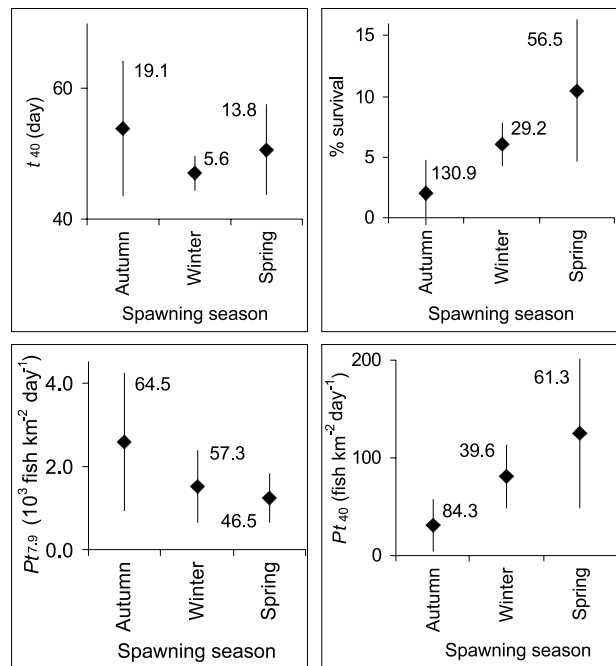


Fig. 7. Mean (diamond) and standard deviation (vertical bar) of growth (t_{40} , top left) and survival (% survival, top right), larval production in the hatching L-class ($P_{t_{7.9}}$, bottom left), and 40 mm juvenile production ($P_{t_{40}}$, bottom right) in the 3 spawning seasons. CV (%) is attached to the vertical bar.

$\text{fish km}^{-2}\text{day}^{-1}$), but the large mortality coefficient (0.107 ± 0.037), effective over longer time duration up to the age of 40 mm juvenile (54.0 ± 10.3 days), resulted in smaller cumulative survival ($2.05 \pm 2.68\%$). This led to a

Table 1. Vital parameters for autumn-spawned cohorts in the transitional waters. # tows, number of net tow samples; $Pt_{7.9}$, larval production in the hatching L-class; Z , daily instantaneous mortality rate; t_{40} , age of 40 mm L juveniles; % survival, cumulative survival % from hatching L-class to 40 mm juveniles.

	# tows	$Pt_{7.9}$	Z	t_{40}	Pt_{40}	% survival
1990	78	1499.9	0.101	76.2	3.6	0.24
1991	180	5988.1	0.129	45.4	70.2	1.17
1992	387	3866.1	0.074	58.7	59.5	1.54
1993	361	2331.2	0.105	57.5	20.8	0.89
1994	342	3239.2	0.159	46.7	7.3	0.23
1995	297	1044.2	0.075	45.0	62.3	5.97
1996	260	2106.5	0.112	49.4	16.3	0.77
1997	307	2541.1	0.156	46.4	6.5	0.26
1998	291	480.6	0.049	60.3	35.5	7.38
Mean		2566.3	0.107	54.0	31.3	2.05
sd		1655.4	0.037	10.3	26.4	2.68
CV (%)		64.5	34.9	19.1	84.3	130.9

Table 2. Vital parameters for winter-spawned cohorts in the Kuroshio waters. Data of $Pt_{7.9}$, Z , Pt_{40} , and % survival in 1995 are excluded from analyses because of outlying $Pt_{7.9}$ and Z . See Table 1 for the labels in the first line.

	# tows	$Pt_{7.9}^*$	Z^*	t_{40}	Pt_{40}^*	% survival*
1990	58	1151.4	0.071	45.6	81.5	7.08
1991	219	411.9	0.073	47.8	29.2	7.09
1992	324	1216.1	0.085	47.8	60.3	4.96
1993	89	791.3	0.072	47.3	61.9	7.82
1994	170	1854.6	0.086	46.8	77.0	4.15
1995	188	5445.2	0.137	47.4	23.4	0.43
1996	366	1141.2	0.063	51.6	90.3	7.92
1997	362	2990.5	0.084	47.0	107.1	3.58
1998	267	2533.3	0.083	42.3	145.0	5.72
Mean		1511.3	0.077	47.1	81.5	6.04
sd		865.8	0.008	2.6	32.3	1.76
CV (%)		57.3	10.3	5.6	39.6	29.2

*Mean, sd, and CV were calculated exclusive of 1995 data.

small production of 40 mm juveniles (31.3 ± 26.4 fish $\text{km}^{-2}\text{day}^{-1}$). CVs in the growth (t_{40}) and survival parameters (% survival) were 19.1% and 130.9%, respectively, which resulted in large CV (84.3%) in 40 mm juvenile production (Pt_{40}) (Fig. 7).

In the Kuroshio waters in the winter spawning season (Table 2), estimated parameters of larval and 40 mm juvenile productions (5445.2 and 23.4 fish $\text{km}^{-2}\text{day}^{-1}$) and mortality ($Z = 0.137$, % survival = 0.43) in 1995 were outliers in the dataset. Excluding these data, the mean \pm sd of larval production in the hatching L-class ($Pt_{7.9}$) was 1511.3 ± 865.8 fish $\text{km}^{-2}\text{day}^{-1}$. The mean age of 40 mm

juvenile (t_{40}) in the 9 years was estimated to be 47.1 ± 2.6 days. CV of t_{40} was small (5.6%) indicating that growth rate of the saury larvae and juveniles was stable in the Kuroshio waters (Fig. 7). Cumulative survival up to the 40 mm juvenile stage (% survival) was $6.04 \pm 1.76\%$ (CV = 29.2%) and 40 mm juvenile production (Pt_{40}) was estimated to be 81.5 ± 32.3 fish $\text{km}^{-2}\text{day}^{-1}$ (CV = 39.6%).

Larval production in the hatching L-class (1234.2 ± 574.2 fish $\text{km}^{-2}\text{day}^{-1}$) in the transitional waters in spring (Table 3) was at the same level as that in the Kuroshio waters in the winter spawning season. The age of 40 mm juveniles ($t_{40} = 50.6 \pm 7.0$ days, CV = 13.8%) was not

Table 3. Vital parameters for spring-spawned cohorts in the transitional waters. See Table 1 for the labels in the first line.

	# tows	$Pt_{7.9}$	Z	t_{40}	Pt_{40}	% survival
1990	239	1186.1	0.045	45.7	256.3	21.61
1991	383	636.4	0.069	45.3	52.4	8.23
1992	231	891.2	0.042	53.1	131.3	14.73
1993	330	1667.4	0.066	65.8	62.7	3.76
1994	391	1942.4	0.060	52.1	190.2	9.79
1995	261	1109.3	0.047	52.3	138.8	12.51
1996	198	1263.7	0.059	43.6	183.0	14.48
1997	142	353.3	0.084	44.5	16.9	4.78
1998	83	2058.0	0.066	53.4	92.7	4.50
Mean		1234.2	0.060	50.6	124.9	10.5
sd		574.2	0.013	7.0	76.6	5.9
CV (%)		46.5	22.5	13.8	61.3	56.5

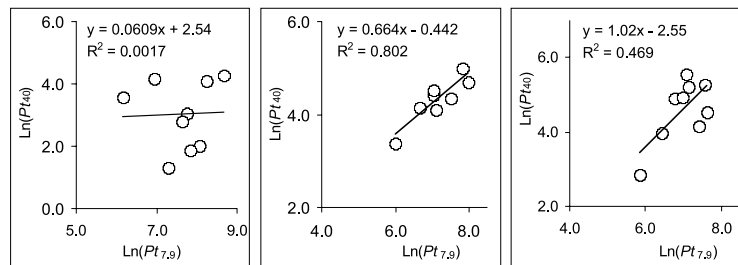


Fig. 8. Regression of 40 mm juvenile production (Pt_{40} km⁻²day⁻¹) to larval production in the hatching L-class ($Pt_{7.9}$ km⁻²day⁻¹) for autumn (left), winter (middle), and spring (right) spawning seasons.

different from that in winter, but the mortality coefficient ($Z = 0.060 \pm 0.013$) was smaller than in the Kuroshio waters ($Z = 0.077 \pm 0.008$), resulting in higher percentage survival (10.5 ± 5.9) in the transitional waters in spring (Fig. 7). The mean production of 40 mm juveniles (Pt_{40}) was estimated to be 124.9 fish km⁻²day⁻¹, which tended to be higher than in the Kuroshio waters in winter but was very variable (sd = 76.6, CV = 61.3%).

3.4 Determinants of 40 mm juvenile production

Production of 40 mm juveniles (Pt_{40}) in the 9 years were regressed to larval production in the hatching L-class ($Pt_{7.9}$) for each spawning season (Fig. 8). In the Kuroshio waters in winter, 80.2% of the interannual variability could be significantly ($P < 0.01$) explained by larval production in the hatching L-class. In the transitional waters, on the other hand, virtually none of the interannual variability was explained by larval production in autumn. In spring 46.9% of juvenile production was explained by larval production.

Regression analyses of 40 mm juvenile production to percent survival from the hatching L-class up to 40

mm showed that 67.1% ($P < 0.01$) and 54.9% ($P < 0.05$) of interannual variabilities in autumn and spring, respectively, could be explained by percentage survival in the transitional waters (Fig. 9), but in the Kuroshio waters in winter, only 10.7% of the variability was explained by percentage survival.

3.5 Density-dependent survival

Cumulative survival from the hatching L-class to 40 mm juvenile (percentage survival = $Pt_{40}/Pt_{7.9}$) was correlated with larval production in the hatching L-class ($Pt_{7.9}$) in order to examine the presence of a density-dependent survival process in larval and juvenile stages (Fig. 10). In the Kuroshio waters in winter, percentage survival was significantly ($R^2 = 0.583$, $P < 0.05$, $n = 8$) correlated with larval production. In the transitional water on the other hand, percentage survival was not correlated with larval production in the hatching L-class. CV in fish production tended to decrease from the hatching L-class (57.3%) to 40 mm juvenile (39.6%) in the Kuroshio waters (Fig. 7), implying the presence of a stabilization mechanism through the survival process in the early life stages. CVs

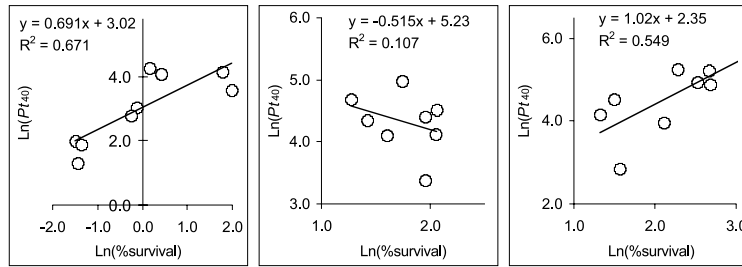


Fig. 9. Regression of 40 mm juvenile production (Pt_{40} $\text{km}^{-2}\text{day}^{-1}$) to percentage survival from hatching to 40 mm juvenile for autumn (left), winter (middle), and spring (right) spawning seasons.

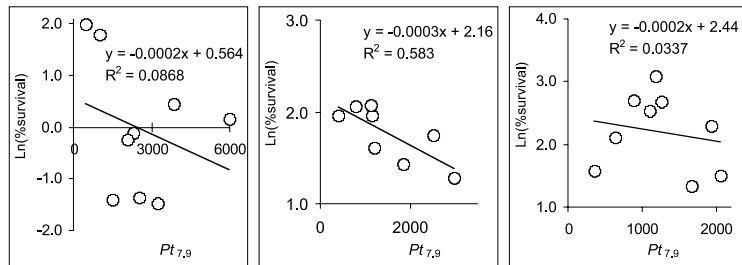


Fig. 10. Regression of percentage survival from the hatching L-class to 40 mm juvenile (% survival) to larval production in the hatching L-class ($Pt_{7.9}$ $\text{km}^{-2}\text{day}^{-1}$) for autumn (left), winter (middle), and spring (right) spawning seasons.

in fish production in the transitional waters tended to increase in these stages, from 64.5% to 84.3% in autumn and from 46.5% to 61.3% in spring.

4. Discussion

4.1 Extensive spawning of saury

The Kuroshio-Oyashio transitional waters are defined as the area between the Kuroshio Extension (14°C at 200 m depth; Kawai, 1972a) and the subarctic Oyashio front (5°C at 100 m depth; Kawai, 1972b). We did not have temperature data at these depths in this study but the 14°C contour at 200 m depth roughly corresponds to the 18°C SST contour and the 5°C contour at 100 m depth roughly corresponds to the 7°C SST in May (see figures 3 and 4 of Shimizu *et al.*, 2001). The distribution ranges of the saury larvae in the transitional waters in the 9 years from 1990–1998 were characterized by latitudinal expansion from the Kuroshio Extension to near to the subarctic Oyashio front.

Small forage fishes such as Japanese sardine, *Sardinops melanostictus*, and round herring, *Etrumeus teres*, spawn in the Kuroshio waters off the Pacific coasts of southern Japan (Zenitani *et al.*, 1995). Eggs and larvae of Japanese anchovy could be collected in the transitional waters when the anchovy population became large, as in the 1950s (Odate, 1957) and 1990s (Takahashi *et al.*,

2001), but their principal spawning grounds are located in the coastal waters inshore of the Kuroshio current in southern Japan (Zenitani *et al.*, 1995). These forage fishes may migrate north to the transitional waters in summer in juvenile and adult stages but do not use the transitional waters for their principal spawning grounds. Predatory fishes such as bluefin tuna, *Thunnus thynnus*, and skipjack tuna, *Katsuwonus pelamis*, immigrate to the transitional waters in spring and summer to feed on these small forage fishes (Yukinawa and Yabuta, 1967; Nihira, 1996), but their spawning grounds are located further south near the Ryukyu Islands for bluefin tuna (Yabe *et al.*, 1966) or the tropical Pacific for skipjack tuna (Ueyanagi, 1969). Among the forage and predatory pelagic fishes, Pacific saury alone uses the transitional waters for its principal spawning grounds in the early (autumn) and late (spring) spawning seasons.

The Kuroshio axis is defined to be the 15°C isotherm at 200 m depth in the Pacific region of southern Japan (Kawai, 1972b), which almost corresponds to 18°C SST. The larval distribution of saury extends through offshore and inshore waters of the Kuroshio axis. The larval distribution is weighted in the offshore waters of the Kuroshio in saury, which is different from the inshore-weighted distribution in Japanese sardine larvae in these waters in February and March (Watanabe *et al.*, 1996). Eggs of mackerels, *Scomber japonicus* and *S.*

australasicus, are mostly distributed in the coastal and inshore waters of the Kuroshio current (Zenitani *et al.*, 1995).

Thus the spawning activity of saury is extensive spatially from the inshore to the offshore oceanic waters in the transitional and Kuroshio waters, and temporally almost all year round. In these large spawning ranges in space and season, substantial differences in environmental conditions were observed, which seemed to be linked to differences in vital parameters of larval and juvenile saury.

The incubation time of the saury from fertilization to hatching is about 17 days at 13.5–15.7°C and 11 days at 16–19°C (Yusa, 1960). Their eggs have filaments and are attached to floating objects such as drifting seaweed. Hatched larvae stay in the epipelagic layers throughout the larval stage (Okuyama, 1965; Odate and Hayashi, 1977). Eggs and larvae may be transported substantially in the strong flow field in the region covered by this study. The spawning grounds of saury were considered to be more restricted to than the distribution range of larvae in this study. But the extensive survey in this study covered the principal distribution range of larvae and juveniles, and therefore the samples of saury larvae and juveniles in this study are considered to represent growth and survival processes in the early life stages of each seasonally-spawned cohort.

4.2 Large variability in environments and vital parameters in the transitional waters

One of the major differences in environmental conditions within the spawning ranges of saury was found in the variability of SST between the Kuroshio waters and the Kuroshio-Oyashio transitional waters. Spatial and interannual variabilities of SST in the Kuroshio waters in winter spawning season were small compared to those in the transitional waters in autumn and spring spawning seasons. Large variabilities in the transitional waters are not surprising when we consider the complexity of the oceanographic structures in these waters, such as the coastal and offshore intrusions of the Oyashio branches (Hirai and Yasuda, 1988; Yasuda and Watanabe, 1994), development and evolution of warm core rings (Yasuda *et al.*, 1992), and associated streamers and filaments between the subarctic Oyashio fronts and the warm Kuroshio Extension. These complex structures in the transitional waters cause the steep SST gradients (Fig. 4) as well as the large interannual SST variability in the transitional waters (Fig. 5).

Growth and survival processes of the Pacific saury were found to be more variable in the transitional waters than in the Kuroshio waters. CVs of the growth rate parameter (t_{40}) in autumn and spring in the transitional waters (>13%) were larger than that in the Kuroshio waters

(5.6%); those of the survival parameter (% survival) in autumn and spring were almost 4 and 2 times as great as that in winter (Fig. 7). These differences in variability in these waters seem to be associated with the variable environmental conditions represented by SST; that is, variable growth and survival under variable conditions in the transitional waters, stable growth and survival under stable conditions in the Kuroshio waters.

4.3 What determines 40 mm juvenile productions?

Pacific saury has a relatively long incubation period from fertilization to hatching (Yusa, 1960). Hatched larvae swim continuously and start feeding within a day of hatching (Watanabe and Kuji, 1991). They start schooling behavior when they attain 45–50 mm L (Watanabe and Kuji, 1991). Through the course of early life history, larval and early juvenile stages are most vulnerable to mass mortality from food limitation and/or predation in general (Houde, 1989). The production of juveniles after these vulnerable stages can be used as a quantitative index of the recruiting cohort. We used 40 mm juvenile production (Pt_{40}) as an index of abundance of recruitment for each seasonally-spawned cohort.

Under stable environments in the Kuroshio waters in winter, 40 mm juvenile production (Pt_{40}) was largely (80.2%) determined by larval production in the hatching L-class, but percentage survival did not explain the juvenile production (Figs. 8 and 9). This result indicated that recruitment of the winter-spawned cohort is a positive function of larval production in the hatching L-class with a slight modification by percentage survival from hatching to recruitment. If it is true for the Pacific saury that larval production is an index of spawning biomass in spite of a long incubation time, recruitment of the saury may be a function of spawning biomass, which constitutes a basis of a functional stock-recruitment relationship in the winter spawned cohort.

Under variable environments in the transitional waters in autumn, on the other hand, virtually none of interannual variability in 40 mm juvenile productions was explained by larval productions in the hatching L-class. Instead, 67.1% of the variability was explained by percentage survival (Figs. 8 and 9). This demonstrated that in autumn-spawned cohorts in the transitional waters, larval productions in the hatching L-class were largely modified by percentage survival from hatching to recruitment, and therefore spawning biomass has no direct relation to recruitment of the new generation in these cohorts. A functional stock-recruitment relationship cannot be expected in autumn-spawned cohorts in the transitional waters.

In the transitional waters in spring, about 50% of the interannual variability in 40 mm juvenile production was explained by larval production in the hatching L-class, and another 50% was explained by percentage survival

from hatching up to 40 mm L. Interannual variabilities in growth (CV = 13.8%) and survival (CV = 56.5%) in the spring spawning season lay in between those in the winter and in autumn spawning seasons. The moderate variabilities in vital parameters in spring resulted in an intermediate determining process of 40 mm juvenile production between winter and autumn. Although the autumn and spring spawning seasons in the transitional waters did not seem to be different in terms of the magnitude of SST variability in this study, variabilities in vital parameters of larval and juvenile saury were different between the two seasons. In order to understand differences in determining processes of growth and survival between autumn and spring, we need to know in detail about the environments of saury spawning grounds, such as primary and secondary productions and predator abundance.

4.4 Density-dependent survival

In the winter-spawned cohorts, percentage survival was negatively correlated with larval production in the hatching L-class (Fig. 10). This implies that survival process from hatching to 40 mm juvenile stage is density-dependent. In the case of 1995 when the adult population produced an exceptionally large amount of offspring (5445.2 fish km⁻²day⁻¹) in the Kuroshio waters (Table 2), instantaneous mortality rate was exceptionally large ($Z = 0.137$) and percentage survival was extremely low (0.43%), indicating an occurrence of strong density-dependent mortality in this year. If the 1995 data (5445.2, 23.4) are added to the plot in Fig. 8, the $P_{t_{7.9}}-P_{t_{40}}$ relationship in winter may be expressed as a dome-shape curve. This may imply the presence of a Ricker type stock-recruitment relationship. We need more data in years of larval production in the hatching L-class greater than 3000 fish km⁻²day⁻¹. Including the 1995 data ($P_{t_{7.9}} = 5445.2$, % survival = 0.43), the correlation between larval production and percentage survival became highly significant ($R^2 = 0.865$, $P < 0.001$, $n = 9$). The survival process in the early life stages of saury is strongly density-dependent under a stable environment in the Kuroshio waters in winter.

The interannual variation in 40 mm preschooling juvenile production in winter (CV = 39.6%) was smaller than those in larval production in the hatching L-class (57.3%, Fig. 7). This could be explained by the density-dependent survival process found in this study in the winter-spawned cohorts of the saury. That is, the density-dependent survival process stabilized the population of the winter-spawned cohorts through the early life stages. A similar reduction in CV was reported in the plaice, *Pleuronectes platessa*, in the Dutch Wadden Sea by van der Veer and Bergman (1987), who demonstrated that CV in the abundance of newly settled plaice was 62–69% during 1973–82, while after the period of predation by

crustaceans from April to June, it dropped to 35%. This drop of CV was considered to be due to density-dependent regulation of the age 0-group plaice population by predation mortality.

Potential major factors of density-dependent survival are food limitation and predation mortality (Shepherd and Cushing, 1980). If food limitation operates as a limiting factor in winter-spawned cohorts of saury, density-dependent growth should be detected. We examined the correlation of growth rate (t_{40}) with the larval production in the hatching L-class for the cohorts for winter spawning season (Table 2), and found it insignificant ($R^2 = 0.0388$, $n = 8$). In the waters along the Kuroshio current, Nakata *et al.* (1995) estimated that production of nauplii and copepodites smaller than 1.0 mm in prosomal length, which are major food items of saury larvae and juveniles (Odate, K., 1977), was nine times greater than the total food requirements of carnivorous zooplankters and sardine larvae. As for the offshore waters of the Kuroshio current, they estimated that food availability for larvae was low. When observed synoptically over the Kuroshio waters, concentrations of copepod nauplii were not different between the inshore and offshore waters of the current axis (Watanabe *et al.*, 1998). Saury larvae can swim continuously upon hatching (Watanabe and Kuji, 1991) and are assumed to have a better ability to search and capture food organisms. Mortality due to food limitation is less probable as a factor of density-dependent survival in the saury.

Another potential factor of density-dependent mortality is predation. Cannibalism of eggs and larvae by the adult populations may be a typical example of density-dependent mortality in early life stages (Alheit, 1987; Young and Davis, 1990), but its consequence for population size to account for the variation of recruitment may be minimal (Smith *et al.*, 1990). There is little evidence that large-scale, density-dependent processes are significant regulators of mortality in the field (Heath, 1992). As for the saury population, we do not have data on predation mortality of larvae. This study has demonstrated circumstantial evidence of density-dependent mortality. We need data on the incidence of saury larvae and juveniles in piscivorous fish such as mackerel and tuna.

Acknowledgements

The extensive census of saury larvae and juveniles was conducted by Tohoku and Nansei National Fisheries Research Institutes, National Research Institute of Fisheries Science, and Prefectural Fisheries Experimental Stations in Hokkaido, Iwate, Miyagi, Fukushima, Ibaraki, Chiba, and Shizuoka with financial supports by Japan Fishery Agency. Otoliths were read by H. Furukawa, K. Takahashi, and K. Asakura.

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