Distribution, feeding condition, and growth of Japanese Spanish mackerel (*Scomberomorus niphonius*) larvae in the Seto Inland Sea

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Abstract—Distribution of eggs and larvae and feeding and growth of larvae of Japanese Spanish mackerel (*Scomberomorus niphonius*) were investigated in relation to their prey in the Sea of Hiuchi, the Seto Inland Sea, Japan, in 1995 and 1996. The abundance of *S. niphonius* eggs and larvae peaked in late May, corresponding with that of clupeid larvae, the major prey organisms of *S. niphonius* larvae. The eggs were abundant in the northwestern waters and the larvae were abundant in the southern waters in late May in both years, indicating a southward drift during egg and yolksac stages by residual flow in the central part of the Sea of Hiuchi. Abundance of clupeid larvae in southern waters, where *S. niphonius* larvae were abundant, may indicate a spawning strategy on the part of first-feeding *S. niphonius* larvae to encounter the spatial and temporal peak in ichthyoplankton prey abundance in the Seto Inland Sea. Abundance of the clupeid larvae was higher in 1995 than in 1996. Feeding incidence (percentage of stomachs with food; 85.3% in 1995 and 67.7% in 1996) and mean growth rate estimated from otolith daily increments (1.05 mm/d in 1995 and 0.85 mm/d in 1996) of *S. niphonius* larvae in late May were significantly higher in 1995. Young-of-the-year *S. niphonius* abundance and catch per unit of fishing effort of 1-year-old *S. niphonius* in the Sea of Hiuchi was higher in 1995, indicating a more successful recruitment in this year. Spatial and temporal correspondence with high ichthyoplankton prey concentration was considered one of the important determinants for the feeding success, growth, and survival of *S. niphonius* larvae.

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Scombrid fishes are considered to have adopted a survival strategy characterized by fast growth and the ability to consume large prey at an early age (Hunter, 1981). Their larvae have morphological features such as large eyes and mouths, with which piscivory and fast growth can be achieved in early life stages. Among scombrids, extremely early piscivory and fast growth have been observed in the early life stages of Spanish mackerels (*Scomberomorus* fishes). Fish larvae were dominant in stomachs of *Scomberomorus* larvae in three regions: 1) *S. semifasciatus, S. queenslandicus,* and *S. commerson*, in Australian waters (Jenkins et al., 1984), 2) Spanish mackerel (*S. maculatus*) and king mackerel (*S. cavalla*) in the southeastern United States (Finucane et al., 1990), and 3) Japanese Spanish mackerel (*S. niphonius*) in the Seto Inland Sea, Japan (Shoji et al., 1997). Larval growth rate was reported to be approximately 1.0 mm/d in king and Spanish mackerels (DeVries et al., 1990; Peters and Schmidt, 1997) and *S. niphonius* (Shoji et al., 2001). Tanaka et al. (1996) demonstrated precocious development of an adult-type digestive system (with a functional stomach and pyloric caecum) occurred in first feeding *S. niphonius* larvae. They suggested that *Scomberomorus* fish have adopted a specialized feeding strategy, namely piscivory and fast growth from the time of first feeding, which reduces the duration of the larval stage, the period of greatest vulnerability to predation (Houde, 1987).

Ichthyoplankton prey seem to be indispensable for growth and survival during larval period of *Scomberomorus* fish. Under laboratory conditions, Fukunaga et al. (1982) reported that *S. niphonius* larvae preferred fish larvae to invertebrate plankton prey (rotifer and *Artemia* nauplii). Shoji and Tanaka (2001) demonstrated that *S. niphonius* larvae began to cannibalize siblings when they were supplied with only invertebrate plankton prey. *Scomberomorus* larvae would need to exert greater searching effort and to swim fast to capture ichthyoplankton prey because they are larger and much less abundant in water than invertebrate plankton prey (Sheldon et al., 1972). *Scomberomorus* larvae with a high swimming performance have been shown to have high levels of larval mortality due to starvation. Margulies (1993) demonstrated by histological analysis that Pacific sierra (*S. sierra*) larvae could not survive beyond 48 hours without feeding in the Panama Bight. Shoji et al. (2002) observed that the point-of-no-return for *S. niphonius* larvae was one day after first feeding in laboratory experiments. *Scomberomorus niphonius* larvae fed after 1- or 2-days starvation showed significantly retarded growth during the following period of adequate feeding compared to fish that had been fed from the time of first feeding. These observations suggest that ichthyoplankton prey availability can strongly influence growth and survival of *S. niphonius* larvae.

Scomberomorus niphonius is distributed in the coastal waters of Japan and supports important commercial fisheries in the Seto Inland Sea. The total catch exceeded 6000 metric tons (t) in the middle 1980s but decreased to less than 1000 t in the late 1990s in the Seto Inland Sea. Spawning migration of *S. niphonius* into the Seto Inland Sea occurs in May (Kishida and Aida, 1989) and the larvae are distributed in May and June in the Sea of Hiuchi, the central Seto Inland Sea (Kishida, 1988). In order to ensure that catches remain at stable levels and to establish more efficient fisheries management, it is necessary to accumulate biological information to elucidate the recruitment process of the species.

The objective of the present study is 1) to investigate spatial and temporal distribution of *S. niphonius* larvae and their prey and 2) to compare feeding conditions and growth of *S. niphonius* larvae for two consecutive years with contrasting levels of recruitment, 1995 and 1996, in the Seto Inland Sea, Japan. The catch-per-unit-of-fishing-effort (CPUE: no. of fish/boat/day) of 1-year-old *S. niphonius* (Fig. 1) fished by drift gill net in May, the major fishing season for the species, at the Kawarazu Fisherman's Association (Fig. 2) has been used as a recruitment index in the Sea of Hiuchi (Kishida, 1991). The CPUE fluctuated tenfold in the 1990s (Ehime Prefecture Chuyo Fisheries Experimental Station Toyo Branch[1]) and indicated recruitment in 1995 was more successful. Egg, larval, and larval prey distributions, larval feeding incidence and growth, and young-of-the-year (YOY) fish abundance were investigated in 1995 and 1996 in the Sea of Hiuchi.

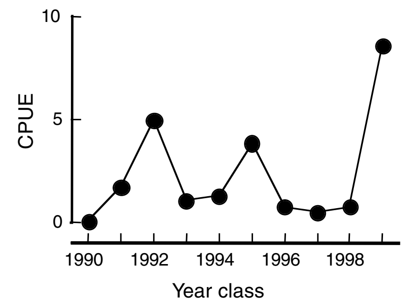

Figure 1

Catch per unit of fishing effort (CPUE: no. of fish/boat/day) of 1-year-old *Scomberomorus niphonius* in the 1990–99 year classes at the Kawarazu Fisherman's Association in the central Seto Inland Sea. Data were obtained from drift gill-net catches in May, the major fishing season for *S. niphonius*.

Materials and methods

Ichthyoplankton sampling

Three research cruises were carried out in 1995 (11–16 April, 24–28 May, and 20–23 June) and in 1996 (10–13 May, 27–30 May, and 18–21 June) in the Sea of Hiuchi (Fig. 2). Ichthyoplankton sampling and hydrographic survey were conducted from the RV *Shirafuji* (138 t) of the National Research Institute of Fisheries and Environment of Inland Sea (NRIFEIS). Double oblique tows from the surface to 5 m above the bottom were made by using a bongo net (0.7-m diameter, 0.315-mm mesh) at 80 stations during the cruises in 1995 and at 50 stations in 1996. Average depth of the Sea of Hiuchi is approximately 17.8 m (Montani, 1996). *Scomberomorus niphonius* larvae were quickly sorted from the samples and were preserved in 95% ethanol. Other ichthyoplankton were fixed in 10% formalin seawater for sorting in the laboratory. Flow meters were mounted in the mouth of the net to determine the filtered volume. Each tow followed a salinity-temperature-depth sensor cast to measure the water temperature and salinity profiles at each station.

YOY fish abundance

YOY *S. niphonius* have been reported to occur in the southern part of the Sea of Hiuchi from late June to early July (Watanabe, 1994). To detect a potential difference in *S. niphonius* recruitment abundance between 1995 and 1996, YOY fish abundance was assessed in the southern part of the Sea of Hiuchi. YOY *S. niphonius* were collected from catches by a seine fishery in the southern part of the Sea of Hiuchi (Fig. 2). The seine fishery primarily targets young and adult Japanese anchovy (*Engraulis japonicus*). The codend of the net has a 2-mm mesh aperture and was towed by two boats for about 1 hour at a ship velocity of 3 to 4 knots. Two to 10 kg of the catch by the seine fishery was sampled weekly (five times each year) from mid June to late July in 1995 and 1996. YOY abundance was expressed as the number of *S. niphonius* per 10 kg of the catch.

Laboratory procedures

Larval SL was measured to the nearest 0.1 mm, and stomach contents were identified under a dissecting microscope. After removal of *S. niphonius* larvae, the bongo-net samples were processed to estimate concentrations (no./100 m^2) of *S. niphonius* eggs. Larvae of two

[1] Ehime Prefecture Chuyo Fisheries Experimental Station Toyo Branch. 2000. Unpubl. data. Kawarazu, Toyo, Ehime 799-1303, Japan.

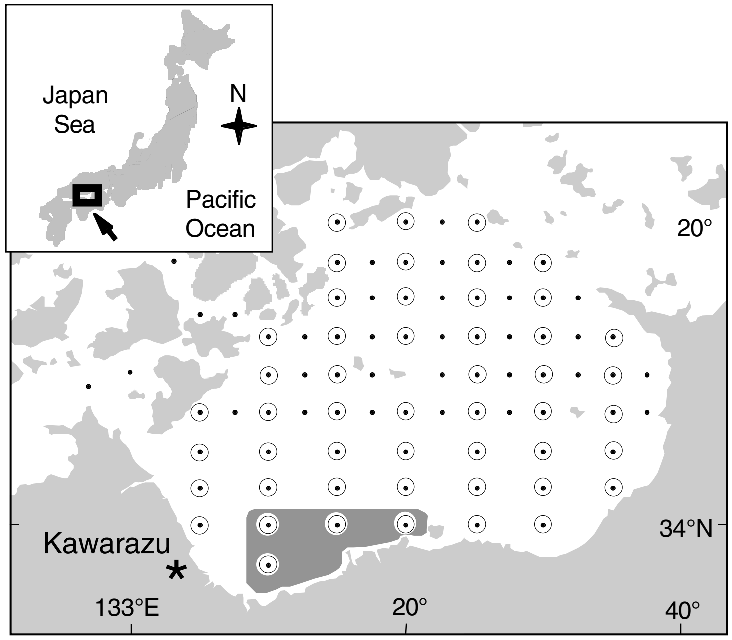

Figure 2

Map of the Sea of Hiuchi, central Seto Inland Sea, showing the sampling stations where ichthyoplankton were collected with a bongo net during the three cruises in 1995 (closed small circles) and in 1996 (large open circles). Catch data for 1-year-old *S. niphonius* were obtained at Kawarazu Fisherman's Association (asterisk). Young-of-the-year Japanese Spanish mackerel were collected by the seine fishery in the southern waters indicated by the shaded area.

clupeid species, gizzard shad (*Konosirus punctatus*) and Japanese sardine (*Sardinops melanostictus*), that were the major prey organisms of the post-first-feeding *S. niphonius* larvae (see "Results" section) were counted to estimate prey concentrations.

Scomberomorus niphonius larvae were aged by counting daily increments on otoliths. Right-side sagittal otoliths were removed under a dissecting microscope and the number of increments on the otolith were counted using an image-analysis system (ARP, version 4.21, Ratoc System Engineering Co., Ltd., Tokyo, Japan) connected to a compound light microscope at 400 to 1000× magnification. Daily increments begin to be deposited on the sagittal otoliths of *S. niphonius* larvae at first feeding (Shoji and Tanaka, 2004). *Scomberomorus niphonius* larvae initiate feeding on day 5 under 19.0°C (Shoji et al., 2001). Larval age was therefore estimated by adding five to the increment count because the water temperature in the southern part of the Sea of Hiuchi where *S. niphonius* larvae were abundant ranged between 18° and 20°C (see "Results" section) in late May. Data from cruises in late May only (the second cruise in both years) were included in the feeding and growth analyses because no *S. niphonius* larvae were collected during the first cruise and too few were collected during the third cruise in both years.

Results

Physical environment

The surface water temperature was higher in the southeastern area and lower in the northwestern area in all cruises. Mean surface temperatures (±SD) were 12.3° (±0.4), 18.6° (±1.2), and 20.5° (±0.6)°C in 11–16 April, 24–28 May, and 20–23 June, 1995, and were 14.3° (±0.6), 19.0° (±1.3), and 19.4° (±1.0)°C in 10–13 May, 27–30 May, and 18–21 June 1996, respectively (Fig. 3). Salinity ranged between 32.5 and 34.3 ppt and was lower in the southeastern area in all cruises. In late May, during the seasonal peak in abundance of *S. niphonius* larvae, the mean surface temperature was slightly higher in 1996 although there was no significant difference between the two years (ANOVA: F=3.14, P=0.08).

Scomberomorus niphonius eggs and larvae

A total of 1018 eggs and 272 larvae of *S. niphonius* were collected during the cruises. No eggs and larvae of *S. niphonius* were collected during the first cruise in both years. The egg and larval abundance peaked in late May and decreased thereafter in both years (Fig. 4, A and B). The eggs were abundant in the northwestern waters in late May where the surface temperature was between 17° and 19°C (Fig. 5). The larvae were abundant in the middle to southern waters, where the surface temperature was between 18° and 20°C in late May (Fig. 6). There was no significant difference in egg and larval abundance in late May between the two years (ANOVA: F=0.03, P=0.87 for eggs; F=0.02, P=0.89 for larvae).

Clupeid larvae

Of the 107,252 larvae collected throughout the cruises, clupeid larvae were most dominant, accounting for 57.2% in number. Gizzard shad and Japanese sardine larvae accounted for 76.4% and 23.6% of clupeid larvae, respectively. A seasonal change in abundance of clupeid larvae and a peak in abundance in late May in both years were evident (Fig. 4C). Maximum abundance (no./m^2) was more than 400 in late May in 1995 in the southern waters and there was no station where the abundance exceeded 300/m^2 in 1996 (Fig. 7). The difference in abundance of clupeid larvae in late May between the two years was significant (ANOVA: F=8.12, P=0.005).

Feeding

Clupeid larvae (gizzard shad, Japanese sardine, and unidentified clupeid larvae) were the most dominant items in the stomachs of *S. niphonius* larvae (Table 1). Feeding incidence (percentage of stomachs with food) was significantly higher in 1995 than in 1996 (chi square test; df=1, chi-square=8.538, P=0.0035).

Growth

Age of *S. niphonius* larvae collected in late May in 1995 and 1996 was estimated to be between 5 and 14 days

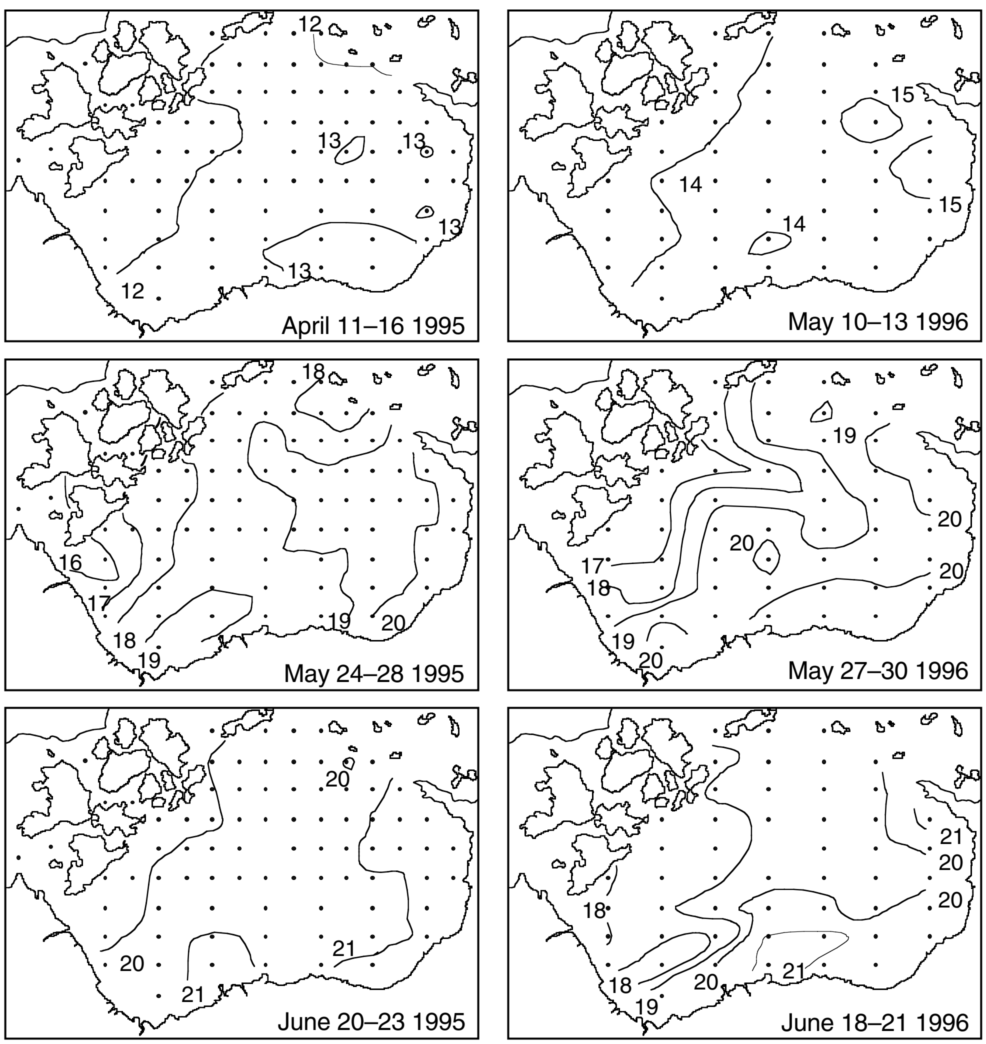

Figure 3

Contour plots of the surface water temperature (°C) of the Sea of Hiuchi during the three cruises in 1995 and 1996.

after hatching. Relationships between larval age (A) and SL (L, mm) were best described by a linear regression for each year (Fig. 8):

1995: $L = 1.05A - 1.39$ (n=102, r^2=0.87, P<0.0001)
1996: $L = 0.85A - 0.15$ (n=93, r^2=0.80, P<0.0001).

The slope of the equation for 1995 was significantly higher than that for 1996 (ANCOVA; df=1, F=11.01, P=0.001).

YOY *S. niphonius* abundance

YOY *S. niphonius* (14.6–122.8 mm in TL) were collected by the seine fishery in the Sea of Hiuchi from late June through late July in 1995 and 1996. Mean (±SE) abundance of YOY *S. niphonius* in 1995 (7.7 [±2.1] individuals/m^2) was significantly higher than that in 1996 (0.6 [±0.4] individuals/m^2; Mann-Whitney U-test; P=0.006, Fig. 9).

Discussion

Spawning strategy

Abundance of *S. niphonius* eggs and larvae peaked in late May in 1995 and 1996. A similar pattern was observed in the abundance of clupeid larvae, indicating that spawning of *S. niphonius* was synchronized with

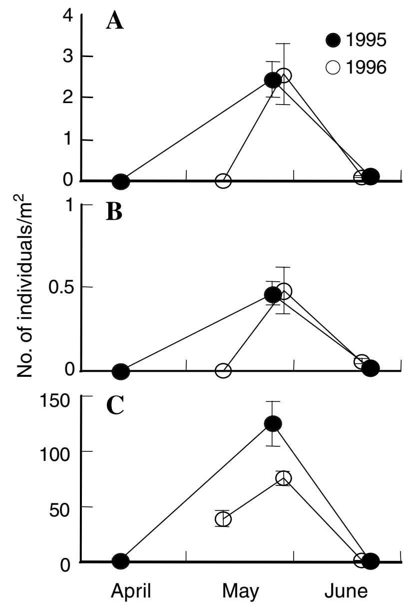

Figure 4

Seasonal change in abundance (no./m^2) of *S. niphonius* eggs (**A**), larvae (**B**) and clupeid prey larvae (**C**) in the Sea of Hiuchi in 1995 and 1996. Bars indicate standard error.

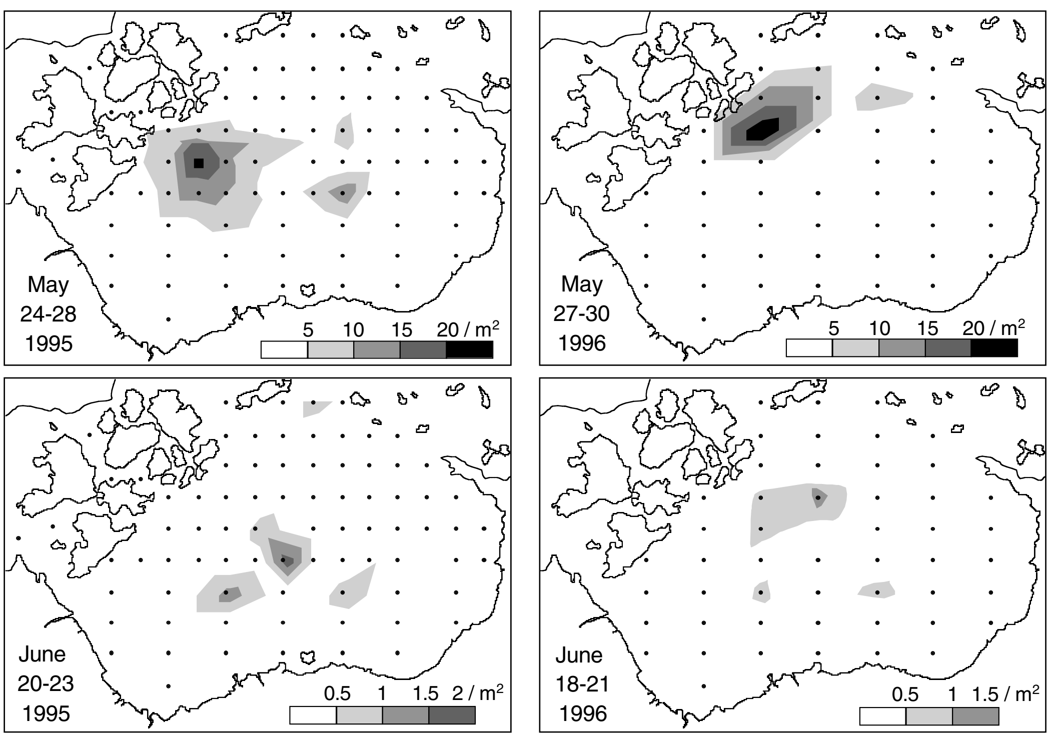

Figure 5

Horizontal distribution of *S. niphonius* eggs in the Sea of Hiuchi in 1995 and 1996.

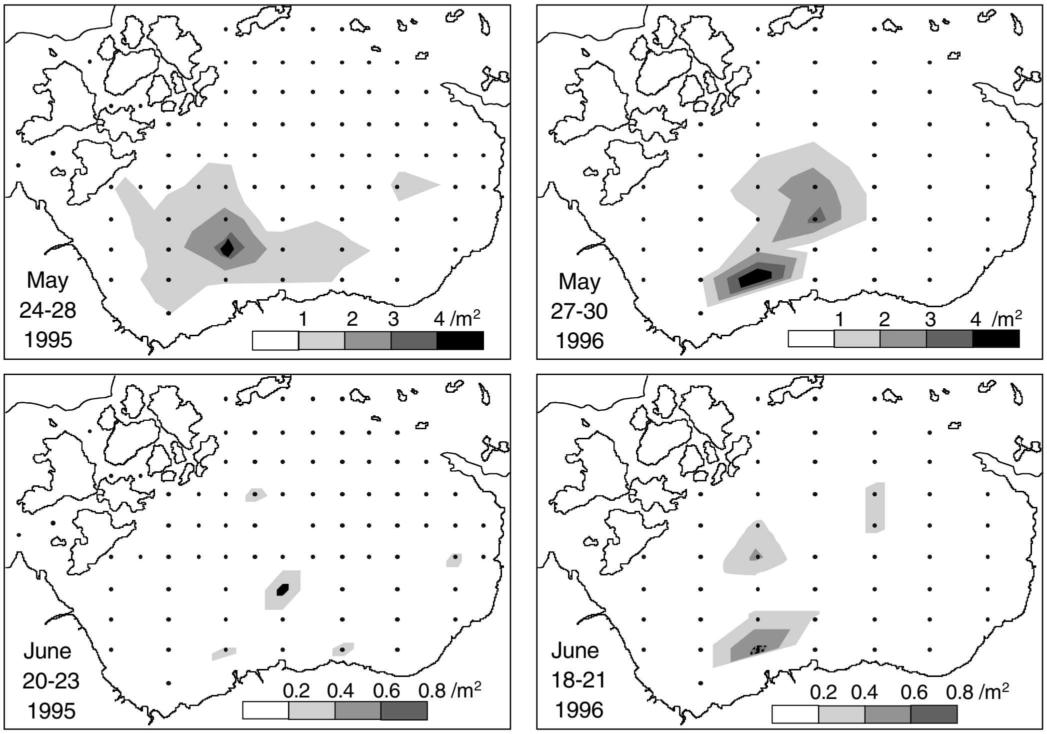

Figure 6

Horizontal distribution of *S. niphonius* larvae in the Sea of Hiuchi in 1995 and 1996.

that of clupeid fishes in the central Seto Inland Sea. Piscivorous fishes tend to spawn earlier than other fishes in freshwater ecosystems so that they attain sufficient size to enable consumption of other young fishes by the onset of piscivory (Keast, 1985). Because *S. niphonius* larvae are piscivorous from the first feeding stage, spawning that is synchronized with the seasonal peak in abundance of clupeid larvae would be advantageous for survival of *S. niphonius* larvae.

Larvae of *S. niphonius* were abundant in the southern part of the Sea of Hiuchi in late May 1995 and 1996 while eggs were abundant in the northwestern waters during the same season. This difference in horizontal distribution patterns of eggs and larvae seems to be associated with the drift by a residual flow (current) from northern to southern waters. In the central part of the Sea of Hiuchi, a residual flow in the middle (5–15 m) layers proceeds southward at a speed of about 5 cm/s (=4.32 km/d; Yanagi et al., 1995). Yolksac larvae of *S. niphonius* are abundant in the 5- to 10-m layers in the Sea of Hiuchi (Kishida, 1988) and do not exhibit diel vertical migration (Shoji et al., 1999). The horizontal distance between the stations with the highest egg and larval abundance in late May was approximately 15 km in 1995 and 20 km in 1996. Given that the yolksac stage is five days for mackerel larvae under 19°C (Shoji et al., 2001), drift distance while larvae are entrained in the southward residual flow during the yolksac stage would be estimated to be approximately 20 km. The estimate for the drift distance during the yolksac stage approximates the horizontal distance between the stations of egg and larval highest abundance. It is therefore plausible that the larvae were transported by the southward residual flow to the southern part of the Sea

Table 1

Feeding incidence (percentage of stomachs with prey) and stomach contents of *S. niphonius* larvae collected in late May of 1995 and 1996 in the Sea of Hiuchi.

	1995	1996
No. of larvae examined	102	93
No. of larvae feeding	87	63
Feeding incidence (%)	85.3	67.7
Size range (SL, mm)	4.2–13.8	4.5–14.2
Stomach contents	*n*	*n*
Sardinops melanostictus	4	2
Konosirus punctatus	21	14
Unidentified clupeids	19	11
Engraulis japonicus	2	4
Unidentified Clupeiformes	34	22
Mugiliidae	3	2
Gobiidae	13	9
Total	96	64

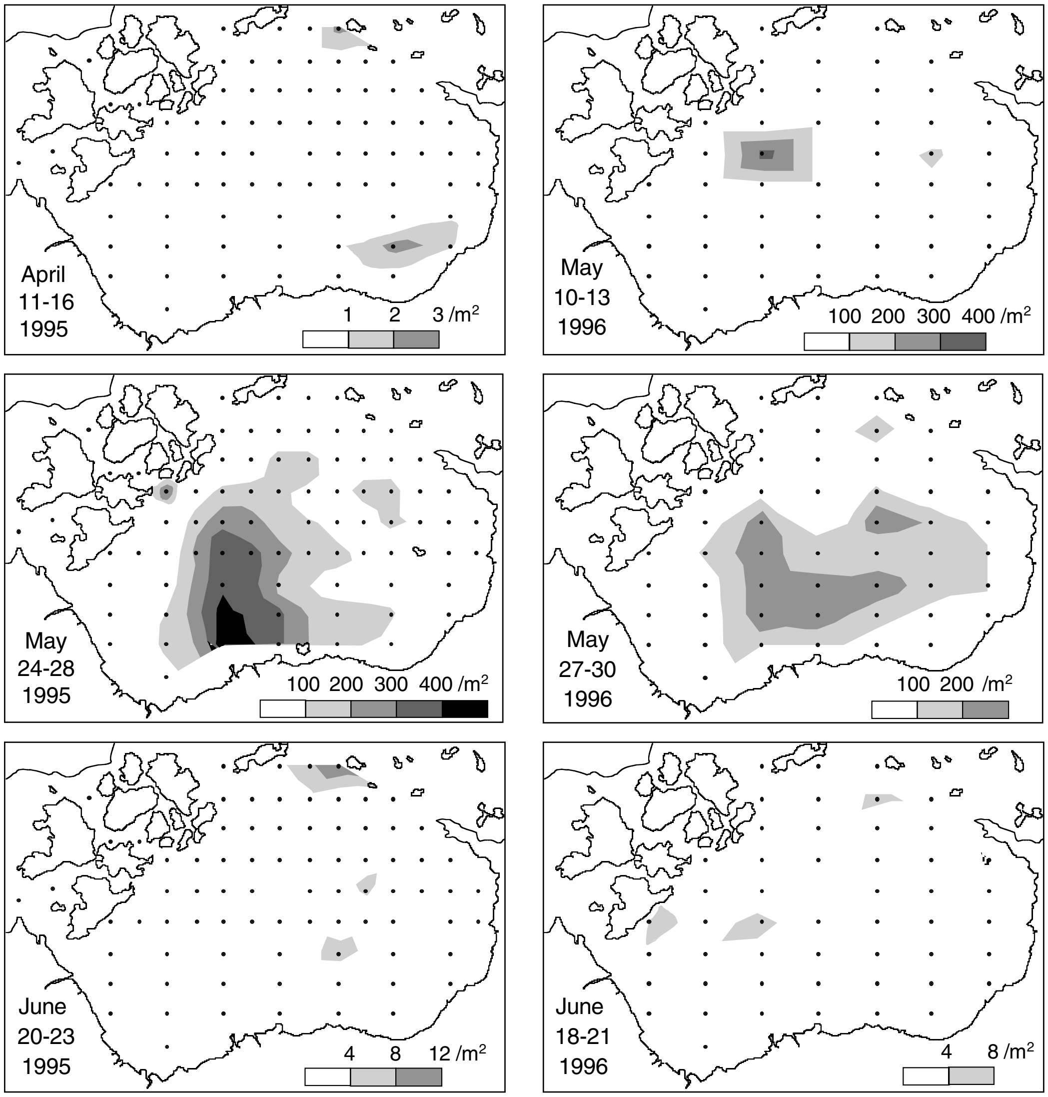

Figure 7

Horizontal distribution of clupeid larvae in the Sea of Hiuchi during the three cruises in 1995 and in 1996.

of Hiuchi where clupeid larva concentration was high in late May. We suggest that spawning of *S. niphonius* in the northern part of the Sea of Hiuchi would enable their first-feeding larvae to meet high prey abundance in the southern part.

Significance of high ichthyoplankton prey

Water temperature and prey concentration would be possible factors that can influence growth rates of *S. niphonius* larvae. In aquaria, the mean absolute growth rate of *S. niphonius* larvae fluctuated between 0.87 and 1.28 mm/d depending on temperature between 18.2° and 22.6°C (Fukunaga et al., 1982; Shoji et al., 2001). In the present study, the mean surface temperature of the Sea of Hiuchi in late May was slightly higher in 1996, although the difference was not significant.

The higher abundance of clupeid larvae in 1995 would better explain the higher larval growth rate in 1995. The mean larval growth rate in late May 1995, 1.05 mm/d, approximates those reported in aquaria at the same temperature (1.03 mm/d at 20.8°C; Fukunaga et al., 1982) where *S. niphonius* larvae were provided with an excess of prey, indicating that the prey concentration in late May 1995 met larval requirements. It is likely that the lower growth rate in late May 1996 resulted from lower prey concentration. This conclusion is supported by results of the stomach content analysis: the larval feeding incidence was significantly lower in May 1996. We conclude that clupeid larvae concentration had a significant effect on growth of the *S. niphonius* larvae.

In the Sea of Hiuchi, clupeid larvae abundance greatly increased from April to May. We suggest that the prey

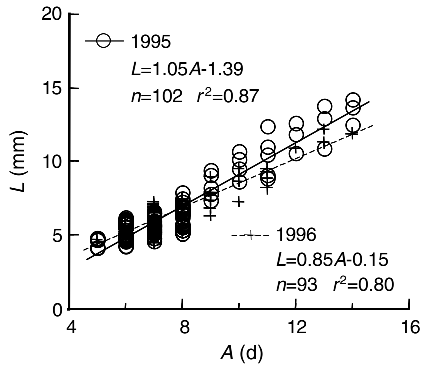

Figure 8

Relationships between standard length (L, mm) and otolith-estimated age (A, d) of *S. niphonius* larvae collected during the cruises in late May of 1995 and 1996 in the Sea of Hiuchi.

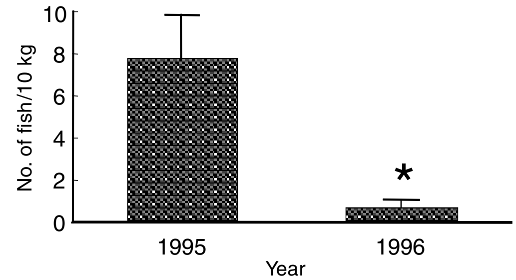

Figure 9

Mean (SE) young-of-the-year *S. niphonius* abundance collected by the seine fishery in 1995 and 1996 in the Sea of Hiuchi. Asterisk indicates a significant difference between the years (Mann-Whitney U-test, $P<0.01$).

availability for *S. niphonius* larvae fluctuated depending for the most part on seasonal change in abundance of gizzard shad larvae that were dominant in the Sea of Hiuchi. The difference in clupeid larval abundance in late May between 1995 and 1996 may be explained by between-year difference in gizzard shad spawning stock biomass. The total catch of gizzard shad in the southern Sea of Hiuchi (coastal waters of Ehime Prefecture) in 1995 (372 t) was higher than that in 1996 (217 t: Ehime Prefecture Agriculture, Forestry and Fisheries Statistics Association, 1998).

Implications for recruitment

Variability in larval growth rate can influence survival during the larval period by affecting the length of the early life stages because total mortality is positively correlated with the length of these early life stages (Houde, 1987). Campana (1996) demonstrated a significant correlation between growth to the end of the pelagic juvenile stage (90 d) and the year-class strength of Atlantic cod on the Georges Bank and suggested that the adult cohort strength could be predicted from growth during early life stages. In the present study, egg and larval *S. niphopius* abundance during their peak-occurrence period did not differ between 1995 and 1996, whereas YOY and 1-year-old *S. niphonius* were more abundant in 1995. These results indicate more successful recruitment and higher larval growth rate in 1995 although there are no data available for years other than 1995 and 1996. Larvae of *S. niphonius* initiate feeding at 5.59 mm SL at 18.5°C (Shoji et al., 2002). Given the mean larval growth rate in 1995 (1.05 mm/d) and 1996 (0.88 mm/d), the critical period (from first feeding to the onset of schooling at the early juvenile stage, 19.6 mm SL; Masuda et al., 2003) is estimated as 13.3 days in 1995 and 16.5 days in 1996. For *S. niphonius*, even a slight increase in larval stage duration due to retarded growth can greatly reduce larval survival because the larval daily mortality coefficient is expected to be extremely high (>0.6: Grimes and Kingsford, 1996). The lower recruitment of *S. niphonius* in 1996 may be partly explained by the prolonged larval period (3.2 d) which could have led to lower survival (1/6.82, assuming the daily mortality coefficient is 0.6) during the larval period of that year.

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