Abstract.–Late larvae (15–30 mm TL) of the Japanese sardine, *Sardinops melanostictus*, are commercially exploited in fishing grounds along the Pacific coast of western and central Japan. Concentrated shoals of late larvae in the shallow (15–30 m deep) coastal (4–6 miles from the coast) fishing grounds enable fishermen to catch as much as several hundred metric tons (t) (several billion larvae in number) per month. Growth trajectories of sardine larvae caught in the fishing ground off Atsumi Peninsula in central Japan were individually backcalculated by using the biological intercept method based on the allometric relationship between otolith radius and fish length. Growth rates for larvae up to 13–21 d were high, ranging from 0.79 to 0.85 mm/d, but declined after reaching size of immigration (13–19 mm TL) from the offshore waters to the coastal fishing grounds. The decline of growth rate in the late larval stage seemed to be related to the concentration of late larvae in the fishing grounds, the result of onshore intrusions of offshore Kuroshio waters. Total lengths at age 20 d were significantly smaller in 1990 (total catch of larval sardine was 720 t) than in 1991 (total catch 300 t) in spite of a higher sea surface temperature in 1990 in the coastal habitat. This may have resulted from a larger population of late larvae on the fishing ground in 1990 than in 1991.

Growth trajectory of the larval Japanese sardine, *Sardinops melanostictus*, transported into the Pacific coastal waters off central Japan

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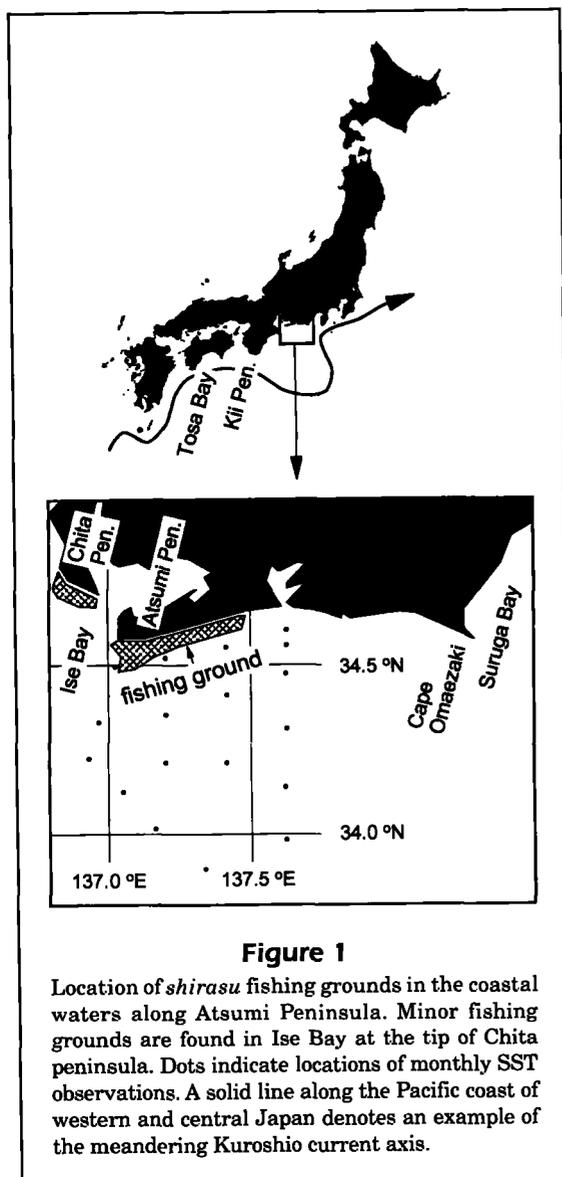
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Late larvae of the Japanese sardine *Sardinops melanostictus* and the Japanese anchovy, *Engraulis japonicus*, termed *shirasu* in Japan, are fished by boat seiners in waters along the Pacific coast of western and central Japan. The coastal waters (4–6 miles from the coast) off Atsumi Peninsula (Fig. 1) are one of the major fishing grounds for *shirasu*. Depth of the sea bed of the fishing grounds is about 20 m, with a range from 15 to 30 m. The *shirasu* fishery for sardine larvae begins in March and continues to December, with the major effort shifting to anchovy in early summer. The annual catch of sardine larvae in the waters ranged from 700 to 2000 metric tons (t), 7–20 billion larvae, 1980–88. However, between 1989 and 1991 the catch declined to 300–700 t (Fig. 2). Since 1992, catches have been as low as several tens of tons, with an exception of about 400 t in 1993.

Growth rates of fish larvae affect their survival and recruitment to the adult population (Anderson, 1988). From life-stage table analyses, growth rate has been shown to be an important determinant 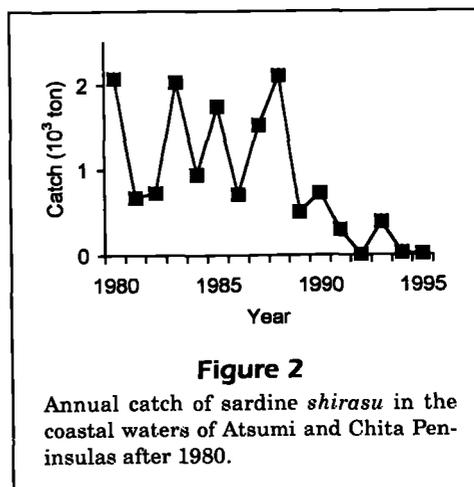of year-class strength by delimiting the duration of a particular life stage with high instantaneous mortality (Lo et al., 1995; Butler et al., 1996). Watanabe et al. (1995) showed that recruitment failures of the Japanese sardine in 1988–91 could not be explained by mass mortality at the first feeding stage. Cumulative mortality after the first feeding stage of the sardine, which may be a function of growth rate, is likely to have determined the recruitment in these years. Meekan and Fortier (1996) examined early life growth and survival of the Atlantic cod, *Gadus morhua*, and showed that fast-growing pelagic larvae survived better through the larval stage and dominated in the cohort of demersal juveniles. Campana (1996) found a positive correlation between growth rates in juvenile Atlantic cod and subsequent year-class strengths, which enabled him to predict recruitment from the juvenile growth rates.

Available population size of late larval sardine in the *shirasu* fishing grounds could be affected by larval growth. The size range of larvae caught in the *shirasu* fishery is usually from 15 to 30 mm TL. Because the duration time of this size

Figure 1

Location of *shirasu* fishing grounds in the coastal waters along Atsumi Peninsula. Minor fishing grounds are found in Ise Bay at the tip of Chita peninsula. Dots indicate locations of monthly SST observations. A solid line along the Pacific coast of western and central Japan denotes an example of the meandering Kuroshio current axis.

Figure 2

Annual catch of sardine *shirasu* in the coastal waters of Atsumi and Chita Peninsulas after 1980.

well as of available stock sizes of *shirasu* larvae of the Japanese sardine. The daily growth rate of fish can be estimated by regressing size-at-age data to a growth model (Campana and Jones, 1992). When we apply this method, we need data points throughout an age range, from first feeding up to the fish size of concern (Watanabe et al., 1997). Because the size range of sardine larvae fished by the boat seine fishery is usually from 15 to 30 mm, we do not have a complete range of data points for early larvae, and therefore the regression method is not applicable to describe the growth history from first feeding to size at capture. Instead, backcalculation of size at age from the relationship between otolith radius and fish length makes it possible to draw a growth trajectory for individual fish (Campana, 1990; Campana and Jones, 1992). We backcalculated growth trajectories of individual larval sardines caught in coastal waters off Atsumi Peninsula, 1990 and 1991, and compared them with growth trajectories of larvae from other waters.

range is a function of growth rate, slower growth results in longer duration time and an increase in the available number of larvae. Watanabe and Kuroki (1997) backcalculated the growth history of larval sardine *Sardinops melanostictus* in the coastal waters off Miyazaki in western Japan. They found that growth rates reached a maximum (0.80–0.85 mm/d) at around 10–12 mm in total length (TL) but slowed thereafter, exhibiting asymptotic growth trajectories. According to this growth pattern, duration time from 15 to 30 mm TL was calculated to be 35 days. If, however, growth rates of 0.80–0.85 mm/d were maintained in the late larval stage, duration time of the same size range could be as short as 18 days.

Growth rate in early life stages is thus important as a potential determinant of year-class strength as

Materials and methods

Larval sampling

Two *shirasu* fishing boats, towing a seine net, were used to sample waters off Atsumi Peninsula and in Ise Bay (Fig. 1). They usually departed before dawn from the fishing port, together with a catch-loading boat, set the net several times in the morning, and returned to the port for offloading. Catches were stored with ice before landing. In our study, we randomly sampled *shirasu* larvae from catches in the ports of Morozaki and Toyohama (tip of Chita Peninsula) four times in 1990 (11, 16, 27 April and 7 May) and four times in 1991 (15, 23 April and 7, 14 May).

The larvae were classified as Japanese sardine, *S. melanostictus*, Japanese anchovy, *E. japonicus*, and round herring, *Etrumeus teres*. Sardine larvae were preserved in 80% ethanol for otolith examinations.

Otolith measurement

Total lengths (TL) of sardine larvae were measured to the nearest 0.1 mm with an optical comparator. Sagittal otoliths were dissected and cleaned under a binocular microscope, mounted on a glass plate with enamel resin, and used for measurements and counts of daily growth rings. We used the otolith measurement system (Ratoc System Engineering Inc.) composed of a light microscope, a video camera and monitor, and an image analyzer controlled by computer. Because the otolith had not yet developed a rostrum and because we were not able to determine its orientation at the larval stage, we measured radii of all daily rings along the maximum radius of the otolith.

Growth backcalculation

The relationship between larval TL and maximum otolith radius (OR) was considered for larvae sampled. Plots of TL against OR can be expressed by an allometric relationship (see "Results" section). An allometric OR-TL relationship has previously been demonstrated in larval *S. melanostictus* from different waters (Watanabe and Kuroki, 1997). Otolith growth rings have been found to be deposited on a daily basis in *S. melanostictus*, with the first ring being formed on the third day of hatching (the day of first feeding) when larvae are reared at 18°C (Hayashi et al., 1989). The relationship of the ith otolith ring radius (OR_i) and TL on the day of the ith ring formation (TL_i) is considered to be expressed by an allometric formula, $TL_i = a \times OR_i^b$, for individual larvae. We determined the allometric parameters a and b for each larva by using the biological intercept method (Campana, 1990; Campana and Jones, 1992) and a size of first feeding larvae (first otolith daily ring deposition) of 5.0 mm TL (Watanabe and Kuroki, 1997). The solution of the following two equations gives us a and b for each larva:

$$TL_1 = a \times OR_1^b \text{ and } TL_{capture} = a \times OR_{capture}^b,$$

where TL_1 = total length (mm) at the first ring deposition which was fixed at 5.0 mm;

OR_1 = the measured radius of the first daily ring;

$TL_{capture}$ = the measured total length (μm) at capture; and

$OR_{capture}$ = otolith radius (μm) at capture.

TL_i of each larva was thus calculated from the formula for each larva independently. Mean ±SD (standard deviation) of TL at ages from 4 d up to a certain age, with at least 10 backcalculated TLs, was calculated for the March- and April-hatched cohorts for the two years of study. Differences in mean TLs at ages 10, 15, 20, and 25 d were examined between the same month of hatch cohorts in 1990 and 1991 by using Student's t-test, when variances were equal, or by Welch's t-test when they were not equal.

Sea surface temperature distribution

Sea surface temperatures (SST) in and around the *shirasu* fishing ground were measured monthly at fixed stations off Atsumi Peninsula (Fig. 1). We used data from April and May, 1990 and 1991, to describe temperature distributions in coastal waters.

Results

The SST in coastal waters off Atsumi Peninsula was in the range of 16–19°C during 23–25 April and 8–9 May 1990. From 23 to 25 April, the isotherms ran nearly parallel to the coast line but from 8 to 9 May offshore waters warmer than 18°C intruded into the coastal fishing ground (Fig. 3). In 1991, the SST during 2–3 April and 8–9 May ranged from 11 to 18°C. Cold waters extruded from Ise Bay covered part of the coastal fishing ground. The SST in the fishing grounds were 1.5–2.5°C lower in 8–9 May 1991 than in the corresponding season in 1990.

Local government permits the *shirasu* fishery to operate year round in these fishing grounds, but catches were zero in January–February 1990 and January–March 1991 (Fig. 4). Japanese sardine larvae were caught mainly in April in these years. The major target species of the *shirasu* fishery shifted to Japanese anchovy after May. A monthly catch of sardine larvae was 430 t in April 1990, declining to 175 t in April 1991. Annual catches of sardine larvae were 724 t and 298 t in 1990 and 1991, respectively.

Total length of larval sardines caught in the *shirasu* fishery were 15–27 mm in mid-April 1990 (Fig. 5). Frequency of larvae smaller than 15 mm TL increased after late April in this year, with sizes of 11–20 mm. In 1991, the modal size and range of the larvae remained relatively constant at 22–25 and 20–27 mm TL, respectively, mid-April to mid-May (Fig. 5).

Sardine larvae fished on 11 and 16 April 1990 were aged from 14 to 39 d after hatching. All of them hatched in March (Fig. 6). Larvae caught on 27 April

and 7 May were young, from 10 to 23 d. Except for one larva hatched on 31 March (not used for backcalculation), all larvae caught on 27 April and 7 May hatched in April 1990. In 1991, ages of sardine larvae were 19–30 d. Larvae caught on 15 April were all hatched in March. Those caught on 23 April were composed of March- and April-hatched fish. All larvae caught on 5 and 14 May were hatched in April except one which was hatched on 24 March (not used for backcalculation).

Plots of TL (mm) on OR (µm) of all individuals could be expressed in an allometric formula (Fig. 7). Size at age of individual larva was backcalculated on the basis of allometric OR-TL relationship for each larva from first feeding to capture. The 1990 March-hatched cohort grew linearly to 25 d when fish reached 20.5 mm TL (Fig. 8). Mean growth rate of the cohort from 4 d (6.3 mm TL) to 25 d was 0.68 mm/d. Growth in the April-hatched cohort in 1990 was linear to about 13 d (13.1 mm TL, 0.83 mm/d), then slowed down. In the 1991 March- and April-hatched cohorts, growth was linear to 21 d (21.2 mm TL, 0.85 mm/d), and 20 d (19.2 mm TL, 0.79 mm/d), respectively, declining thereafter. Larval TL at which growth started to decline occurred at the approximate size when immigration into the coastal fishing grounds occurred in both months.
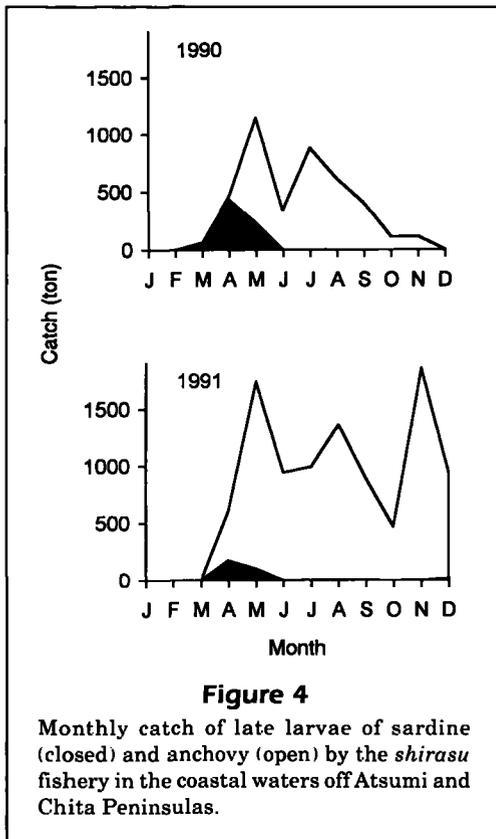
Total lengths at 15 d in the 1990 March- and April-hatched cohorts were 14.2 ±1.2 and 14.9 ±1.4 mm, respectively, whereas in 1991 the March-hatched cohort reached 16.3 ±1.5, and the April cohort 15.8 ±1.3 mm. Backcalculated TLs of March- and April-hatched cohorts were significantly smaller in 1990 than in corresponding hatching month in 1991 at 15, 20, and 25 d (Table 1).

Discussion

Larvae of *S. melanostictus* and *E. japonicus* have been reported to be transported from the offshore Kuroshio area to the coastal fishing grounds along the Pacific coast in central Japan by onshore intrusions of Kuroshio waters (Tsuji, 1983; Muranaka, 1984; Mitani, 1990). This is the case in the coastal fishing grounds off Atsumi Peninsula, because great densities of *S. melanostictus* eggs were detected in the offshore waters along the Kuroshio Current in 1990 and 1991 (Ishida and Kikuchi, 1992; Zenitani

Figure 3

Sea surface temperature distribution off Atsumi Peninsula in April and May of 1990 and 1991.
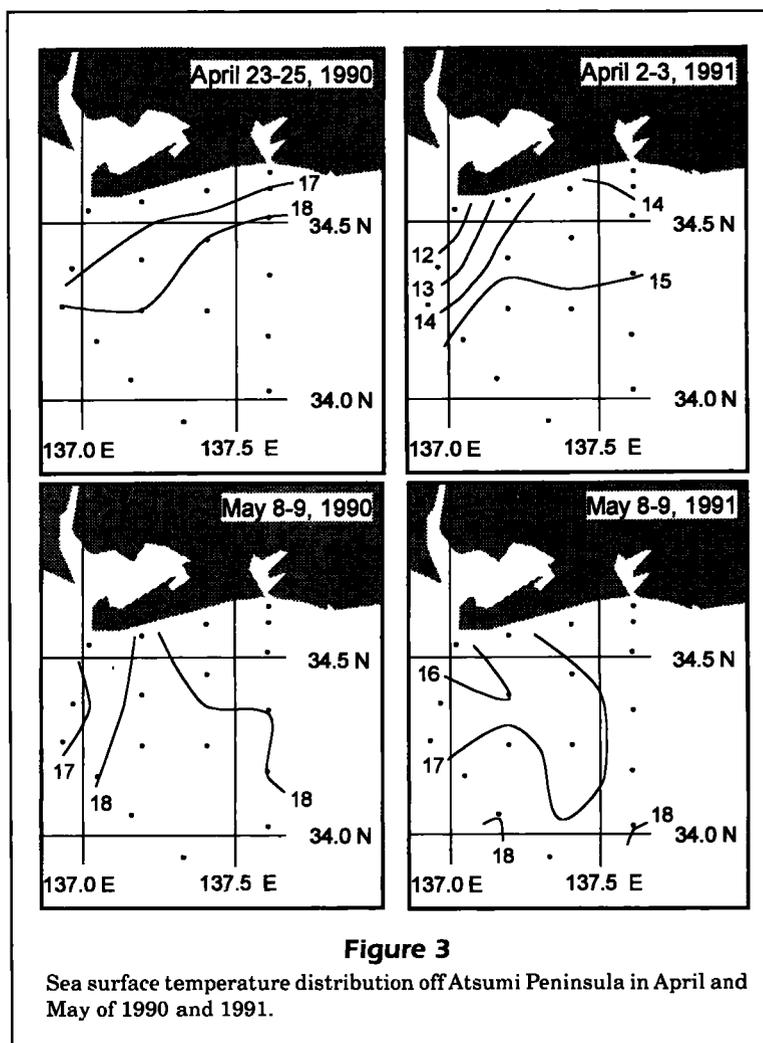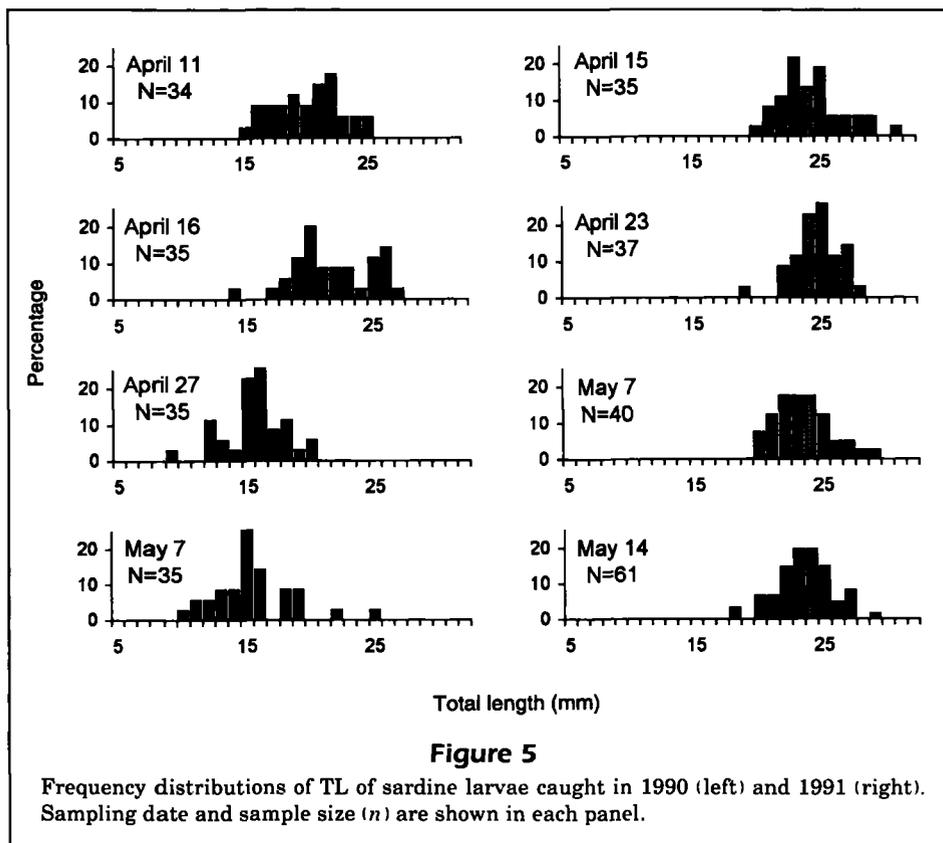
et al., 1995; Watanabe et al., 1996). Onshore intrusions of Kuroshio waters often develop when the Kuroshio meanders in the waters off central Japan (Kobayashi et al., 1986; Kasai, 1995). The available population size of *S. melanostictus* larvae in coastal fishing grounds off Atsumi Peninsula and adjacent waters is a positive function of the latitudinal distance from Cape Omaezaki to the Kuroshio axis (Fig. 1) (Kishida et al., 1994). This distance in April and May 1991 measured approximately 125 nautical miles (n mi) (Maritime Safety Agency, 1991), which was less than that in 1990 (200 n mi) (Maritime Safety Agency, 1990). Oceanic conditions were less favorable for onshore larval transport in 1991 than in 1990. As seen in Figure 3, SSTs in coastal waters were lower in 1991 than in 1990, a feature that was indicative of limited intrusion of the warm Kuroshio waters to the coastal area. Annual catch of sardine *shirasu* in 1991 in the waters off Atsumi Peninsula (including small catches in Ise Bay) decreased to 41%

Figure 4

Monthly catch of late larvae of sardine (closed) and anchovy (open) by the *shirasu* fishery in the coastal waters off Atsumi and Chita Peninsulas.

of the 1990 catch. This was due partly to unfavorable oceanic conditions.

Growth rates of sardine larvae estimated in this study were 0.79–0.85 mm/d to a size when they immigrated to the fishing grounds as 1990 April- and 1991 March- and April-hatched cohorts, but later declined to 0.6–0.7 mm/d (Fig. 8). This decline in growth was similar to the asymptotic growth of larval *S. melanostictus* in the *shirasu* fishing grounds in western Japan (Watanabe and Kuroki, 1997). Fishermen for *shirasu* locate a concentrated larval shoal by echo sounder (Mitani, 1987) and catch large numbers of larvae in relatively narrow fishing grounds (Fig. 1). In mid-April 1990, 100 t (ca. one billion in number) per day of sardine larvae were caught in the fishing ground in our study.[1] Turbidity is a factor that helps to retain concentrated larval shoals in the coastal fishing grounds (Funakoshi, 1988). Uotani et al. (1993) demonstrated experimentally that *E. japonicus* larvae showed a strong positive taxis to turbidity and tended to stay in the turbid water. Reduction of larval growth, after reaching the size when immigration to the *shirasu* fishing grounds occurred, is likely to be related to concentrations of large numbers of larval sardines in the narrow fishing grounds as a result of intrusions of offshore waters (Muranaka, 1984).

The modal size of sardine larvae caught on April 27 and May 7 (April-hatched cohort) in 1990 was exceptionally smaller (15–16 mm TL) than those in the other larval groups (Fig. 5). The mesh aperture of the net of the *shirasu* fishery is 2.1 mm at the codend. The diagonal of the mesh is 3.0 mm, which is much larger than the body depth of 15–16 mm sardine larvae (about 1.3 mm). A large proportion of larvae smaller than 15 mm could, therefore, be extruded from the mesh at the codend (Smith and Richardson, 1970). Nevertheless, many larvae smaller than 15 mm

Total length (mm)

Figure 5

Frequency distributions of TL of sardine larvae caught in 1990 (left) and 1991 (right). Sampling date and sample size (*n*) are shown in each panel.

Figure 6

Frequency distribution of age of sardine larvae caught on different dates in 1990 (left) and 1991 (right). Boxes show the earliest or latest hatch date of the group.
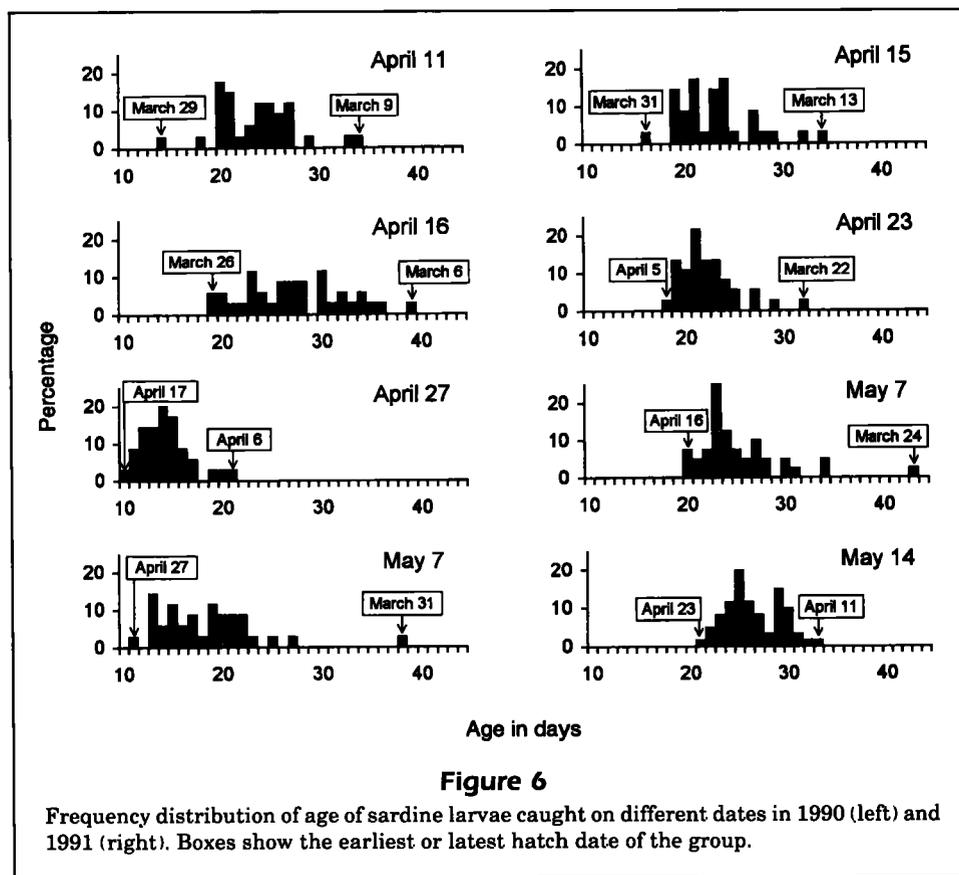
Table 1

Back-calculated TLs (in mm) of sardine larvae at ages 10, 15, 20, and 25 d after hatching.

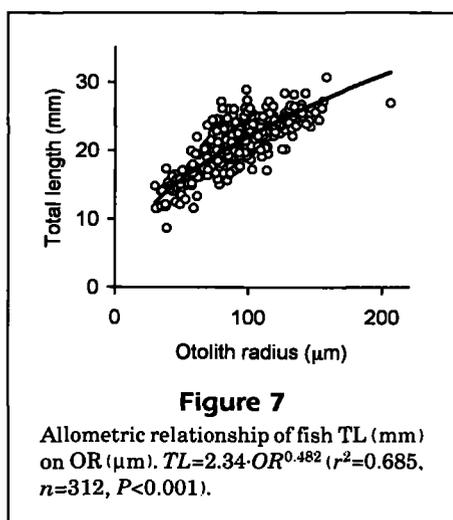| Hatching month		10			15			20			25		
		Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n
1990	March	10.8**	0.9	69	14.1**	1.2	68	17.5**	1.4	65	20.5**	1.3	35
	April	11.5	1.0	69	14.9**	1.4	39	17.9*	2.0	14			
1991	March	12.3	1.1	62	16.3	1.5	62	20.4	2.1	61	23.1	2.6	33
	April	11.7	0.9	110	15.8	1.3	110	19.2	1.7	110	21.6	1.8	74

* Significantly smaller ($P<0.01$) than the same hatching month cohort in 1991.
** Significantly smaller $P<0.001$ than the same hatching month cohort in 1991.

(April-hatched cohort) were caught from late April to early May. This finding indicates that large numbers of small larvae were carried to the coastal fishing grounds after April 16 in 1990. The SST distribution in 8–9 May indicated that there was a substantial amount of intrusion of the offshore warm water after 23–25 April. Because the size of immigration to the fishing ground was smaller in this April-hatched cohort than in others, decline of growth in this cohort started earlier, at 13 d old (13.1 mm

TL), compared with other cohorts from 20 to 21 d (19–20 mm TL) (Fig. 8).

Larval TLs at 20 d were 20.4 ±2.1 and 19.2 ±1.7 mm, as March- and April-hatched cohorts in 1991, respectively, which were comparable to the sizes at 20 d (19.1 ±0.6–19.4 ±1.6 mm) of the January- to March-hatched cohorts of *S. melanostictus* in the waters off Miyazaki in 1991 (Watanabe and Kuroki, 1997). In our current study, however, TLs of the 1990 larvae at 20 d ranged from 17.5 to 17.9 mm, significantly

Figure 7

Allometric relationship of fish TL (mm) on OR (μm). $TL=2.34 \cdot OR^{0.482}$ (r^2=0.685, n=312, P<0.001).

Figure 8

Backcalculated growth trajectories of sardine larvae hatched in March and April in 1990 and 1991. Small diamond represents mean TL at age and vertical bar one SD of the m

smaller than the sizes in 1991. The difference in growth rates between 1990 and 1991 could not be explained by SST because in our study area, slower growth was recorded in 1990, when SST was higher, than in 1991. Relative abundance of sardine *shirasu* in the coastal waters of central Japan in 1991 decreased to about 50% of the 1990 (Kishida et al., 1994). The catch of sardine larvae in 1991 declined to 41% of that in 1990 (Fig. 2). Funakoshi (1996) demonstrated that abundance of macrozooplankton was negatively correlated with the biomass of young-of-the-year sardines in Ise Bay (Fig. 1). He considered that large biomasses of young-of-the-year sardines resulted in a reduced abundance of macrozooplankton, followed by a decline in growth of the sardines through density-dependent processes. The greater population of sardine larvae in the *shirasu* fishing grounds in 1990 than in 1991 may have resulted in the slower growth of the sardine larvae in 1990. We need to study the density of food items for sardine larvae in the *shirasu* fishing grounds to examine if sardine larval growth is limited by food availability. We also need to know interspecific competition for food between sardine and anchovy larvae in a coastal ecosystem, because they coincided in April and May in our study area (Fig. 4).

The offshore Kuroshio frontal waters provide sardine larvae with sufficient foods. Nakata et al. (1995) calculated that the total food requirement of carnivorous macrozooplankters and sardine larvae was about 11% of the total production of small copepods (<1.0 mm prosome length) in Kuroshio frontal waters. This resulted in a higher feeding incidence in the early larval stage of *S. melanostictus* in the frontal waters compared with the inshore and offshore waters of the frontal area (Nakata, 1995). Juvenile *S. melanostictus* (32–48 mm fork length) collected in
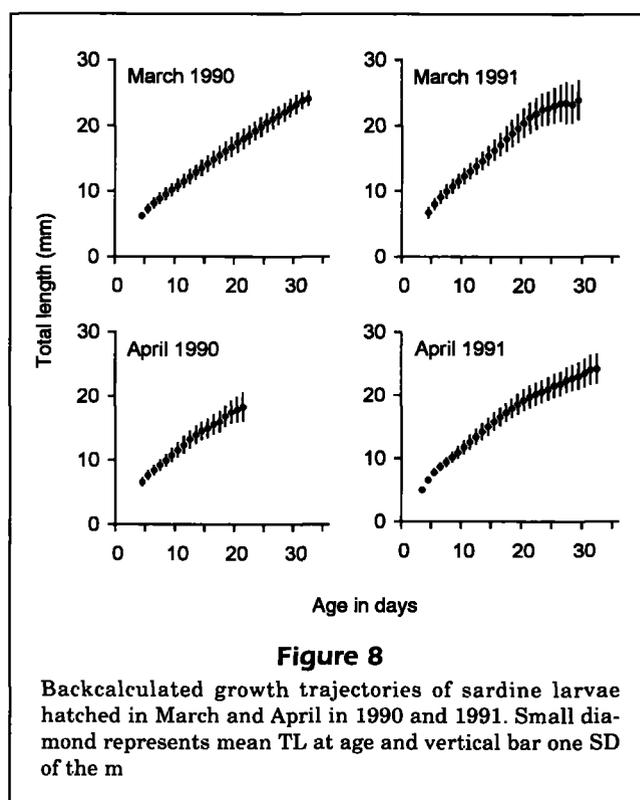
the Kuroshio frontal waters had stomach contents (mostly copepods and larvaceans) of 7–10% of wet body weight and were backcalculated to have grown at 0.8–0.9 mm/d in the larval stage (Watanabe and Saito, 1998). Perhaps the coastal waters in and around the *shirasu* fishing grounds are a less favorable feeding area for sardine larvae than the Kuroshio frontal waters.

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