

Environmental factors affecting larval growth of Pacific saury, *Cololabis saira*, in the northwestern Pacific Ocean

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ABSTRACT

Environmental factors affecting larval growth of the Pacific saury, *Cololabis saira*, were analyzed from specimens sampled in the northwestern Pacific Ocean in winter, spring and autumn, 1992–94. Body length at 5 days before sampling was individually estimated by back-calculation from otolith increment widths and recent growth rate was determined. Recent growth rates of saury larvae were significantly different among seasons and years. Results of multiple regression analysis between the recent growth rate and environmental factors indicated that sea surface temperature, chlorophyll *a* concentration and copepodite stage Copepoda concentration were positively correlated with the growth rate of saury larvae. Annual and seasonal variations of larval growth were largely explained by these environmental factors.

Key words: back-calculation, *Cololabis saira*, growth, larvae, otolith increment, Pacific saury

INTRODUCTION

Pacific saury, *Cololabis saira* (Brevoort), is widely distributed in the northwestern Pacific Ocean and supports a major pelagic fishery, with annual harvests ranging from 159 to 359 000 metric tonnes (t) in 1992–98 in Japan (Anonymous, 1999). Fluctuation in stock size is the major factor affecting catch variability and stock size is related to the degree of reproductive

success (Matsumiya and Tanaka, 1978). The saury population in the northwestern Pacific is composed of autumn-, winter-, and spring-spawned cohorts and these cohorts appear to correspond to the large (29.0–31.9 cm in body length), medium (24.0–28.9 cm), and small size (20.0–23.9 cm) categories of landed saury in the fishing season from mid August to late December (Fukushima *et al.*, 1990). Recruitment levels of the three seasonal cohorts need to be estimated for forecasting stock size; however, because the saury lay adhesive eggs attached to floating objects it is difficult to estimate egg abundance quantitatively. Larval production rates have been estimated from plankton sampling using mortality curves constructed from data on abundance of fish in various size-class and daily growth rates estimated from otolith readings (Watanabe *et al.*, 1997).

Seasonal and annual variations in larval production have been analyzed based on the cumulated dataset from 1990 to 1998 (Watanabe *et al.*, 2003). Growth and survival processes of saury larvae and juveniles described from a 9-yr data set indicated that high larval production, low growth rate and high mortality rate resulted in a small cumulative survival in the autumn spawning season (Watanabe *et al.*, 2003). A stable high growth rate and low mortality coefficient resulted in stable high survival in the Kuroshio waters in the winter spawning season. The 9-yr data set of larval parameters also showed the survival process after hatching controlled recruitment of the autumn- and the spring-spawned cohorts in the transitional waters. The variable growth rates and survival rates in these spawning seasons seemed to be associated with the large environmental variability in the transitional waters (Watanabe *et al.*, 2003). This hypothesis, that environmental variability in the transitional waters is a major factor affecting growth and survival, can be verified from detailed analyses of larval growth and survival processes. Methot and Kramer (1979) first suggested that recent growth rate estimated from otolith increment width is a useful method for evaluating the effects of environmental factors on larval growth. Oozeki and Watanabe (2000) reported that somatic growth of saury larvae could be estimated from otolith increment widths. In the case of Pacific saury,

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recent growth rate before sampling is expected to yield accurate information for detecting the effect of environmental factors on larval growth. In this paper, we estimated the recent growth rate during the larval stage of individual Pacific saury, *Cololabis saira*, using otolith increment width and then analyzed relationships between larval growth and environmental factors.

MATERIALS AND METHODS

Sampling

Saury larvae were collected in Kuroshio waters mainly between 30–35°N and 132–142°E in February, in Kuroshio–Oyashio transitional waters mainly between 37–39°N and 143–172°E in May and June and in transitional waters between 35–40°N and 141–160°E in November of 1992, 1993 and 1994 (Fig. 1). A

5.5-m long cylindrical–conical net with a 1.3-m mouth diameter and 0.45 mm mesh aperture was used for fish sampling. The net was towed on the sea surface for 10 min at two knots. Saury larvae were removed from the samples and preserved in 80% ethanol for both body-length measurements and otolith readings.

Sea surface temperature (SST) was measured at the sampling stations and water samples for determining the concentrations of chlorophyll *a* and nutrients were collected from the surface. A 250 mL water sample was filtered with a glass fiber filter (Whatman GF/F) and the concentrated phytoplankton cells with the filter were stored in a dark bottle with 2 mL of 90% acetone at –40°C. The cells were lysed by ultrasonic treatment and chlorophyll *a* was extracted by placing the sample in 10 mL of 90% acetone for 24 h after which the concentration determined by fluorometry

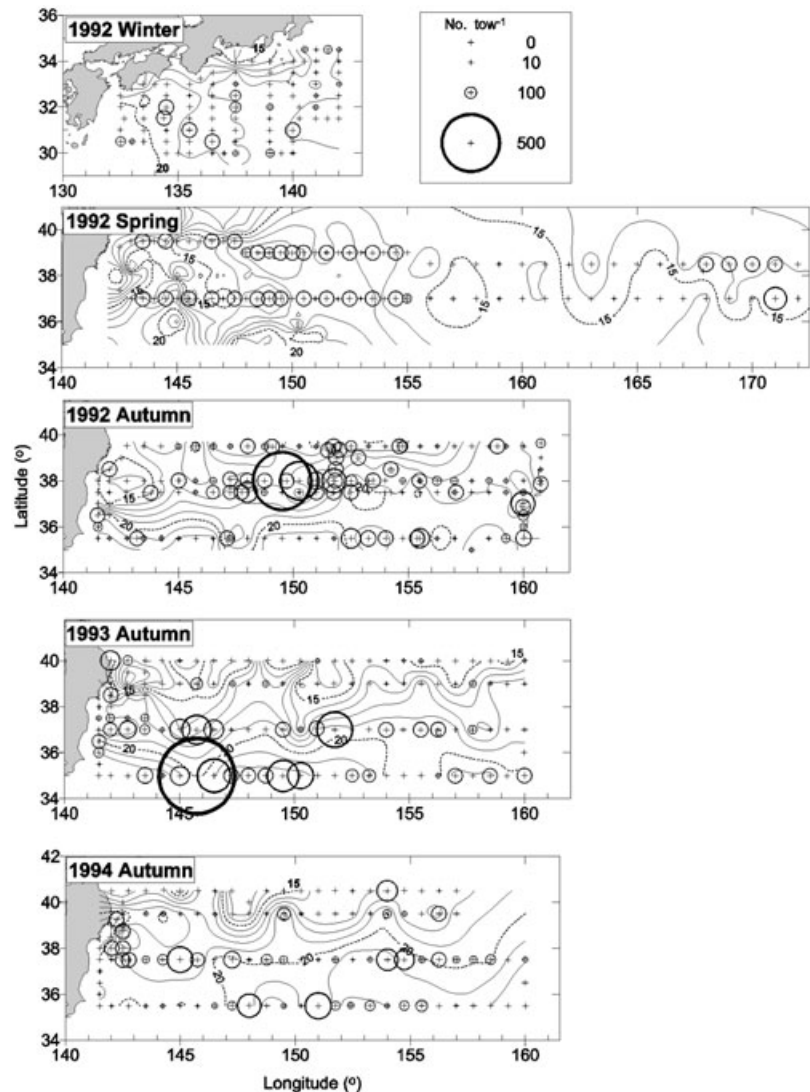


Figure 1. Sampling stations and distributions of saury *Cololabis saira* larvae (no. tow⁻¹) in winter, spring and autumn in 1992, and in autumn 1993 and 1994. Contours in each panel indicate the sea surface temperature (SST) (°C).

(Turner Design Model 10-AU, Turner Designs, Inc., CA, USA)(Holms-Hansen *et al.*, 1965). About 10 mL of the water sample was filtered with a cellulose acetate filter (DISMIC-25 cs, 0.45 µm pore size; Advantec Toyo, Tokyo, Japan) and stored frozen at -40°C in a test tube for nutrient analysis. Concentrations of nitrate ($\text{NO}_3\text{-N}$), nitrite ($\text{NO}_2\text{-N}$), phosphate ($\text{PO}_4\text{-P}$) and silicate ($\text{SiO}_2\text{-Si}$) were determined by continuous flow analysis (TRRAACS 800; Bran Luebbe, Nordstedt, Germany). Samples for nutrient analyses were not taken in winter and spring 1993 and 1994.

Food organism concentrations for saury larvae were analyzed mainly from a Norpac net (45-cm mouth diameter, 100-µm mesh aperture) towed from 10-m depth to the surface, and additionally from a Norpac net (335-µm mesh aperture; 1992 spring) towed from 150-m depth or a 20-L van Dorn water bottle samples (filtered by 25 µm mesh aperture; 1992 winter) from 2-m depth. Samples were preserved in 5% formalin. Copepod concentrations were counted in three categories as nauplius, copepodite and adult stage and were expressed as number L^{-1} .

Growth analysis

Knob length (KnL: distance from the tip of lower jaw to the posterior end of muscular knob on the caudal peduncle; Kimura, 1956) was measured on the preserved specimens. In Pacific saury, standard length (SL) or notochord length is not easily measured because of the presence of melanophores, KnL closely approximates the SL from hatching to 60 mm KnL. Both sagittal otoliths were dissected from each larva and embedded in enamel resin on a glass slide. Otolith radii were measured along the maximum radius of the post-rostrum part (posterior axis) using a video-image analyzer (Image Command 4198; Ratoc System Engineering Co. Ltd., Tokyo, Japan). The number of otolith increments and otolith increment widths were measured along multiple axes, on which increments were clearly observed for analysis, around the posterior

axis. Two different researchers independently repeated the otolith increment measurements and the data when the two counts agreed were adopted. Transformation to values at the otolith radius of the posterior axis was indicated as follows:

$$O_{t \text{ post}} = (O_t - O_h) \cdot (O_{c \text{ post}} - O_{h \text{ post}}) \cdot (O_c - O_h)^{-1} + O_{h \text{ post}}$$

where O_t and O_c are the otolith radii at age t and at collection on the analyzed axis; $O_{t \text{ post}}$ and $O_{c \text{ post}}$ are the otolith radii at age t and at capture on the posterior axis; O_h and $O_{h \text{ post}}$ are the otolith radii at hatching on the analyzed axis and on the posterior axis, respectively. The Biological Intercept Method (Campana, 1990) was used for back-calculation of KnL at age following the method detailed in Oozeki and Watanabe (2000). Knob length (KnL) at age was back-calculated by solving the two equations:

$$\text{KnL}_h = a \cdot O_{h \text{ post}}^b \quad \text{and} \quad \text{KnL}_c = a \cdot O_{c \text{ post}}^b$$

where KnL_h and KnL_c are the knob lengths at hatching and at catch. Otolith radius and KnL at hatching were assumed as 21.0 µm from Nemoto *et al.* (2001) and 5.9 mm from Watanabe *et al.* (1988), respectively.

Recent growth rate for 5 days before collection was estimated from the back-calculated KnL data set. Recent growth rate was expressed as the absolute growth rate (AGR mm day^{-1}) and the instantaneous growth rate (IGR $\% \text{ day}^{-1}$):

$$\text{AGR} (\text{mm day}^{-1}) = (\text{KnL}_c - \text{KnL}_{c-5})/5$$

$$\text{IGR} (\% \text{ day}^{-1}) = (\ln \text{KnL}_c - \ln \text{KnL}_{c-5})/5$$

where KnL_c and $\text{KnL}_{\{c\}-5}$ are the KnLs at collection and at 5 days before collection, respectively. The recent growth rates were calculated on specimens older than 6 days.

All measured environmental factors were taken into account for our stepwise multiple linear regression

Table 1. Summary of sampling and specimens used in the otolith analysis.

Year	1992			1993			1994		
Season	Winter	Spring	Autumn	Winter	Spring	Autumn	Winter	Spring	Autumn
No. of stations surveyed	85	102	139	126	104	118	159	80	108
Larval sampling									
Number of net tows	80	72	111	98	100	107	159	71	101
Number of fish	1211	849	5346	879	1722	5284	4721	3518	3834
Otolith readings									
Number of stations	8	18	10	2	12	12	8	5	6
Number of fish	194	185	239	33	177	237	175	234	208

analysis on IGR, considering the multi-collinearity between independent variables. Independent variables included in the analysis were SST, three nutrient concentrations [$\text{SiO}_2\text{-Si}$, $\text{PO}_4\text{-P}$, $(\text{NO}_2 + \text{NO}_3)\text{-N}$], chlorophyll *a* concentration and the three copepod concentrations (nauplius, copepodite and adult stage). KnL was also included as an independent factor because IGR was highly correlated with KnL (see Results). A multiple non-linear regression on IGR was also estimated because of trends in the residual scatter plot for KnL (see Results). The criterion for selecting appropriate coefficient parameters was the smallest residual sum of squares (RSS) and only significant environmental parameters in the multiple linear regression analysis were chosen. All statistical analyses were conducted using SPSS (Base 11.0J; SPSS, Inc., IL, USA).

RESULTS

Distribution of larvae

Oceanographic surveys were conducted at more than 80 stations in each season (Table 1). Saury larvae distributions are shown for three seasons of 1992, and for autumn 1993 and 1994 as typical examples

(Fig. 1). In the winter of 1992, the Kuroshio Current exhibited a meandering path around the Izu Islands along the Pacific coast of central Japan, estimated from the contour of 18°C SST (Fig. 1). Saury larvae were abundant both along and outside of the Kuroshio axis. Saury larvae were distributed in a similar pattern in winter 1993 and 1994. In spring 1992, warm water ($>15^\circ\text{C}$) were present from 145 to 162°E in the survey area and saury larvae were patchily distributed throughout the region. An aggregation of larvae was also observed at 171°E ($>13^\circ\text{C}$ and $<15^\circ\text{C}$). Similar patchy distributions of saury larvae in warm water were observed in spring 1993 and 1994. In autumn, warm water ($>20^\circ\text{C}$) covered a larger area in 1994 than in 1992 or 1993 and cold water ($<15^\circ\text{C}$) did not occur in the survey area in 1992. Saury larvae were rarely collected in the cold water area ($<15^\circ\text{C}$) in autumn, although the larval distributions varied among years.

Environmental parameters

Significant differences in SST at stations where saury larvae were collected were observed throughout the 3 yrs and seasons ($P < 0.01$). Average SSTs at stations where saury larvae were collected were lowest in spring

Table 2. Sea surface temperatures (SST), concentrations of nutrients, chlorophyll *a*, and densities of copepods at stations where saury larvae were collected. Numerical values indicate mean and SD in parentheses for each year and season. Summary values indicate mean and CV (%).

Year			Nutrients				Copepods		
Season	No.	SST($^\circ\text{C}$)	($\text{NO}_2 + \text{NO}_3$)-N ($\mu\text{g L}^{-1}$)	$\text{SiO}_2\text{-Si}$ ($\mu\text{g L}^{-1}$)	$\text{PO}_4\text{-P}$ ($\mu\text{g L}^{-1}$)	chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$)	Nauplii (no. L^{-1})	Copepodites (no. L^{-1})	Adults (no. L^{-1})
1992									
Winter	62	19.2 (0.67)	1.09 (0.61)	2.22 (0.68)	0.03 (0.05)	0.46 (0.21)	2.77 (2.10)	1.74 (1.77)	0.40 (0.57)
Spring	53	15.5 (1.25)	2.36 (1.52)	5.50 (2.23)	0.19 (0.08)	1.28 (0.93)	0.01 (0.01)	0.10 (0.12)	0.06 (0.08)
Autumn	107	18.1 (2.19)	0.96 (0.64)	3.43 (1.37)	0.16 (0.07)	0.64 (0.30)	0.12 (0.05)	0.09 (0.05)	0.02 (0.02)
1993									
Winter	90	19.1 (1.53)	—	—	—	0.59 (0.22)	0.84 (0.99)	1.82 (2.94)	0.34 (0.53)
Spring	88	14.9 (1.57)	—	—	—	0.58 (0.26)	7.99 (5.50)	1.50 (10.1)	3.99 (3.37)
Autumn	106	17.5 (3.00)	1.18 (1.08)	6.21 (2.31)	0.24 (0.17)	0.56 (0.24)	0.74 (0.73)	2.35 (1.80)	0.69 (0.63)
1994									
Winter	133	18.7 (1.85)	—	—	—	0.94 (0.82)	0.85 (1.03)	1.73 (1.30)	0.50 (0.46)
Spring	68	16.6 (1.74)	—	—	—	0.70 (0.56)	5.59 (5.15)	6.73 (7.43)	2.56 (2.11)
Autumn	92	19.3 (2.14)	0.65 (0.81)	2.42 (2.14)	0.15 (0.13)	0.52 (0.17)	2.35 (2.07)	4.00 (2.97)	1.66 (1.41)
Mean (CV %)									
1992		17.8 ^a (12.2)	1.33 (82.0)	3.20 (52.3)	0.13 (70.5)	0.74 ^a (80.5)	1.00 ^a (181)	0.67 ^a (197)	0.20 ^a (184)
1993		17.2 ^b (16.1)	—	—	—	0.57 ^b (42.9)	1.61 ^b (197)	3.52 ^b (137)	6.09 ^b (145)
1994		18.4 ^c (11.8)	—	—	—	0.70 ^a (83.1)	1.97 ^b (135)	2.68 ^b (140)	3.84 ^c (130)
Winter		18.9 ^a (8.3)	—	—	—	0.69 ^a (121)	1.37 ^a (120)	1.39 ^a (147)	0.86 ^a (122)
Spring		15.6 ^b (11.1)	—	—	—	0.80 ^a (82.0)	2.58 ^b (159)	5.70 ^b (98.7)	9.43 ^b (106)
Autumn		18.2 ^c (14.2)	0.94 (94.4)	3.76 (67.0)	0.18 (73.2)	0.57 ^b (43.4)	0.90 ^c (187)	0.89 ^c (154)	1.93 ^c (122)

^{a-c}Mean values, within a column, not sharing the same superscript are significantly different at $P < 0.05$ for each group.

1993 (14.9°C) and highest (19.3°C) in autumn 1994 (Table 2). High mean SST with the smallest canonical variates (CV) of SST was observed in winter and the CV of SST was largest in autumn.

Comparatively high concentrations of (NO₂ + NO₃)-N were detected in spring, although no significant difference was observed among seasons and years in autumn (Table 2). The concentration of (SiO₂)-Si varied among seasons and years and the highest average value of 6.21 µg L⁻¹ was recorded in autumn 1993. The concentration of (PO₄)-P was lowest at 0.03 µg L⁻¹ in winter 1992.

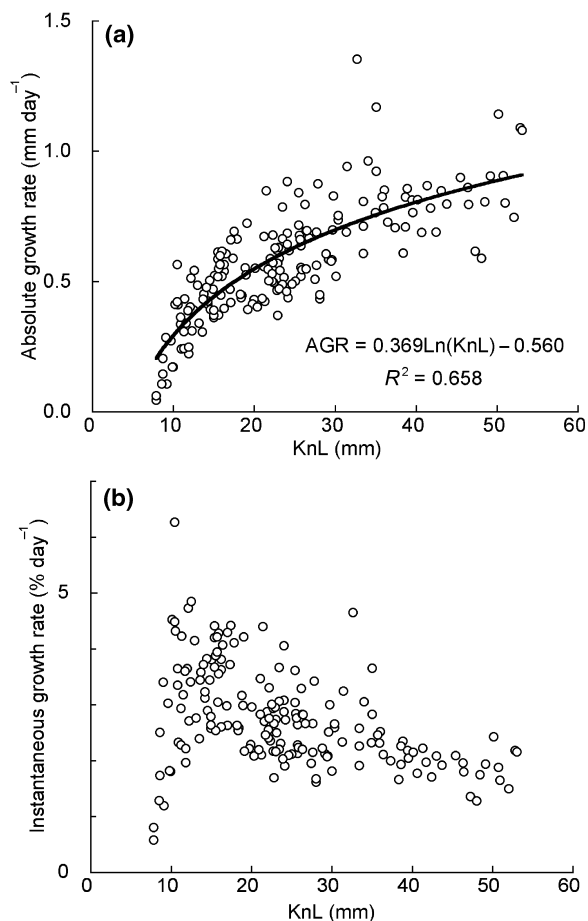
Chlorophyll *a* concentrations indicated annual differences and the mean concentration was significantly lower in 1993 than in 1992 and 1994 ($P < 0.01$, Table 2). Mean concentration of chlorophyll *a* in spring was highest at 0.80 µg L⁻¹, and the lowest value and smallest CV was observed in autumn (Table 2).

The mean concentration of nauplii marked seasonal and annual variations. The highest mean concentrations of nauplii were observed in spring 1993 (7.99 L⁻¹) and the nauplii concentration in 1992 was significantly lower than in the other 2 yrs ($P < 0.05$, Table 2). At the copepodite stage, the highest concentration was recorded in spring 1994 (6.73 L⁻¹) and the lowest in autumn 1992 (0.09 L⁻¹). The density of the copepodite stage was significantly lower in 1992 than in 1993 and 1994 ($P < 0.001$). Mean concentrations of adult copepods indicated highly significant differences among the 3 yrs ($P < 0.001$, Table 2). The autumn season had the lowest values among three seasons for all stages of copepods ($P < 0.01$).

Growth rate

Recent absolute growth rate (AGR mm day⁻¹) indicated an exponential shape against KnL in all seasons as seen in the example of spring 1992 (Fig. 2a). Recent instantaneous growth rate (IGR % day⁻¹; Fig. 2b) was calculated to cancel the exponential trend against KnL by natural logarithm transformation of size (Busacker *et al.*, 1990). IGR was, however, still affected by KnL and a plot produced a dome shape that was shifted to the left in each season. The IGR increased sharply from 7–15 mm KnL and then slowly decreased to around 2 % day⁻¹ asymptotically. The peak level of the IGR varied among seasons and years, although the IGR of large size larvae was not markedly different among seasons and years (Fig. 3). Comparison of IGR among seasons and years indicated significant variation, although the number of data for winter 1993 was small. Differences of the average values were tested by Tamhane's T2 because of the lack of homo-

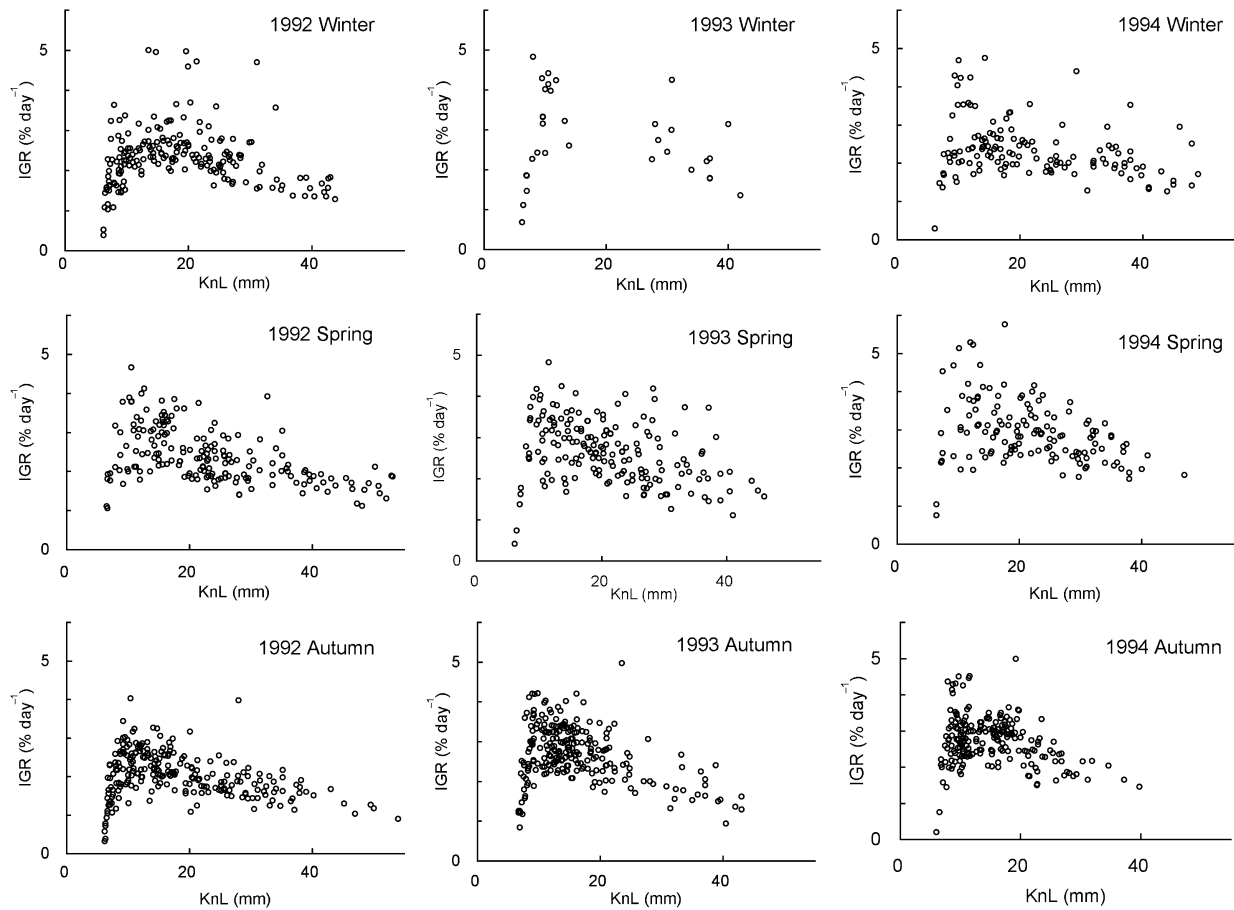
Figure 2. Recent growth rate of saury *Cololabis saira* larvae in spring 1992. Panel (a) indicates the recent absolute growth rate (AGR mm day⁻¹) and panel (b) indicates the recent instantaneous growth rate (IGR % day⁻¹) against the knob length (KnL mm) on the sampling date.



geneity. IGR in spring was significantly higher than in the other two seasons ($P < 0.01$) and the IGR in 1992 was significantly lower than in the other 2 yr ($P < 0.001$, Table 3).

Stepwise multiple linear regression analysis eliminated several environmental parameters for multicollinearity. The final regression model was expressed by SST, copepodite stage Copepoda concentration, chlorophyll *a* concentration, and KnL (Table 4). The linear regression model was significant and well expressed the variance of IGR ($R^2 = 0.919$); however, the residual plot against KnL still indicated a dome shape that was shifted to the left (Fig. 4a). Multiple non-linear regression analysis provided acceptable results for this problem ($R^2 = 0.939$, Table 4). The (RSS: 567.9) was smaller than that of the linear

Figure 3. Relationships between knob length (KnL) and instantaneous growth rate (IGR % day⁻¹) of saury *Cololabis saira* larvae in winter, spring and autumn of 1992, 1993 and 1994.



regression (755.5) and the residual plot against KnL scattered more uniformly than the linear regression (Fig. 4b).

DISCUSSION

Abundant distributions of saury larvae were observed along and on the oceanic side of the Kuroshio axis in winter. A similar pattern of larval distribution has been reported in previous papers and the oceanic side of the Kuroshio Current is thought to be the main spawning ground of the Pacific saury off Japan (Hayashi and Odate, 1981; Watanabe *et al.*, 1997, 2003). Larvae were distributed only in warm waters in spring and the distribution was defined by the 15°C surface isotherm. Larval distribution in autumn indicated a similar dependency on SST as seen in spring; however, the density of larvae varied among years even in the same SST area. Annual differences between SST and larval distribution might be

explained by the migration pattern of spawners, because the migration of adult saury is affected not only by SST but also by the position of warm core rings and the Oyashio intrusion (Fukushima, 1979). Larval distributions in this study showed typical distribution patterns of saury larvae; therefore, the relationships between larval growth and environmental factors described in the present study might be applicable beyond 3 yrs (1992–94) and area (the northwestern Pacific) analyzed in this study.

Nutrient concentrations of N and Si were highest in spring and were able to support the high chlorophyll *a* concentration of spring blooms. In the winter season, nutrient concentration of N, P and Si had low values with small CVs. Watanabe *et al.* (1998) reported that the concentration of N, P and Si in the upper 100 m in offshore waters of the Kuroshio Current in winter 1993 were 1.11 (SD 0.29), 0.19 (0.15) and 2.09 (0.56), respectively. Values in both 1993 and 1994 from Watanabe *et al.* (1998) were similar to the present

Table 3. ANOVA of the instantaneous growth rate among seasons and years. Differences of the average values were tested by Tamhane's T2 because of the lack of homogeneity.

Season

Source of variation	DF	Sum of Squares	Mean Squares	F	P
Between seasons	2	14.692	7.346	12.992	<0.001
Within seasons	1579	892.803	0.565		
Total	1581	907.495			
Season	N	Mean (SD)			
Winter	402	2.39 (0.773) ^a			
Spring	496	2.64 (0.768) ^b			
Autumn	684	2.48 (0.727) ^a			

Year

Source of variation	DF	Sum of Squares	Mean Squares	F	P
Between years	2	71.206	35.603	67.222	<0.001
Within years	1579	836.289	0.530		
Total	1581	907.495			
Year	n	Mean (SD)			
1992	618	2.24 (0.705) ^a			
1993	447	2.70 (0.737) ^b			
1994	517	2.65 (0.747) ^b			

^{a,b} Mean values within a column not sharing the same superscript are significantly different at $P < 0.01$ for each group.

results. Annual differences in nutrient concentrations were observed in autumn with large spatial variances.

Linkages between chlorophyll *a* concentration and the distribution of saury larvae were not found. In winter, chlorophyll *a* concentrations in the inshore sides of the Kuroshio Current were higher than those values in the offshore side (Watanabe *et al.*, 1998), although saury larvae were mainly distributed offshore of the Kuroshio Current. The highest chlorophyll *a* concentration was observed in spring and was related to the occurrence of spring blooms along the northern front of the Kuroshio Extension. The effect of cross frontal flows associated with meanders of the Kuroshio Extension was indicated by the high chlorophyll *a* concentration along this area (Ito *et al.*, 2000). The concentration of saury larvae, however, did not coincide with the position of northern front of the Kuroshio Extension where high chlorophyll *a* concentrations were recorded in this study.

The lowest average copepod densities and largest annual fluctuation of copepod densities were observed in the autumn. This means that food conditions are not usually good for saury larvae in autumn and supported the idea that low growth rate and high mortality rate in autumn were associated with high

environmental variability in the transitional waters (Watanabe *et al.*, 2003). High environmental variability was also observed in spring in the transitional waters; however, high average copepod densities supported by the high primary production level could cancel the negative effect on larval growth.

Temperature, copepodite-stage copepod density, and chlorophyll *a* concentration were positively correlated to the growth of saury larvae. Relationships between growth or metabolism and environmental factors have been studied in many papers and Fry (1971) categorized environmental factors into five groups: limiting, controlling, masking, directive and lethal factors. Dissolved oxygen, salinity, daily feeding period, food quality and pollutants were included in these environmental factors as well as the factors analyzed in this study. Based on these five categories, Yamashita *et al.* (2001) discussed effects of environmental variability on the growth of juvenile flatfish in nursery grounds and reported that dissolved oxygen was an important factor controlling fish growth in addition to food, temperature and body size. Although several papers mentioned the effects of temperature and prey abundance on larval growth (i.e. Haldorsen *et al.*, 1989; Bailey *et al.*, 1995, 1996; Oozeki and

Table 4. Results of the multiple regression analysis of the instantaneous recent growth rate (IGR).Model-1: $IGR = SST + \text{Copepodite} + \text{Chlorophyll-}a + \text{KnL}$

Source of variation	DF	Sum of Squares	Mean Squares	F	P
Regression	4	8590.362	2147.590	3800.8	<0.0001
Residuals	1337	755.461	0.565		
Total	1341	9345.822			

Parameters	Regression coefficient	Standardized partial regression coefficient	Partial correlation coefficient
SST	0.140	0.929	0.813
Copepodite	3.897×10^{-2}	0.111	0.318
Chlorophyll- <i>a</i>	0.355	0.116	0.238
KnL	0.0174	-0.143	-0.229

Model-2: $IGR = SST + \text{Copepodite} + \text{Chlorophyll-}a + (\text{KnL-c}) e^{(a-b(\text{KnL-c}))}$

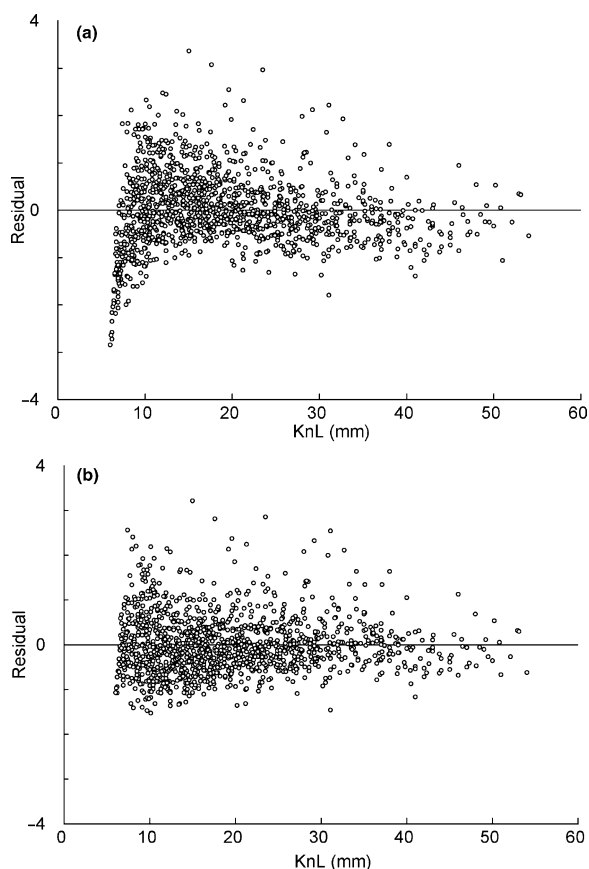
Source of variation	DF	Sum of Squares	Mean Squares	F	P
Regression	6	8777.873	1462.979	3442.3	<0.0001
Residuals	1335	567.949	0.425		
Total	1341	9345.822			

Parameters	Regression coefficient	Asymptotic standard error
SST	0.0911	0.00335
Copepodite	3.09×10^{-2}	2.75×10^{-3}
Chlorophyll- <i>a</i>	0.209	0.0348
KnL		
a	-0.594	0.0507
b	0.174	0.00927
c	7.10	0.164

Zenitani, 1996), it might be difficult to demonstrate linkages between larval growth and environmental parameters from field data on pelagic fishes in the ocean, because most environmental parameters were thought to be more stable in oceanic than in the coastal area, and other parameters including dissolved oxygen, salinity and feeding period, might rarely change in the ocean. Furthermore, age- and size-selective mortality significantly influenced the growth inferred from length-at-age. Bailey *et al.* (1996) mentioned the necessity of analysis over smaller time and space scales to discuss the relationship between larval growth and environmental factors in the ocean. Recent growth rate analysis just before collection is a promising method to conduct the fine scale analysis on the relationship between growth and the environmental factors, because the size-selective mortality may not affect short-time growth rate changes. Our results showed a positive relationship between larval growth and three environmental parameters – temperature, prey abundance and primary production.

Temperature highly affected the growth of saury larvae and the regression coefficient was around 0.1 (% day⁻¹ °C⁻¹). However, Methot and Kramer (1979) reported no clear relationship between growth rate and temperature in *Engraulis mordax* larvae. Takahashi *et al.* (2001) also noted that growth rates of *E. japonicus* were mainly affected by food availability rather than ambient temperature. These discrepancies on the effect of temperature might be related to the larval distribution area and duration of the spawning season of the target species. Methot and Kramer (1979) mentioned that the narrow temperature range that they used, from 13.0 to 16.2°C, would be one of the reasons for not detecting a temperature effect on larval growth. The spawning season of the saury is protracted from autumn to spring and shifts latitudinally with the spawning ground. Saury larvae, therefore, are distributed in waters ranging from 10 to 25°C along the North Pacific coast of Japan (Odate, 1956). This study indicated that the temperature of stations where saury larvae were collected varied from 10.4 to 23.6°C.

Figure 4. Residuals of the instantaneous growth rate (IGR % day⁻¹) of saury *Cololabis saira* larvae plotted against the knob length (KnL). Panel (a) indicates residuals calculated by the multiple linear regression model and panel (b) indicates the residuals by the multiple non-linear regression model.



The estimated regression model between larval growth and environmental parameters was biologically appropriate from the point of the feeding ecology of saury larvae. Saury larvae eat larger zooplankton compared with other marine fish larvae, that is, Japanese sardine *Sardinops melanostictus*, and successfully feed on *Artemia* nauplii (body length 0.43–0.52 mm; Vanhaecke and Sorgeloos, 1980) from 2 days after hatching (Watanabe and Kuji, 1991; Oozeki and Watanabe, 2000). The abundance at copepodite stage Copepoda indicated a positive effect on growth of saury larvae in the present study, whereas a positive correlation between nauplius densities and growth rate have been observed in the early larval period of Japanese sardine *S. melanostictus* (Oozeki and Zenitani, 1996). Odate (1977) qualitatively reported that the size of food organisms in juvenile stage saury (25–60 mm KnL: based on her stage definition) expanded to larger items, such as adult copepods up to

1.5 mm in body length. Based on this information, a high abundance of adult stage copepods would be expected to produce a positive effect on the growth rate of older larvae. Significant effects on larval growth were, however, not observed for adult stage copepod density in this study. Gut contents of saury larvae should be analyzed in order to discuss this issue in the future.

Chlorophyll *a* concentration was the third positive factor on larval growth and is an appropriate proxy for primary production that supports food production for saury larvae. Nakata *et al.* (1994) reported significant positive correlations both between the chlorophyll *a* concentration and the RNA/DNA ratio of female *Paracalanus* sp. and between chlorophyll *a* concentration and *Paracalanus* sp. egg productivity in the frontal waters of the Kuroshio Current. Although chlorophyll *a* concentration did not indicate a significant positive relationship with the three Copepoda densities in the multiple linear regression analysis in this study, the concentration of chlorophyll *a* might be an important parameter to support the copepod production as food of saury larvae.

In this study, seasonal and annual variations of larval growth were described and differences of larval growth were explained by the differences of SST, chlorophyll *a* concentration and copepod densities. Average IGR in spring (2.64) was higher than in the other two seasons and was supported by significantly higher chlorophyll *a* concentrations and copepod densities than in the other seasons. The low IGR value in 1992 (2.24) can also be explained by the low copepod densities. Large environmental variability was shown in the transitional waters and it was thought to be the cause of the low growth rate reported by Watanabe *et al.* (1997, 2003), although the low growth rate in autumn was not directly confirmed in this study.

The relationship between larval growth of saury and environmental conditions revealed in this study provides effective information not only for establishing ecosystem models of Pacific saury, but also for studying the effect of decadal changes in environmental variables on fluctuations in the saury population. The results of the present study confirmed that growth ability is delimited by the physical and biological environment.

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