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Developmental and growth rates of Japanese anchovy *Engraulis japonicus* during metamorphosis in the Kuroshio-Oyashio transitional waters

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ABSTRACT: Stage duration and growth rate during the late larval stage can be key parameters of recruitment dynamics in the Japanese anchovy *Engraulis japonicus* in the Kuroshio-Oyashio transition region of the western North Pacific. The developmental rate was defined as a reciprocal of the duration in days of the metamorphosing stage, and was a positive function of the growth rate after the onset of metamorphosis. The growth rate after the onset of metamorphosis in the early juvenile stage fish corresponded with higher growth rates in the early metamorphosing stage fish. The results indicate that larvae with a faster growth rate during the late larval stage metamorphosed at a younger age than the larvae with a slower growth rate. Developmental and growth rates were faster in the southwestern waters than in the northern and eastern waters in the Kuroshio-Oyashio transition region. Survival during metamorphosis depends on the developmental and growth rates, and we conclude that the larvae with faster developmental and growth rates in the southwestern waters had a higher probability of successful metamorphosis and recruitment to the spawning stock, and constituted the major part of the population of *E. japonicus* in the Kuroshio-Oyashio transition region.

KEY WORDS: Developmental rate · Growth rate · Otolith · Metamorphosis · Japanese anchovy

INTRODUCTION

The total annual catch of the Japanese anchovy *Engraulis japonicus* in the Japanese Pacific coastal waters was 100 000 to 250 000 metric tons (t) from the 1960s to the mid 1970s. The catch declined to 50 000 to 100 000 t through the 1980s and sharply increased from 88 000 t in 1989 to 212 000 t in 1990 (Statistics and Information Department 1963–2001).

The main spawning ground of *Engraulis japonicus* was located in the Pacific coastal waters in the early 1980s (TRFRL 1988). It expanded to the Kuroshio Current region in the 1990s when the population was large (NRIFS 1995). The Kuroshio Current flows eastward off the Pacific coast of southern Japan and breaks away from the coastal waters as the Kuroshio Extension, which delimits the southern margin of the Kuroshio-Oyashio transition region. Pelagic eggs and larvae distributed around the Kuroshio Current region off the Pacific coastal spawning grounds are swiftly transported eastward to the Kuroshio Extension (Kasai et al. 1992, Heath et al. 1998). The northward intrusion of warm water from the Kuroshio Extension further transports eggs and larvae into the Kuroshio-Oyashio transition region (Okazaki et al. 2002). In the 1950s and 1990s, the distribution range of larval and juvenile *E. japonicus* expanded eastward from the coastal waters at the waters of 170° E in the transition region (Odate 1957, Takahashi et al. 2001). The abundance of *E. japonicus* at Age 1 in the Pacific coastal waters has been suggested to be dependent on the survival processes in the late larval and early juvenile stages in the transition region (Takahashi 2001).

Survival probabilities during the larval and juvenile stages in fishes have been hypothesized to be a function of the growth rate and the stage duration in early

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life stages. Anderson (1988) proposed the 'growth-mortality' hypothesis that bigger larvae of a faster growth rate in a population have a shorter duration of the larval stage over which high mortality rates are hypothesized to occur, and faster growth rates result in a higher recruitment probability. In Atlantic cod *Gadus morhua*, faster-growing larvae survived better than slower-growing larvae until the juvenile stage (Meekan & Fortier 1996). Campana (1996) demonstrated in *G. morhua* that the larval growth rate was positively correlated with the abundance of fish at Age 1.

The mean larval growth rate in *Engraulis japonicus* was found to be faster in the western waters of 140 to 155° E than in the eastern waters of 155 to 170° E in the Kuroshio-Oyashio transition region (Takahashi et al. 2001). Larvae with a faster growth rate have been shown to have a shorter stage duration of the larval stage in many marine fishes (Benoît et al. 2000). The stage duration of the larval stage in *E. japonicus* may be different among variable environmental conditions and can be a key parameter of the recruitment dynamics in the Kuroshio-Oyashio transition region.

We focused on the stage duration and growth rate after the onset of metamorphosis in late larval *Engraulis japonicus*. The developmental rate was defined as a reciprocal of the number of days in the metamorphosing stage and used as a parameter of the duration of the metamorphosing stage in this study. We aimed to demonstrate the relationship between the developmental and growth rates during metamorphosis, and to examine the effect of the developmental and growth rates on the survival process during the late larval and early juvenile stages in *E. japonicus* in the Kuroshio-Oyashio transition region.

MATERIALS AND METHODS

Field sampling. Samples of larval and early juvenile *Engraulis japonicus* in the Kuroshio-Oyashio transition region were obtained from subsurface trawl surveys conducted by the National Research Institute of Fisheries Science, Fisheries Research Agency, from 24 May to 25 June 1997 and 14 May to 14 June 1998. The trawl net used in these surveys had a 25 × 25 m opening and a 10 mm mesh aperture at the cod end, and was towed for 30 min at 3 to 4 knots; 3 hauls a night were made at depths shallower than 25 m. A random subsample of about 200 to 300 anchovy larvae and early juveniles was taken from each trawl catch and preserved at –25° C. The number of larvae and early juveniles collected in each haul was enumerated by the gravimetric method based on the wet weight and fish counts in a subsample.

Sample processing. A random sample of up to 100 individuals was taken from the subsample for the analysis of developmental and growth rates for each haul. The standard length (*L*) of each fish was measured to the nearest 0.1 mm with digital calipers and was assigned to 1 of 3 development stages depending on the degree of guanine deposition on the peritoneal surface of the body cavity and lateral surface of the trunk; the fish without any guanine deposition on the peritoneal and trunk surfaces corresponded to the larval and early metamorphosing stage (Stage Gu-0), fish with guanine deposition on the peritoneal surface but not on the trunk surface corresponded to the end of metamorphosing stage (Stage Gu-1), and fish with guanine deposition on the peritoneal and trunk surfaces corresponded to the juvenile stage (Stage Gu-2) (Takahashi & Watanabe 2004a).

Sagittal otoliths were removed under a binocular microscope from 50 random specimens and mounted on a glass slide with enamel resin. Counts and measurements of the otolith daily increments were conducted under a light microscope at 100 to 500× magnification with the otolith measurement system controlled by a personal computer (RATOC System Engineering). For individual fish <50 mm *L*, we counted the total number of daily increments and measured the radius of each increment from the nucleus along the postrostrum transect of an otolith.

Developmental rates. Developmental rates were analyzed using up to 10 otoliths of fish for each of the Gu-0, Gu-1 and Gu-2 stages from the 50 specimens in each haul. The first daily increment of the otolith is deposited 3 to 4 d after hatching in *Engraulis japonicus* (Tsuji & Aoyama 1984). The age in days at capture of each Gu-0, Gu-1 and Gu-2 stage fish was calculated by adding 3 to the total number of otolith daily increments. The relationship between *L* and otolith radius is represented by an allometric equation within the current *L* range (Takahashi et al. 2001). We determined the allometric parameters of the relationship between *L* and otolith radius for each of the Gu-0, Gu-1 and Gu-2 stage fish by using the biological intercept method (Campana 1990, Campana & Jones 1992), and calculated *L* at ages from hatching to capture following Watanabe & Kuroki (1997). Since Fukuhara (1983) showed that *L* at the first feeding stage was 3.76 ± 0.29 mm, we assumed *L* at the first increment deposition to be 3.5 mm in this study.

As morphological changes of metamorphosis from the larval to the adult pattern start at *L* > 20 mm and terminated at the end of the Gu-1 stage in *Engraulis japonicus* (Takahashi & Watanabe 2004a), we defined the duration of the metamorphosing stage in days (d_m) from age at 20 mm *L* to age at capture in the

Gu-1 stage fish. The developmental rate D (% d^{-1}) was calculated for Gu-1 stage fish as:

$$D = 100/d_m$$

and the mean growth rate after the onset of metamorphosis for Gu-0, Gu-1 and Gu-2 stage fish (G) as:

$$G = (L - 20)/d_m$$

where L is the standard length at capture. The growth rate at age i (G_i) was calculated for Gu-1 stage fish as:

$$G_i = L_i - L_{i-1}$$

where L_i and L_{i-1} are the back-calculated L at ages i and (i – 1) d, respectively (i = 2, 3…, t – 1, age at capture t).

Each Gu-1 stage fish was assigned to a D class and a G class for the analysis of geographic variability in developmental and growth rates in the transition region. The data of mean L, age, D and G were tested statistically by analysis of variance and a *post hoc* test, Fisher's PLSD (Zar 1996).

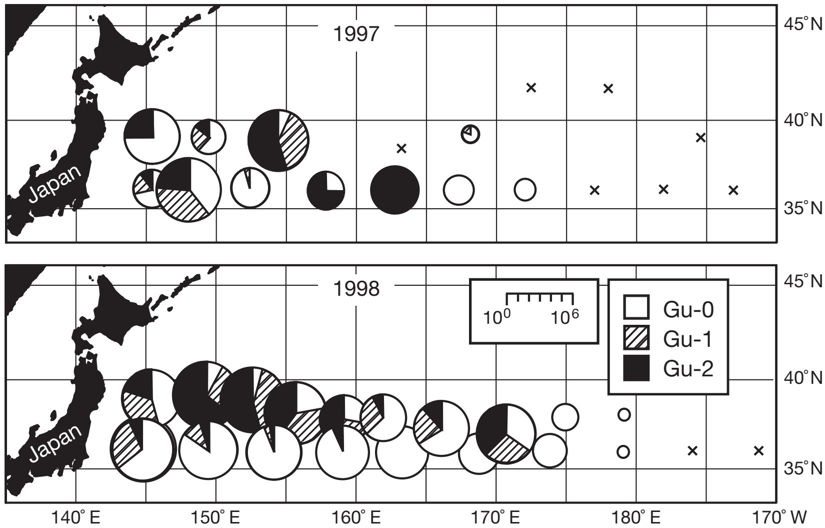

Fig. 1. *Engraulis japonicus.* Proportion in number of Gu-0, Gu-1 and Gu-2 stage anchovy caught in the Kuroshio-Oyashio transition region in 1997 (top) and 1998 (bottom). ×: location at which the Gu-0, Gu-1 and Gu-2 stage anchovy <50 mm standard length (L) were not collected. Scale bar indicates no. of fish

RESULTS

Distribution of Gu-0, Gu-1 and Gu-2 stage anchovy

The sum of Gu-0, Gu-1 and Gu-2 stage fish collected in the 3 hauls a night decreased from western to eastern waters (Fig. 1), except for the 37° N, 171° E station in 1998 where a large catch of about 1.5 × 10^5 was recorded. The proportion of Gu-0 stage fish to all fish of the Gu-0, Gu-1 and Gu-2 stages ranged from 65 to 100 % in the southern waters (36° N), while from 5 to 66 % in the northern area (37 to 39° N, 140 to 170° E) in 1998. The number of Gu-2 stage fish was about 10^5 to 10^6 per net haul in the northwestern waters (37 to 39° N, 140 to 155° E), and about 10^3 to 10^4 per net haul in the southern waters in 1998. The Gu-2 stage fish were distributed at a higher density in the northern waters compared to the Gu-0 stage fish.

Size and age of Gu-0, Gu-1 and Gu-2 stage anchovy

Modes of L increased from 25.1 to 30.0 mm in the Gu-0 stage fish to 35.1 to 40.0 mm in the Gu-2 stage fish (Fig. 2). All the fish <25 mm L were in the Gu-0 stage. L of the Gu-1 stage fish ranged from 26.4 to 47.0 mm and averaged 34.4 ± 3.6 mm (±SD). The minimum L of the Gu-2 stage fish was 30.8 mm.

The age ranges of the 3 guanine stages were ca. 30 to 90 d, though the modes of age increased from 31 to 40 d in the Gu-0 stage fish to 51 to 60 d in the Gu-2 stage fish. Ages of the Gu-1 stage fish ranged from 29 to 83 d and averaged 54.7 ± 8.5 d. Gu-2 stage fish first

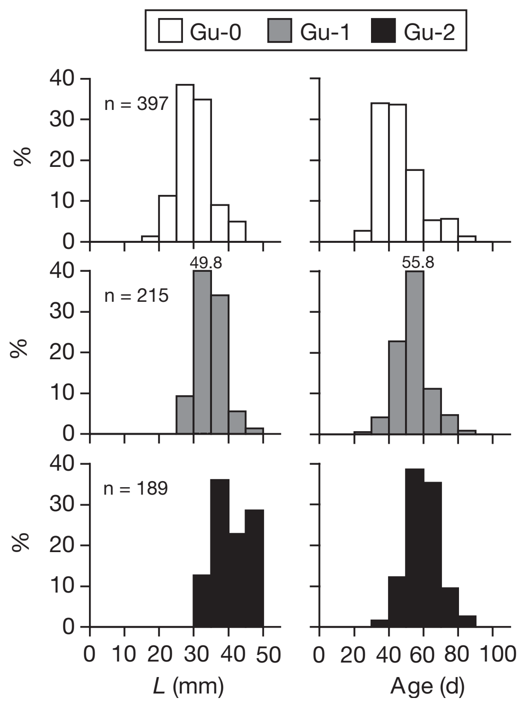

Fig. 2. *Engraulis japonicus.* Frequency distribution of standard length (L) and age in the Gu-0, Gu-1 and Gu-2 stage fish

Table 1. *Engraulis japonicus.* Standard length (*L*), age and growth (*G*) or developmental (*D*) rates from 20 mm to the end of metamorphosis of the Gu-1 stage larvae in the *D* and *G* classes (mean ± SD). n: ind. per sample. Within columns and groups, different letters indicate significant differences (p < 0.01); data without superscript letter were excluded from statistical analysis

Class	*L* (mm)	Age (d)	*G* (mm d^{-1})	*D* (% d^{-1})	n
$D_{2.0}$	41.2 ± 2.9[a]	71.8 ± 6.9[a]	0.50 ± 0.05[a]		22
$D_{4.0}$	34.8 ± 2.4[b]	55.1 ± 4.9[b]	0.59 ± 0.09[b]		144
$D_{6.0}$	31.0 ± 2.1[c]	50.3 ± 4.8[c]	0.62 ± 0.12[b]		40
$D_{8.0}$	30.9 ± 2.2	39.7 ± 5.4	0.81 ± 0.18		8
$D_{10.0}$	28.8	30.0	0.82		1
$G_{0.4}$	33.3 ± 4.8[a]	61.4 ± 8.9[a]		4.1 ± 1.5[a]	42
$G_{0.6}$	34.6 ± 3.3[a]	55.4 ± 6.0[b]		4.3 ± 1.0[a]	134
$G_{0.8}$	34.8 ± 3.2[a]	46.1 ± 7.0[c]		5.6 ± 1.5[b]	35
$G_{1.0}$	33.4 ± 1.7	37.0 ± 1.4		7.9 ± 1.2	4

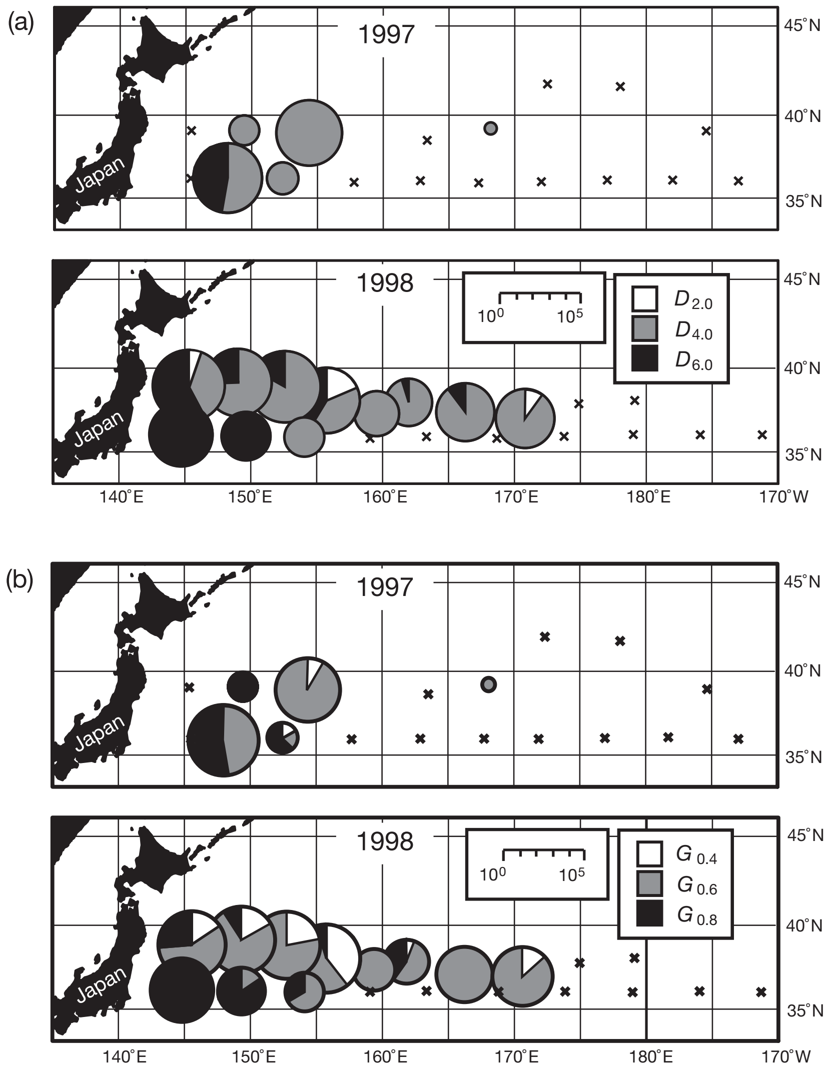

Fig. 3. *Engraulis japonicus.* (a) Proportion of developmental (*D*) and (b) growth (*G*) classes of the Gu-1 stage anchovy caught in the Kuroshio-Oyashio transition region in 1997 (top) and 1998 (bottom). ×: location at which the Gu-1 stage anchovy were not collected. Scale bar indicates no. of fish

occurred in the age range of 31 to 40 d at 1.6% and the proportion sharply increased to 38.6% by 51 to 60 d. The minimum age of Gu-2 stage fish was 37 d.

Geographical variability in developmental and growth rates of Gu-1 stage anchovy

The developmental rate (*D*) of the Gu-1 stage fish ranged from 1.9 to 10.0% d^{-1}. Each Gu-1 stage fish was assigned to 1 of 5 *D* classes by 2% d^{-1} interval; $1.1 < D < 3.0$ ($D_{2.0}$), $3.1 < D < 5.0$ ($D_{4.0}$), … $9.1 < D < 11.0$ ($D_{10.0}$) (Table 1). The $D_{8.0}$ and $D_{10.0}$ classes contained only 8 and 1 fish, respectively, and were excluded from the analysis. Mean *L* and age of the $D_{2.0}$, $D_{4.0}$ and $D_{6.0}$ classes ranged from 31.0 to 41.2 mm and 50.3 to 71.8 d, respectively, and were significantly larger in the lower *D* classes (Table 1). Gu-1 stage fish in the $D_{6.0}$ class were distributed in the southwestern waters (36° N, 144 to 149° E) in proportions of 48.9 to 100% in the years studied (Fig. 3a), while those in the $D_{2.0}$ class occurred in the northern or eastern waters in proportions of 5.3 to 18.6% in 1998.

The mean growth rate after the onset of metamorphosis (*G*) of the Gu-1 stage fish ranged from 0.38 to 1.07 mm d^{-1}. Each Gu-1 stage fish was assigned to 1 of 4 *G* classes of 0.2 mm d^{-1} interval; $0.31 < G < 0.50$ ($G_{0.4}$), $0.51 < G < 0.70$ ($G_{0.6}$), … $0.91 < G < 1.10$ ($G_{1.0}$) (Table 1). The $G_{1.0}$ class contained only 4 fish and was excluded from the analysis. Mean *L* of the $G_{0.4}$, $G_{0.6}$ and $G_{0.8}$ classes ranged from 33.3 to 34.8 mm and were not different from each other. Mean ages of the *G* classes ranged from 46.1 to 61.4 d, and were significantly older in the lower *G* classes. Gu-1 stage fish in the $G_{0.8}$ class occurred in the southwestern waters (36° N, 144 to 154° E) in proportions of 33.3 to 100% (Fig. 3b), while those in the $G_{0.4}$ and $G_{0.6}$ classes were distributed in the northeastern waters (37 to 39° N, 156 to 171° E) in proportions of 58.8 to 100%.

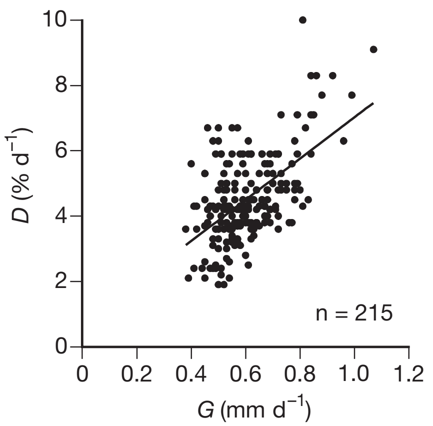

Fig. 4. *Engraulis japonicus.* Relationships between development (D) and growth (G) rates of the Gu-1 stage anchovy

Relationship between developmental and growth rates

The mean G of the Gu-1 stage fish in the 3 D classes ranged from 0.50 to 0.62 mm d^{-1} and was significantly faster in the greater D classes, except between the $D_{4.0}$ and $D_{6.0}$ values (Table 1). The mean D of the Gu-1 stage fish in the $G_{0.8}$ class was significantly greater than in the lower G classes. G of the Gu-1 stage fish was positively correlated with D and had a best fit with a linear equation: $D = 6.31G + 0.715$ ($r^2 = 0.314$, $p < 0.001$, n = 215) (Fig. 4).

The growth rates (G_i) of the Gu-1 stage fish were about 0.6 mm d^{-1} at ages from 10 to 30 d in the $D_{2.0}$, $D_{4.0}$ and $D_{6.0}$ classes (Fig. 5). The mean back-calculated L at 30 d of the Gu-1 stage fish ranged from 19.3 to 19.9 mm in the 3 D classes and was not different between the D classes. The G_i in the $D_{6.0}$ class gradually increased after 30 d to 0.73 mm d^{-1} by 50 d, while in the $D_{2.0}$ class tended to decrease after 30 d to 0.47 mm d^{-1} by 70 d of age.

Growth rate after the onset of metamorphosis Gu-0, Gu-1 and Gu-2 stage anchovy

The growth rate after the onset of metamorphosis (G) was compared between Gu-0, Gu-1 and Gu-2 stage fish within an L range from 20 to 45 mm, which includes 98.7% of Gu-0, 98.6% of Gu-1 and 71.4% of Gu-2 fish (Fig. 2). G of the Gu-0 stage fish ranged from 0.16 to 1.00 mm d^{-1} and averaged 0.56 ± 0.13 mm d^{-1} (±SD), while that of the Gu-2 stage fish from 0.45 to 0.99 mm d^{-1} and averaged 0.67 ± 0.18 mm d^{-1} (Fig. 6). The mean G of the Gu-2 stage fish was significantly greater than that of the Gu-0 stage fish ($p < 0.001$). The proportion of the Gu-2 stage fish with G greater than the mode of the G distribution in the Gu-0 stage fish (0.55 mm d^{-1}) was 87.3%.

The mean G of the Gu-1 stage fish in the $D_{6.0}$ class was 0.62 ± 0.12 mm d^{-1} and significantly greater than that in the $D_{2.0}$ class (0.50 ± 0.05 mm d^{-1}, $p < 0.001$), though not significantly greater than in the $D_{4.0}$ class (0.59 ± 0.09 mm d^{-1}, $p > 0.1$). The proportions of the Gu-1 stage fish with G greater than the mode of G distribution in the Gu-0 stage fish (0.55 mm d^{-1}) were 70.5% in the $D_{6.0}$ class, while only 10.0% in the $D_{2.0}$ class.

DISCUSSION

Growth and development in metamorphosing anchovy

The developmental rate (D) of *Engraulis japonicus* from a length of 20 mm to the end of metamorphosis

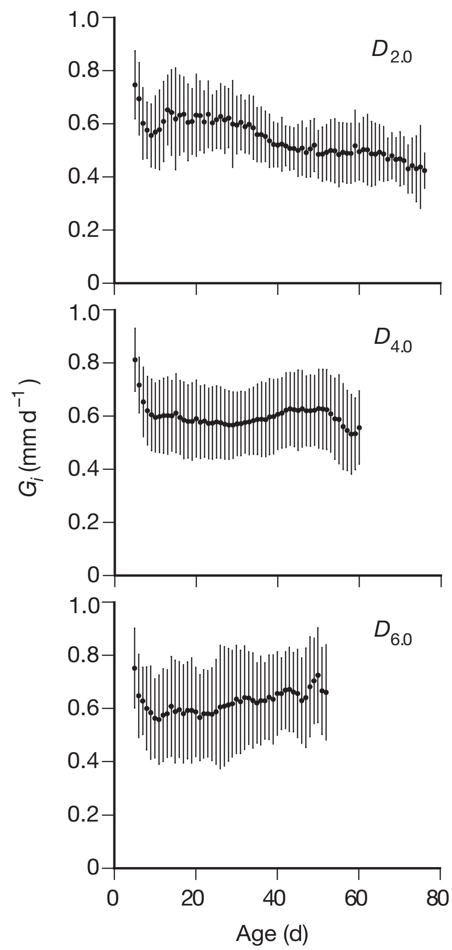

Fig. 5. *Engraulis japonicus.* Growth rates at ages (G_i) in the 3 development (D) classes of Gu-1 stage anchovy. Vertical bars indicate ±SD

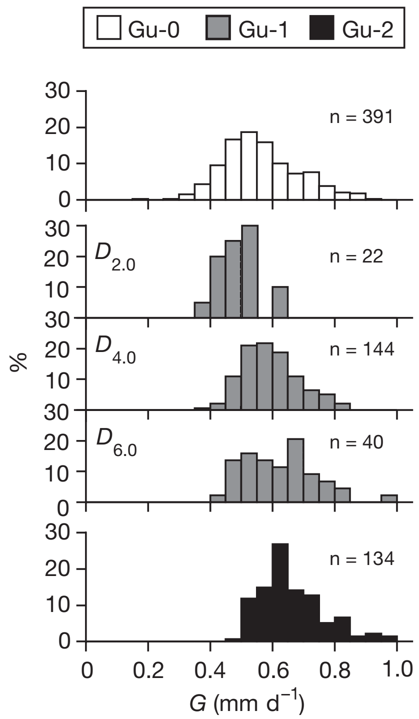

Fig. 6. *Engraulis japonicus*. Frequency distribution of growth rate (G) in the Gu-0, Gu-1 and Gu-2 stage anchovy within 20 to 45 mm standard length (L). G distribution of the Gu-1 stage anchovy was separated into the 3 development (D) classes

(Gu-1) was a positive function of the growth rate (Fig. 4), implying that a slower growth rate during the late larval stage results in a longer duration of the metamorphosing stage in *E. japonicus*. G_i of the Gu-1 stage fish in the $D_{2.0}$ class declined at age >30 d, though G_i at age <30 d in age were at the same level as those of the higher D classes (Fig. 5). The back-calculated length at 30 d was about 20 mm and corresponded to the onset of metamorphosis in *E. japonicus* (Takahashi & Watanabe 2004a). These results indicate that the decline in growth rate after the onset of metamorphosis (L = 20 mm) resulted in a delayed completion of metamorphosis in *E. japonicus* in the Kuroshio-Oyashio transition region. The mean growth rate after the onset of metamorphosis (G) of the Gu-2 stage fish was faster than that of the Gu-0 stage fish (Fig. 6), within the same age ranges from 30 to 90 d. This indicates that the larvae with faster growth rates in this age range successfully metamorphosed to the juvenile stage, while those with slower growth rates remained in the larval stage for a longer period. That is, *E. japonicus* larvae with faster growth rates during the late larval stage completed metamorphosis at a younger age than the larvae with a slower growth rate.

Larval and juvenile *Engraulis japonicus* are reported to constitute a major prey item of skipjack tuna *Katsuwonus pelamis* and mackerels *Scomber japonicus* and *S. australasicus* in the Kuroshio-Oyashio transition region (Nihira 1996, Watanabe et al. 1999). The ability of larval and juvenile northern anchovy *Engraulis mordax* to escape from predatory juvenile *S. japonicus* sharply increased by 30 mm *SL* in a rearing experiment (Folkvord & Hunter 1986). Slower-growing *E. japonicus* larvae (L = 10 to 30 mm) to a higher probability of being eaten when they encounter predatory fish species relative to faster-growing larvae in a cohort in the spawning ground in the coastal waters off central Japan (Takasuka et al. 2003). The larvae (Gu-0 stage fish) with a relatively slower growth rate during metamorphosis in a cohort may, therefore, have a higher probability of being eaten by these predatory fishes before the end of the metamorphosing stage (completion of the Gu-1 stage) in the Kuroshio-Oyashio transition region.

Absolute mesh retention of larvae occurs for specimens larger than the diagonal of a given mesh aperture (Smith & Richardson 1977). The diagonal of the mesh at the cod end of the trawl net in this study was 14 mm, which corresponds to the body depth at the pectoral fin of 80 mm L adult anchovy. Body length of the fish for growth analysis ranged from 20.0 to 45.0 mm and therefore, all the size classes had a probability to slip through the mesh aperture. Nevertheless, we collected many larval and early juvenile anchovies by the trawl net. We do not know the difference of the probability by L size classes of anchovy, but the effects of mesh size selectivity on our results, if they exist, are assumed to be minimal.

Slower-growing larvae of winter flounder *Pseudopleuronectes americanus* had a longer larval duration than the faster-growing larvae (Chambers & Leggett 1987). In the tropical goatfish *Upeneus tragula*, fish that settled at an older age tended to have a slower growth rate over the pelagic phase than the fish that were younger at settlement (McCormick 1994). Benoît et al. (2000) reviewed the variabilities in age and length at metamorphosis of marine fishes at various resolution levels: taxonomic, population and individual, and concluded that faster growth rates result in a shorter duration of the larval stage. These previous studies have shown that a faster growth rate throughout the entire larval stage results in the completion of metamorphosis at a younger age and have generally concluded that faster growth and developmental rates result in a subsequent higher survival probability to the adult population. Houde (1987, 1989) demonstrated that a small decline in the growth rate during the larval stage leads to a substantially longer stage duration over which high mortality rates continued to occur, resulting in higher cumulative total mortality rates in the larval stage.

Recent studies on growth, development and survival traits during the early life stages, however, have revealed that successful survival of juvenile fish results from a faster growth rate during the late larval stage in some fishes. Meekan & Fortier (1996) found in Atlantic cod *Gadus morhua* that planktonic larvae with faster growth rates in the late larval stage (40 to 80 d) survived to the epibenthic juvenile stage better than those with slower growth rates during this period. Searcy & Sponaugle (2001) demonstrated in 2 Caribbean coral reef fishes *Thalassoma bifasciatum* and *Halichoeres bivittatus* (Labridae) that the settled juveniles had faster growth rates during metamorphosis. In this study, we demonstrated that the growth rate in the metamorphosing stage, not in the early larval stage, is strongly associated with successful metamorphosis at a younger age. Based on the above and the current data, growth rate-dependent survival processes are concluded to be potentially more critical during the metamorphosing stage than in the early larval stage.

Distribution of anchovy larvae and juveniles in the Kuroshio-Oyashio transition region

The growth rate at ages (G_i) of the Gu-1 stage fish in the $D_{2.0}$ class was at the same level (about 0.6 mm d^{-1}) as the faster D classes in the early larval stage <30 d in age, but declined in the late larval stage (Fig. 5). The D of the Gu-1 stage fish was slower in the northern and eastern waters than in the southwestern waters in the Kuroshio-Oyashio transition region (Fig. 3a). The Gu-1 stage fish with a slower D in the northern and eastern waters seem to have traced a similar growth history as those with a faster D in the southwestern range in the early larval stage. Based on the general eastward transportation of the eggs and newly hatched larvae from the Pacific coastal waters in the prevailing current flow, the larvae and early juveniles in the transition region are suggested to have hatched in the coastal and/or southwestern ranges of the study area.

The Gu-0 stage fish were distributed at higher densities in the southern waters than in the northern waters in the transition region (Fig. 1). On the other hand, the Gu-2 stage fish were distributed at higher densities in the northern waters. The stage-specific spatial gradient and the growth rate trajectories in the D classes (Fig. 5) indicate that most of the larval and juvenile *Engraulis japonicus* were transported eastwards from the coastal spawning grounds by the Kuroshio and the Kuroshio Extension, and are dispersed into the extended Kuroshio-Oyashio transition region.

The D of the Gu-1 stage fish was faster in the southwestern waters than in the northern or eastern waters in the Kuroshio-Oyashio transition region (Fig. 3a), similar to the distribution of the G (Fig. 3b). Based on the developmental- and growth rate-dependent survival in the metamorphosing stage in fishes discussed above, the results of this study show that among the larvae hatched in spring in the coastal waters off central Japan and transported to the transition region, those that remained in the southwestern waters in the metamorphosing stage had a faster D and G, and had a higher probability of surviving to the juvenile stage in the transition region. In contrast, those swiftly transported to the northern or eastern waters had a slower D and G, resulting in a longer larval duration and a potentially lower probability of survival to the juvenile stage. Takahashi & Watanabe (2004b) elucidated that adult *Engraulis japonicus* in the transition region had relatively faster growth rates in the late larval and early juvenile stages among fish in the same cohort based on the width of otolith growth increments, which were positively correlated with the daily somatic growth rate. The larvae with a faster D and G in the southwestern waters seemed to have expanded their distribution range after metamorphosis (Gu-2, Fig. 1) to northern waters of higher food availability (Odate 1994) and constitute a major component of the population of *E. japonicus* in the Kurosho-Oyashio transition region.

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LITERATURE CITED

Anderson JT (1988) A review of size-dependent survival during pre-recruit stages of fishes in relation to recruitment. J Northwest Atl Fish Sci 8:55–66

Benoît HP, Pepin P, Brown JA (2000) Patterns of metamorphic age and length in marine fishes, from individuals to taxa. Can J Fish Aquat Sci 57:856–869

Campana SE (1990) How reliable are growth back-calculations based on otoliths? Can J Fish Aquat Sci 47: 2219–2227

Campana SE (1996) Year-class strength and growth rate in young Atlantic cod *Gadus morhua*. Mar Ecol Prog Ser 135: 21–26

Campana SE, Jones CM (1992) Analysis of otolith microstructure data. In: Stevenson DK, Campana SE (eds) Otolith microstructure examination and analysis. Can Spec Publ Fish Aquat Sci 117:73–100

Chambers RC, Leggett WC (1987) Size and age at metamorphosis in marine fishes: an analysis of laboratory-reared winter flounder (*Pseudopleuronectes americanus*) with a review of variation in other species. Can J Fish Aquat Sci 44:1936–1947

Folkvord A, Hunter JR (1986) Size-specific vulnerability of northern anchovy, *Engraulis mordax*, larvae to predation by fishes. Fish Bull (US) 84:859–869

Fukuhara O (1983) Development and growth of laboratory reared, *Engraulis japonicus* (Houttuyn), larvae. J Fish Biol 23:641–652

Heath MH, Zenitani Y, Watanabe Y, Kimura R, Ishida M (1998) Modelling the dispersal of larval Japanese sardine, *Sardinops melanostictus*, by the Kuroshio current in 1993 and 1994. Fish Oceanogr 7:335–346

Houde ED (1987) Fish early life dynamics and recruitment variability. Am Fish Soc Symp 2:17–29

Houde ED (1989) Subtleties and episodes in the early life of fishes. J Fish Biol 35 (Suppl A):29–38

Kasai A, Kishi JJ, Sugimoto T (1992) Modelling the transport and survival of Japanese sardine larvae in and around the Kuroshio Current. Fish Oceanogr 1:1–10

McCormick MI (1994) Variability in age and size at settlement of the tropical goatfish *Upeneus tragula* (Mullidae) in the northern Great Barrier Reef lagoon. Mar Ecol Prog Ser 103:1–15

Meekan MG, Fortier L (1996) Selection for fast growth during the larval life of Atlantic cod *Gadus morphua* on the Scotian Shelf. Mar Ecol Prog Ser 137:25–37

Nihira A (1996) Studies of the behavioral ecology and physiology of migratory fish schools of skipjack tuna (*Katsuwonus pelamis*) in the oceanic frontal area. Bull Tohoku Natl Fish Res Inst 58:137–233

NRIFS (1995) Distribution of eggs and larvae of Japanese sardine, Japanese anchovy, mackerels, round herring, Japanese horse mackerel, and Japanese common squid in the waters around Japan, 1991 through 1993. Zenitani H, Ishida M, Konishi Y, Goto T, Watanabe Y, Kimura R (eds) National Research Institute of Fisheries Science, Tokyo

Odate K (1994) Zooplankton biomass and its long-term variation in the western North Pacific Ocean, Tohoku sea area, Japan. Bull Tohoku Natl Fish Res Inst 56:115–173

Odate S (1957) Study on the larval fish of the Japanese anchovy, *Engraulis japonica* (Houttuyn), in the northeastern sea area of Japan. Bull Tohoku Natl Fish Res Inst 9:111–128

Okazaki Y, Nakata H, Kimura S (2002) Effects of eddies on the distribution and food availability of anchovy larvae in the Kuroshio Extension. Mar Freshw Res 53:403–410

Searcy SP, Sponaugle S (2001) Selective mortality during the larval-juvenile transition in two coral reef fishes. Ecology 82:2452–2470

Smith PE, Richardson SL (1977) Standard techniques for pelagic fish egg and larva survey. FAO Fish Tech Pap No. 175

Statistics and Information Department (1963–2001) Annual statistics on fisheries and aquaculture production. Tokyo

Takahashi M (2001) Growth and development of larval and juvenile Japanese anchovy (*Engraulis japonicus*) and their implications for recruitment to spawning population. PhD thesis, University of Tokyo, Tokyo

Takahashi M, Watanabe Y (2004a) Staging larval and early juvenile Japanese anchovy based on the degree of guanine deposition. J Fish Biol 64:262–267

Takahashi M, Watanabe Y (2004b) Growth rate dependent recruitment of Japanese anchovy *Engraulis japonicus* in the Kuroshio-Oyashio transitional waters. Mar Ecol Prog Ser 266:227–238

Takahashi M, Watanabe Y, Kinoshita T, Watanabe C (2001) Growth of larval and early juvenile Japanese anchovy, *Engraulis japonicus*, in the Kuroshio-Oyashio transition region. Fish Oceanogr 10:235–247

Takasuka A, Aoki I, Mitani I (2003) Evidence of growth-selective predation on larval Japanese anchovy *Engraulis japonicus* in Sagami Bay. Mar Ecol Prog Ser 252:223–238

TRFRL (1988) Monthly egg productions of the Japanese sardine, anchovy, and mackerels off the southern coast of Japan by egg censuses: January, 1978 through December, 1986. Mori K, Kuroda K, Konishi Y (eds) Tokai Regional Fisheries Research Laboratory, Tokyo

Tsuji S, Aoyama T (1984) Daily growth increments in otoliths of Japanese anchovy larvae, *Engraulis japonicus*. Bull Jpn Soc Sci Fish 50:1105–1108

Watanabe C, Kawabata A, Wada T (1999) Distribution of 0-year cohorts in scomber fish in the Kuroshio-Oyashio transition region. Kaiyo Monthly 31:236–240

Watanabe Y, Kuroki T (1997) Asymptotic growth trajectories of larval sardine *Sardinops melanostictus* in the coastal waters off western Japan. Mar Biol 127:369–378

Zar JH (1996) Biological analysis, 3rd edn. Prentice-Hall, Englewood Cliffs, NJ

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