

# Three synergistic growth-related mechanisms in the short-term survival of larval Japanese anchovy *Engraulis japonicus* in Sagami Bay

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**ABSTRACT:** The 'growth–mortality' hypothesis, which holds that larger and/or faster growing individuals will have a higher probability of survival, currently includes 3 functional mechanisms (hypotheses) in its theoretical framework: 'bigger is better', 'stage duration' and the recently proposed 'growth-selective predation', which are based on size, time and per se growth rate, respectively. Through otolith microstructure analysis, we tested these 3 synergistic growth-related mechanisms according to growth characteristics of the survivors vs the original population in the short-term (ca. 2 wk) survival process of larval Japanese anchovy *Engraulis japonicus* in the 'shirasu' (larval anchovy) fishing ground in Sagami Bay, Japan. Back-calculated standard length (growth trajectory) and growth rate (growth history) were compared between the survivors (SV) captured on 18 July 2001 and the presumed original population (OP) captured on 1 and 5 July 2001. The larvae from SV were consistently smaller than the larvae from OP until at least the start of the ca. 2 wk survival process (1 July). Daily growth rates, however, were higher for SV than for OP at least at the start of the survival period. Therefore, faster growing individuals survived even if they were smaller than slower-growing conspecifics. This was probably mediated by predation. Growth histories were generally similar between the metamorphosing larvae and non-metamorphosing larvae older than 40 d, the minimum age for metamorphosis, except for the period immediately after hatching. As such, we failed to detect a clear relationship between growth rates and the timing of metamorphosis (stage duration) as a whole. The results supported and extended the 'growth-selective predation' hypothesis but not the 'bigger is better' hypothesis. The 'stage duration' hypothesis was not unequivocally supported by the present findings.

**KEY WORDS:** Growth rate · Otolith microstructure analysis · Short-term survival · Growth-selective predation hypothesis · Larval Japanese anchovy

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## INTRODUCTION

Growth rate during early life history is a determinant of recruitment dynamics of marine and freshwater fish. Simulation and field studies suggest that even subtle variations in growth rate can lead to great fluctuations in population size (Houde 1987, 1989, Campana 1996), and if so, early life growth rates would be a predictor of recruitment success (Houde 1987). A paradigm for larval

and juvenile survival processes is summarized in the 'growth–mortality' hypothesis (Anderson 1988), which holds that larger and/or faster growing individuals (or cohorts) will have a higher probability of survival. This scenario has been supported by many field tests (Healey 1982, Post & Prankevicius 1987, West & Larkin 1987, Hovenkamp 1992, Campana 1996, Meekan & Fortier 1996, Hare & Cowen 1997, Sirois & Dodson 2000, Searcy & Sponaugle 2001, Wilson & Meekan 2002, Allain et al.

2003, Baumann et al. 2003, Oozeki et al. 2003), laboratory experiments (Rosenberg & Haugen 1982) and simulation studies (Rice et al. 1993). Anderson (1988) concluded that the 'growth–mortality' hypothesis provides a rational theoretical framework for future studies.

The 'growth–mortality' hypothesis includes several functional mechanisms within its theoretical framework (Hovenkamp 1992, Hare & Cowen 1997, Searcy & Sponaugle 2001). The 'bigger is better' and 'stage duration' hypotheses (mechanisms) have explained the relationship between growth and survival according to 2 concepts: size and time (Takasuka et al. 2003). In the 'bigger is better' hypothesis, mortality is assumed to be negatively size-dependent. Larvae with higher growth rates (higher growth larvae) will be larger than those with lower growth rates (lower growth larvae) at the same age, leading to a survival advantage for higher growth larvae (Miller et al. 1988). The 'stage duration' hypothesis, also known as the 'growth-dependent' hypothesis, focuses on the relationship between growth rate and larval stage duration. If growth rates shorten larval stage duration, higher growth larvae should selectively survive, since the probabilities of mortality events will be much decreased (Chambers & Leggett 1987, Houde 1987). From 2 standpoints, however, these 2 concepts indirectly link growth rate with survival. First, size is just an output of growth rate. Second, the stage duration idea depends solely on the time-integrated cumulative probabilities of lethal events occurring throughout high mortality stages. Moreover, until recently, no direct evidence existed in the field to support the relationship between growth rate and predation mortality, even though predation pressure has been recognized as the primary and direct source of mortality (Bailey & Houde 1989, Leggett & DeBlois 1994). Here emerged 2 questions: Is a fish larva with a lower growth rate actually removed by predation at a given moment in the sea? If so, is the mortality size-dependent?

Our previous study (Takasuka et al. 2003) demonstrated direct impacts of growth rates on vulnerability to predation for larval Japanese anchovy *Engraulis japonicus* through field research. In that study, sympatric larvae and their predatory fish were captured simultaneously by the same tows of a trawler in the 'shirasu' ('larval anchovy' in Japanese) fishing ground in Sagami Bay, Japan. Growth rates, analyzed by otolith microstructure, and larval sizes were compared between the larvae dissected from the stomach contents of their predators (ingested larvae) and the larvae captured simultaneously with the predators (surviving larvae from the original population). The growth rates of the ingested larvae were shown to be significantly lower than those of the surviving larvae, presenting the first snapshot evidence to support the relationship be-

tween growth rate and predation mortality in field conditions. The observed selective mortalities were not explained by size-selective mortality. Alternatively, the existence of non-size-related predation mortality was detected by comparing growth rates at the same larval size. Therefore, slower growing individuals were more vulnerable to predation mortality than faster growing conspecifics, even if they were the same size, at a given moment in the sea. This means that growth rates themselves directly affect predation mortality, independently of both negative size-selective mortality and high mortality stage duration. The 'growth-selective predation' hypothesis has been proposed. To date, 3 functional mechanisms — 'bigger is better', 'stage duration' and 'growth-selective predation', based on size, time and per se growth rate, respectively — coexist in the framework of the general 'growth–mortality' theory. These 3 mechanisms are theoretically independent of, and synergistic with, one another.

Earlier studies on the growth–survival relationship have all targeted the time-integrated cumulative mortality, comparing growth features between survivors and the original population (i.e. characteristics of the survivors vs. original population). This is why no direct evidence of a growth–predation relationship had yet been obtained. On the other hand, our previous study included direct examination of the growth rates of the larvae actually ingested by predators. This allowed us to detect 'growth-selective predation'. Conversely, though, 'growth-selective predation' remains to be demonstrated in the time-integrated survival process. If the 'growth-selective predation' mechanism has significant effects on the recruitment dynamics of Japanese anchovy, the mechanism should be detected in the short-term survival process.

In the present study, we tested the 3 synergistic growth-related mechanisms according to characteristics of the survivors vs. original population (i.e. using the traditional method) in a short-term (ca. 2 wk) survival process of larval Japanese anchovy in the shirasu fishing ground in Sagami Bay. First, we investigated the existence of negative size- and growth-rate-selective mortalities by comparing the growth trajectories and histories between survivors and the original population in order to test the 'bigger is better' and 'growth-selective predation' hypotheses. Second, the relationship between growth rates and metamorphosis (i.e. larval stage duration) was examined in order to test the 'stage duration' hypothesis.

## MATERIALS AND METHODS

**Field sampling.** Larval Japanese anchovy were captured by a commercial shirasu trawler in the shirasu

fishing ground, the same area that we visited in our previous study (Takasuka et al. 2003), near the mouth of the Sagami River in Sagami Bay, Japan (Fig. 1). The first sampling was conducted on 1 and 5 July 2001, and the second was done approximately 2 wk later, on 18 July 2001. Our field samplings were conducted using the methods of the commercial shirasu fishery, which usually targets shoals of Japanese anchovy larvae larger than ca. 13 mm (standard length, SL) (see 'Discussion'). After sunrise, a net with a cod-end mesh size of 2.3 mm was towed just above the seabed (ca. 10 m at deepest), where larval anchovy forage during the daytime (Mitani 1988a). Randomly selected larval anchovy were frozen at  $-20^{\circ}\text{C}$  immediately after the trawler landed.

**Otolith microstructure measurements.** SL of each larva was measured to the nearest 0.1 mm, and then sagittal otoliths were dissected from each individual using a needle. Assuming symmetry of bilateral otoliths (Wang & Tzeng 1999), the left otolith was fundamentally prepared for growth analysis, although the right one was used if the left one was lost or broken. The otoliths mounted on a glass slide with euparal were observed by a transmitted light microscope with a video camera connected to a computer and monitor. Otolith microstructure measurements were obtained using an otolith measurement system (RATOC System Engineering). In this system, the microscope's field of view is captured on a monitor, allowing a series of otolith microstructure measurements. After a measurement transect was set from the otolith nucleus to the outermost margin, maximum otolith radius (OR) and each daily growth increment width were measured to the nearest 0.1  $\mu\text{m}$ . According to a previous report, the first growth increment for Japanese anchovy begins at 3 to 4 d after hatching, when external feeding begins (Tsuji & Aoyama 1984). Hence, the number of daily growth increments plus 3 was regarded as age in days, hereafter referred to as 'age' alone (Aoki & Miyashita 2000, Takasuka & Aoki 2002). Hatching date was determined according to age and date of capture. SL and daily growth rate at each age were back-calculated by the biological intercept method (Campana 1990, Campana & Jones 1992, Watanabe & Kuroki 1997, Oozeki & Watanabe 2000) in order to obtain the growth trajectories and histories of individual larvae. Since the relationship between OR and SL was well expressed as an allometric relationship (data not shown), the back-calculation procedure used an allometric formula that was separately determined for individual larvae, with SL at the first ring deposition fixed at 5.6 mm (Fukuhara 1983).

**Survivors and original population.** Hatching date distributions ranged from 15 May to 13 June (30 d) for the larvae captured on 1 and 5 July ( $n = 120$ ) and from

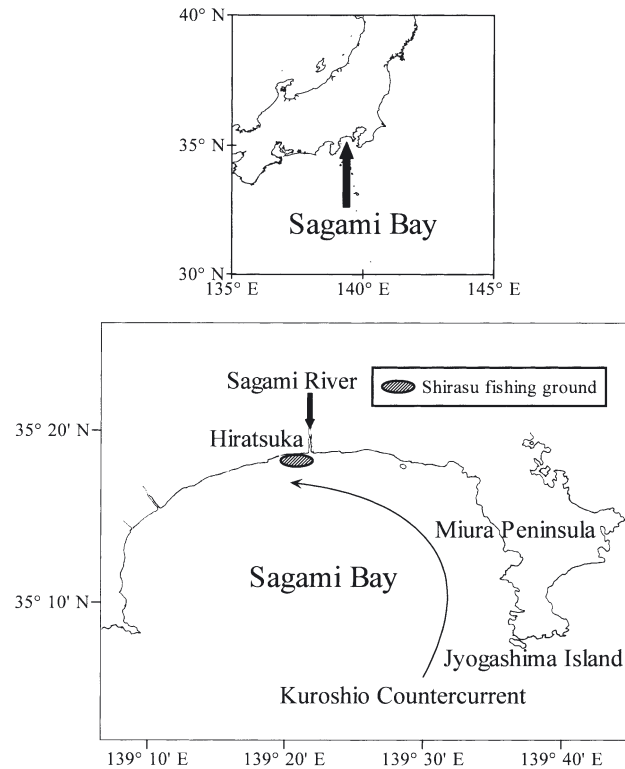


Fig. 1. Shirasu fishing ground near the mouth of Sagami River in Sagami Bay, Japan. Schematic pattern of the current indicated by the curved arrow

30 May to 27 June (29 d) for the larvae captured on 18 July ( $n = 120$ ), with the exception of a larva hatching on 26 May (Fig. 2). The overlapping period ranged from 30 May to 13 June (15 d). We assumed that the larval anchovy were retained in the shirasu fishing ground throughout the larval stage after recruitment into the fishing ground (Mitani 1988a, 1990), and thus that the larvae hatching during the same period originated from the same population or cohort regardless of when they were caught, at least during their retention in the fishing ground (see 'Discussion' for details). Accordingly, the larvae hatching from 30 May to 13 June and captured on 18 July ( $n = 76$ ) were regarded as the individuals surviving ca. 2 wk longer than the larvae hatching during the same period and captured on 1 or 5 July ( $n = 55$ ). The former individuals were designated as the survivors (SV) and the latter as the larvae from the original population (OP). Furthermore, the larvae from SV were divided into 3 sub-cohorts (SV-I, SV-II and SV-III), each with a 5 d hatching period; likewise, the larvae from OP were divided into 3 sub-cohorts (OP-I, OP-II and OP-III) (Table 1).

Back-calculated growth data can be pooled and rearranged in 2 ways: by calendar date and age. Date-based growth data will better represent tempo-

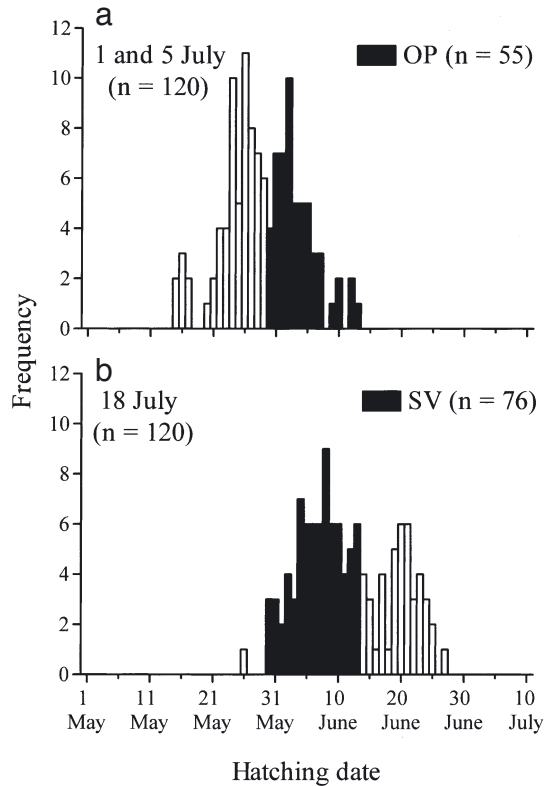


Fig. 2. *Engraulis japonicus*. Hatching date distributions of the larvae captured on (a) 1 and 5 July and (b) 18 July 2001. Larvae within the common range of hatching dates (30 May to 13 June), which were designated as survivors (SV) or from the original population (OP), are indicated as solid bars. Sample sizes indicated in parentheses

ral changes in growth features with time, while age-based growth data will better match stage-specific changes (Takasuka et al. 2003). Hence we adopted

date-based data in order to test the 'bigger is better' and 'growth-selective predation' hypotheses, since we focus on the sizes and growth rates directly prior to the targeted survival period (see below). Daily increment width, back-calculated standard length (growth trajectory) and daily growth rate (growth history), all arranged by calendar date, were compared between SV and the OP. Assuming predation as the source of mortality (see 'Discussion'), standard lengths and growth rates at each encounter with a predator will directly determine the size- and growth-rate-selective mortalities. Those growth features of the larvae from OP at a given moment during the targeted survival period (ca. 2 wk) were not directly estimated by the method based on the characteristics of the survivors vs. original population. Accordingly, we focused on the growth features directly before the start of the survival period. However, the previous study detected the 'growth-selective predation' by using mean growth rates from hatching up to capture or predation (Takasuka et al. 2003). Regarding 1 July as the start date of survival, standard lengths on 1 July ( $SL_{1 \text{ July}}$ ), mean growth rates from hatching up to 1 July ( $GR_{m-1 \text{ July}}$ ), and 3 d (28 to 30 June) mean increment widths and growth rates before 1 July ( $IW_{3d-1 \text{ July}}$  and  $GR_{3d-1 \text{ July}}$  respectively) were compared between SV and the OP. SL at hatching was fixed at 2.9 mm (Fukuhara & Takao 1988), and  $GR_{m-1 \text{ July}}$  was calculated by dividing  $SL_{1 \text{ July}}$  minus 2.9 by daily age on 1 July. All of these parameters were also compared between the corresponding sub-cohorts (SV-I vs. OP-I, SV-II vs. OP-II, and SV-III vs. OP-III).

**Growth rates and metamorphosis.** Guanine was observed on the inside wall of the abdominal cavity in some of the larvae captured on 18 July (see 'Results'). Although the timing of metamorphosis is generally judged

Table 1. *Engraulis japonicus*. Date of capture, hatching date range, sample size and size and growth data for the larvae as survivors (SV), the original population (OP) and their sub-cohorts (SV-I, SV-II, SV-III; OP-I, OP-II, OP-III).  $SL_{1 \text{ July}}$ : standard length on 1 July;  $GR_{m-1 \text{ July}}$ : mean growth rate from hatching up to 1 July;  $IW_{3d-1 \text{ July}}$ : 3 d mean increment width before 1 July;  $GR_{3d-1 \text{ July}}$ : 3 d mean growth rate before 1 July. + and -: size, growth rate or increment width of SV were significantly larger, higher or wider (+) and smaller, lower or narrower (-) than those of the OP on average; \* $p < 0.05$ , \*\* $p < 0.01$  after  $t$ -tests

Sample	Date of capture 2001	Hatching date	n	Age (d)	SL (mm)	$SL_{1 \text{ July}}$ (mm)	$GR_{m-1 \text{ July}}$ (mm d <sup>-1</sup> )	$IW_{3d-1 \text{ July}}$ (μm)	$GR_{3d-1 \text{ July}}$ (mm d <sup>-1</sup> )
<b>Cohort</b>									
OP	1 and 5 July	30 May–13 June	55	22–36	15.6–27.8	21.8 ± 3.0	0.69 ± 0.06	6.45 ± 1.20	0.50 ± 0.10
SV	18 July	30 May–13 June	76	35–49	21.5–32.4	19.3 ± 2.3	0.68 ± 0.05	6.80 ± 1.21	0.59 ± 0.11 +**
<b>Sub-cohort</b>									
OP-I	1 and 5 July	30 May–3 June	33	28–36	20.6–27.8	23.2 ± 2.0	0.68 ± 0.05	6.49 ± 1.21	0.47 ± 0.09
SV-I	18 July	30 May–3 June	15	45–49	26.5–32.4	22.2 ± 1.5	0.64 ± 0.04	7.13 ± 1.09	0.49 ± 0.06
OP-II	1 and 5 July	4–8 June	16	24–31	15.9–26.7	20.9 ± 2.5	0.70 ± 0.09	6.67 ± 1.13	0.54 ± 0.12
SV-II	18 July	4–8 June	34	40–44	23.8–29.4	19.8 ± 1.2	0.68 ± 0.05	7.17 ± 1.19	0.60 ± 0.09 +*
OP-III	1 and 5 July	9–13 June	6	22–26	15.6–20.9	16.6 ± 2.0	0.68 ± 0.06	5.62 ± 1.17	0.56 ± 0.05
SV-III	18 July	9–13 June	27	35–39	21.5–28.5	17.1 ± 1.4	0.71 ± 0.05	6.16 ± 1.05	0.65 ± 0.11

by a meristic character such as the number of fin rays (Youson 1988), Takahashi & Watanabe (2004a) proposed that presence of guanine on the inside wall of the abdominal cavity or on the surface of the body could be an indicator of the timing of metamorphosis in clupeoid species, on the grounds that the timing of the number of fin rays being constant does not always correspond to that of metamorphosis. In our study, none of the individuals with guanine on the inside wall of the abdominal cavity had morphologically reached the juvenile stage, and so they were determined as the metamorphosing larvae. The youngest metamorphosing larva was 40 d old (see 'Results'). Therefore, mean growth rates from hatching up to 40 d ( $GR_{m-40d}$ ), which were calculated by dividing SL at 40 d, minus 2.9, by 40, and daily growth histories from 5 to 40 d were compared between the metamorphosing larvae and non-metamorphosing larvae older than 40 d. We adopted age-based data in order to test the 'stage duration' hypothesis, since metamorphosis must be a physiological phenomenon, which is closely related to developmental stage.

## RESULTS

### Size- and growth-rate-selective mortalities

Daily increment widths of SV ( $n = 76$ ) were narrower than those of the OP ( $n = 55$ ) for more than 10 d around mid-June, although their widths were similar immediately after hatching (Fig. 3). However, daily increment widths of SV became wider rapidly, finally to exceed those of the OP in late June. The 3 d (28 to 30 June) mean increment widths before 1 July ( $IW_{3d-1 July}$ ) were  $6.80 \pm 1.21$  (mean  $\pm$  SD)  $\mu\text{m}$  for SV, which were wider than  $6.45 \pm 1.20$   $\mu\text{m}$  for the OP (Table 1), though the differences were not significant, owing to high variance (Student's  $t$ -test,  $p = 0.101$ ). On the other hand, a comparison of growth trajectories showed that SLs of SV were consistently smaller than those of the OP until at least 1 July. The differences in SLs between SV and the OP averaged ca. 2.5 to 3.0 mm, and SLs on 1 July ( $SL_{1 July}$ ) differed significantly between these 2 groups (Student's  $t$ -test,  $p < 0.001$ ). There were no significant differences in the mean growth rate from hatching up to 1 July ( $GR_{m-1 July}$ ) between SV and the OP ( $p = 0.754$ ); however, their growth history patterns differed distinctly. Daily growth rates were lower for SV than for the OP from immediately after hatching up to mid-June, but temporal decreases in growth rates of SV were moderate, while those of the OP were dramatic. Consequently, the daily growth rates of SV were consistently higher than those of the OP after 20 June, when the mean value of daily growth rates of SV exceeded that of the OP. The 3 d (28 to 30 June) mean

growth rates before 1 July ( $GR_{3d-1 July}$ ) were  $0.59 \pm 0.10$  (mean  $\pm$  SD)  $\text{mm d}^{-1}$  for SV, which were significantly higher than  $0.50 \pm 0.10$   $\text{mm d}^{-1}$  for the OP (Student's  $t$ -test,  $p < 0.001$ ).

Comparison of daily increment widths, growth trajectories and histories and related parameters ( $IW_{3d-1 July}$ ,  $SL_{1 July}$ ,  $GR_{m-1 July}$  and  $GR_{3d-1 July}$ ) between corresponding sub-cohorts (SV-I vs. OP-I, SV-II vs. OP-II and SV-III vs. OP-III) showed trends similar to those of the cohorts overall (SV vs. OP), though the differences between corresponding sub-cohorts were not always significant (Table 1, Fig. 4). Generally, the larvae from sub-cohorts of SV (SV-I, SV-II and SV-III) had smaller sizes ( $SL_{1 July}$ ) but higher-growth rates ( $GR_{3d-1 July}$ ) than the larvae from sub-cohorts of the OP (OP-I, OP-II and OP-III) as of 1 July or just prior to it.

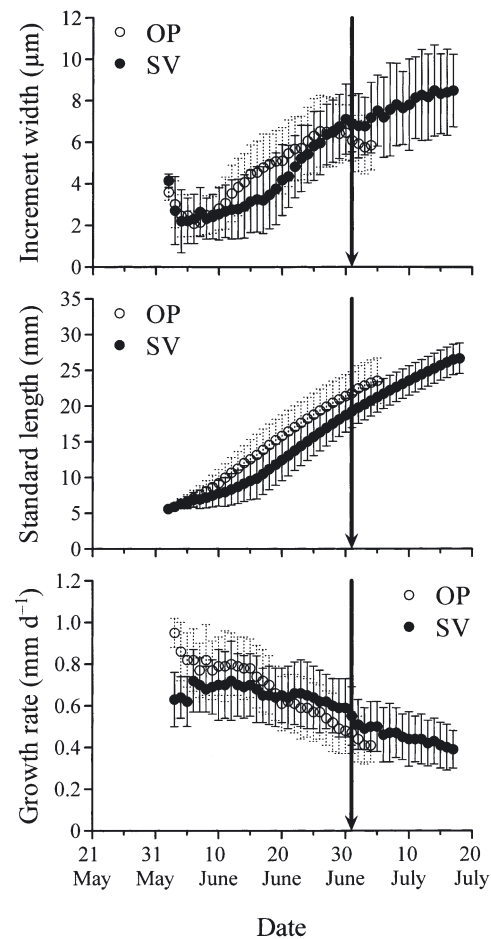


Fig. 3. *Engraulis japonicus*. Comparison of daily increment width, back-calculated standard length (growth trajectory) and daily growth rate (growth history) between survivors (SV) captured on 18 July 2001 and the original population (OP) captured on 1 and 5 July 2001. Data are pooled by calendar date. Mean  $\pm$  SD shown at each date, with at least 3 individual data available. Downward arrows indicate July 1, the start date of the 2 wk survival period

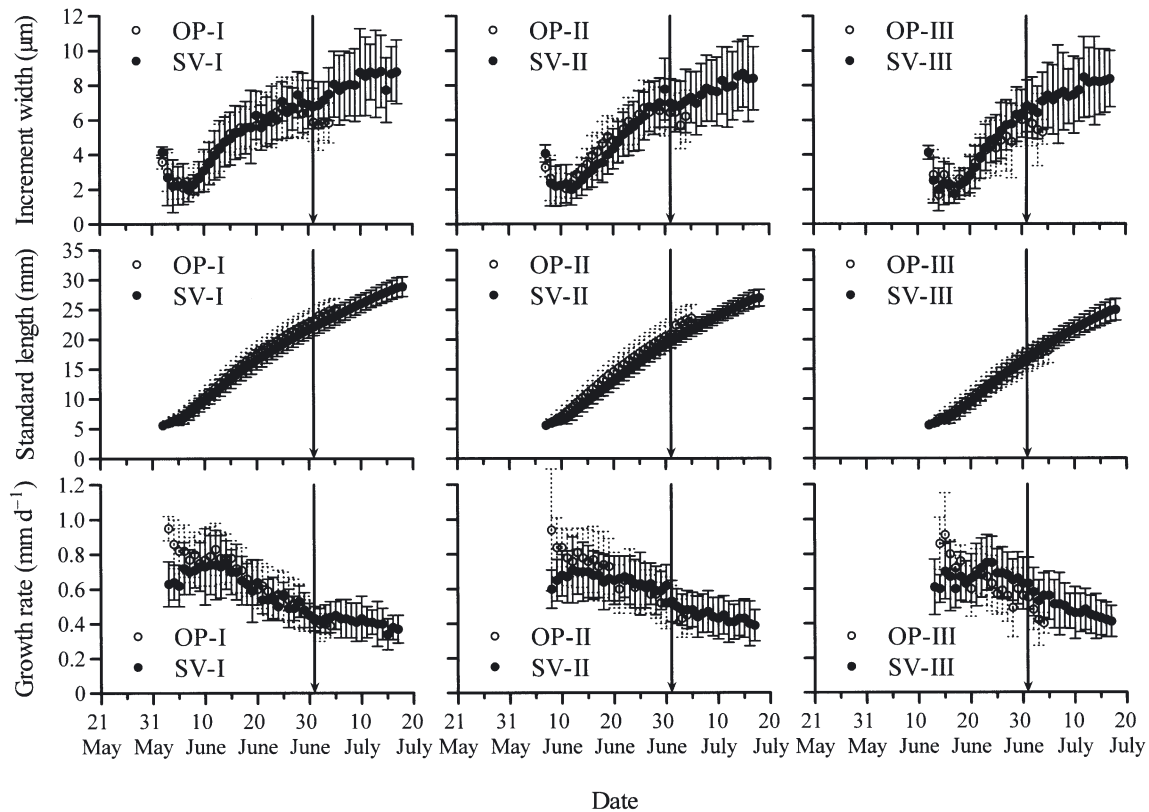


Fig. 4. *Engraulis japonicus*. Comparison of daily increment width, back-calculated standard length (growth trajectory) and daily growth rate (growth history) between sub-cohorts of survivors (SV-I, SV-II and SV-III) captured on 18 July 2001 and sub-cohorts of the original population (OP-I, OP-II and OP-III) captured on 1 and 5 July 2001. Data are pooled by calendar date. Mean  $\pm$  SD shown at each date with at least 3 individual data available. Downward arrows indicate July 1, the start date of the 2 wk survival period

### Growth rates and metamorphosis

Guanine was observed on the inside wall of the abdominal cavity (but not on the surface of the body) in 16 individuals captured on 18 July, which were then determined as the metamorphosing larvae. The minimum size and age of the metamorphosing larvae were 26.4 mm (SL) and 40 d, respectively, while the maximum size and age of the non-metamorphosing larvae were 30.2 mm (SL) and 49 d, respectively (Fig. 5).

The growth histories of the metamorphosing larvae, pooled by age, were consistent with those of the non-metamorphosing larvae up to 40 d, except for the period immediately after hatching (Fig. 6). Comparison of 5 d mean growth rates (i.e. mean growth rates during 5 to 10, 11 to 15, ... and 36 to 40 d) showed no significant differences between the metamorphosing and non-metamorphosing larvae (MANOVA,  $p > 0.05$ ), though the former had significantly higher-growth rates than the latter only during 11 to 15 d ( $p < 0.001$ ). The mean growth rates from hatching up to 40 d ( $GR_{m-40d}$ ) were  $0.59 \pm 0.03$  (mean  $\pm$  SD)  $\text{mm d}^{-1}$  for the

metamorphosing larvae ( $n = 16$ ) and  $0.58 \pm 0.04 \text{ mm d}^{-1}$  for the non-metamorphosing larvae ( $n = 34$ ). No significant differences were found between these 2 groups (Student's  $t$ -test,  $p = 0.064$ ).

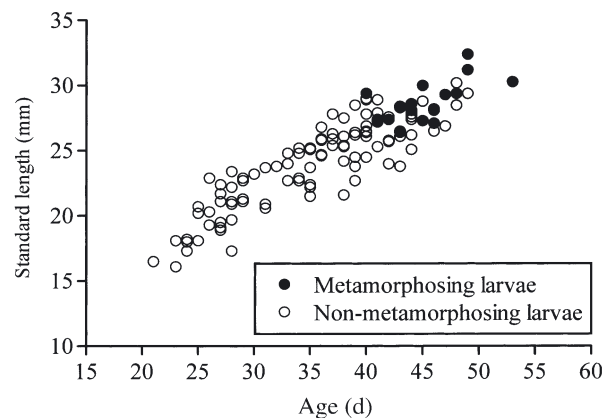


Fig. 5. *Engraulis japonicus*. Size-at-age data for the metamorphosing larvae ( $n = 16$ ) and non-metamorphosing larvae ( $n = 104$ ) captured on 18 July 2001

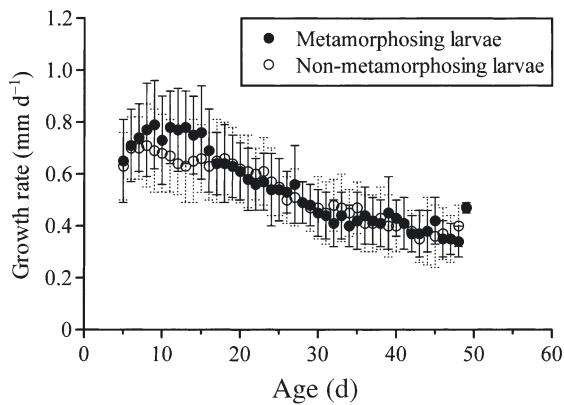


Fig. 6. *Engraulis japonicus*. Comparison of back-calculated growth histories between the metamorphosing larvae and non-metamorphosing larvae >40 d in age and captured on 18 July 2001. Data are pooled by age (ind.). Mean  $\pm$  SD shown at each age, with at least 3 individual data available

## DISCUSSION

### Survivors vs. original population

In field tests of the 'growth–mortality' hypothesis, which were based on characteristics of survivors vs. the original population, an assumption that both of them originated from the same population or cohort should be essential (Hovenkamp 1992, Meekan & Fortier 1996). We assumed that larval anchovy were retained in the shirasu fishing ground and hence that the larvae from SV and the OP originated from the same population or cohort, supported by some lines of circumstantial evidence. Mitani (1990) reported the recruitment process into the shirasu fishing ground for Japanese anchovy during early life history stages. Anchovy females spawn in offshore areas. The eggs are concentrated mainly off Jyogashima Island and are then transported into the bay by the counter-clockwise current (Fig. 1). The larvae entering into the nearshore shirasu fishing ground after crossing the front formed by Sagami River runoff grow to at least 13 mm (SL), which is considered potentially large enough for active swimming. Larval anchovy have positive taxis toward turbid waters; this is a key factor in the formation of the shirasu fishing ground (Uotani et al. 1994, 2000). Moreover, the larvae are provided with higher prey availability here (Mitani 1988b, 1990). Therefore, we found no reason for positive emigration from such an optimal nursery ground during the larval stage. Also, our assumption seemed to be supported by the hatching date distributions in our 2 samples, which were collected at the ca. 2 wk interval. The hatching date distributions of both samples appeared to be bimodal.

This suggested that each sample would include roughly 2 cohorts, which intermittently recruited into the shirasu fishing ground, probably because of fluctuations in current intensity (Mitani 1988a, 1990). The common range of hatching dates (15 d) between 2 samples corresponded to those of the younger cohort of the sample collected on 1 and 5 July (i.e. the OP) and the older cohort of the sample collected on 18 July (i.e. SV). This, too, would support the assumption that SV was the surviving part of OP.

Previous comparisons between survivors vs. original population have generally targeted the long-term survival processes through either larval or larval and juvenile stages (e.g. Healey 1982, Post & Prankevicius 1987, Meekan & Fortier 1996, Good et al. 2001, Takahashi & Watanabe 2004b). Another focus of previous studies has been the selective survival during horizontal migrations (e.g. Hovenkamp 1992) or settlement with metamorphosis (e.g. Searcy & Sponaugle 2001). Conversely, we targeted the short-term survival process in the shirasu fishing ground, a relatively closed area. The ranges of hatching date distributions suggested that larval anchovy forage in the shirasu fishing ground for approximately 1 mo. The age of SV and OP ranged from 22 to 36 d and from 35 to 49 d, respectively. The targeted (2 wk) survival process represents half of the time that the larvae spend in the shirasu fishing ground.

### Samples and biases

Daily growth histories were back-calculated by the biological intercept method, using an allometric formula. We cannot absolutely deny the possibility that this process introduced a bias to the comparison of earlier growth rates between the survivors and the original population, whose ages differed considerably at the time of capture. Previous studies avoided this possibility by using only daily increment widths as an indicator of growth rates (e.g. Thorrold & Milicich 1990, Searcy & Sponaugle 2000, 2001, Shima & Findlay 2002). Comparison of daily increment widths would truly provide the relative merits and demerits of the growth rates of the groups, but not absolute values of those growth rates. Also, if the OR-SL relationship is not linear, the differences in increment widths would not always correspond to those in growth rates between the groups. Accordingly, we used the absolute values of standard lengths and growth rates through back-calculation in order to examine the size- and growth-rate-selective mortalities separately. However, given the possibility of bias as mentioned above, we also used daily increment widths for confirmation. Comparison of daily increment width histories showed that the relative trends between

SV and the OP were similar to the case in daily growth histories. This supports the results of our comparison of daily growth histories (Fig. 3).

The larvae of various ages, sizes and growth rates are mixed in the natural population in the sea. Nonetheless, experimental studies have often dealt with larvae of the same age or within a narrow age range. In such conditions, variations in growth rates will simply lead to variations in sizes; therefore, the existence of non-size-related mortality will be masked. In other words, the target population or cohort must include the larvae of a wider age range in order to detect the 'growth-selective predation' hypothesis. The present samples (SV and the OP) had an age range of 15 d, which we considered sufficient. However, the frequencies of ages were not uniform; the OP included more of the younger larvae, while SV included more of the older, within each sample (Fig. 2). This could bias a comparison of growth features between SV and the OP. In light of such a viewpoint, we confirmed the results of our overall comparison between SV and the OP (Fig. 3) by comparing SV and the OP at the sub-cohort level, with an age range of 5 d (Fig. 4). The results at the sub-cohort level were not always sustained by the significance levels owing to rather small sample sizes; however, the similar trends indicated that the lopsided hatching date distributions would not be critical to the date-based comparison of growth features between SV and the OP.

### Sources of mortality

In the traditional approach based on the characteristics of survivors, it is inherently impossible to directly identify the sources of mortality (see 'Introduction'). Without emigration, the possible sources of mortality, other than predation, are starvation and fishing. However, we ignored the possibility of starvation for several reasons. The shirasu fishing ground is an optimal nursery ground by virtue of prey availability (Mitani 1988b, 1990). In fact, feeding incidence calculated as occurrence of feeding individuals surpassed 40% for the larvae larger than 20 mm (SL) (Takasuka 2003). Also, starvation mortality is limited to a critical period directly after the start of the external feeding (Hewitt et al. 1985). Feeding failure, if it occurs, could not lead to starvation directly but could affect conditions and growth rates. Larvae with deteriorated conditions and growth rates would be more likely to suffer from predation mortality, owing to lowered potential for anti-predator behaviors (Frank & Leggett 1982, Yin & Blaxter 1987, Booman et al. 1991, Mesa et al. 1994, Booth & Hixon 1999, Chick & Van Den Avyle 2000, Takasuka et al. 2003). On the other hand, commercial

fishing intensity cannot be ignored. A shirasu trawler, however, is quite unlikely to select larval growth rates, since it usually sweeps large shoals of larval anchovy. Even if such a selection were to occur, it would be negligible compared to the selection by predators (Takasuka et al. 2003). In short, we can assume that the shirasu fishery does not impact growth-selective mortality, though it does impact mortality rate itself. From all of the above, the observed selective mortality would be attributed directly to predation. If selective mortality on growth rates is observed, it illustrates the existence of 'growth-selective predation'.

### 'Bigger is better' and 'growth-selective predation' hypotheses

The 'growth-mortality' scenario posits that environmental factors affect growth rates, which ultimately determine survival. For larval Japanese anchovy, sea temperature was the principal environmental factor, influencing growth rates positively when it was lower than 21°C (Takasuka 2003). Feeding success might also be influential, especially when temperature was higher than 21°C. From 30 May to 18 July, sea surface temperature increased from 18.8 to 25.5°C, with some fluctuations in Sagami Bay. Thus, variations in both temperature and feeding success would cause the observed substantial variations in growth rates. Such variations in growth rates, and thus sizes, can potentially determine larval survival via the 3 synergistic growth-related mechanisms.

The survivors were consistently smaller than the larvae from the original population until at least the start of the 2 wk survival period, as revealed by a comparison of growth trajectories. This showed that the cumulative size-selective mortality was positively directed such that smaller individuals were more likely to survive. The higher probabilities of mortality among larger individuals have already been reported (Fuiman 1989, Litvak & Leggett 1992, Pepin et al. 1992, 2003). There are various reasons for positive size-selective mortality. For example, larger body size and the appearance of melanophores may increase conspicuousness (Folkvord & Hunter 1986, Fuiman 1989). Progress in swimming ability can increase encounter rate with predators (Bailey & Houde 1989, Cowan & Houde 1992, Fuiman & Magurran 1994, Cowan et al. 1996, Paradis et al. 1996). Size-selective mortality is neither universal nor unidirectional (Takasuka et al. 2003): bigger is not always better. The cause of higher mortality of larger larvae cannot be specified in the present study. A simple inference will be that predators would have selected larger larvae to maximize their energy gain (see below).



On the other hand, the selective mortality on growth rates was directed negatively. Comparison of growth histories showed that the survivors had higher growth rates than the larvae from the original population at least at the start of survival, although the growth histories were somewhat complicated and the survivors had inversely lower growth rates during earlier times. This trend was supported by a comparison of absolute values of daily increment widths. The faster growing individuals at the start of the survival process would have consistently sustained their higher growth rates during the survival period and therefore survived selectively. Here emerged the question of why faster growing larvae survived, while larger larvae did not. Variations in potential for anti-predator behaviors would be the causal background of the 'growth-selective predation' (Takasuka et al. 2003). Slower growing larvae are considered to have lower responsiveness to predator attacks and lower swimming ability, and tend to be isolated from shoals, leading to them being more vulnerable to predation mortality. This would also be true in the case of negative size-selective mortality, since smaller size will also reduce potential for anti-predator behaviors. In this sense, the greater survivorship of faster growing smaller individuals may appear paradoxical at first glance. However, it would be rational from the standpoint of the optimal foraging theory on the side of predators. Size preference by predators will be determined by a trade-off between benefit and cost (Hart 1993, Gerking 1994, Wootton 1998). If predators select larger individuals, they will benefit by obtaining more energy. At the same time, however, the energy cost of pursuing and capturing a larger individual will be greater. Negative selection on prey growth rates will reduce energy loss, since slower growing individuals would be less-capable swimmers and thus easier to catch. Slower growing larger larvae will be preferable to the predators in light of net energy gain.

Another question may be why the survivors had lower-growth rates than the larvae from the original population at earlier stages. Both larvae survived at least until the start date of survival, in spite of their growth differences. The SL of the larvae around 20 June, when the relative merits and demerits of SV and the OP were reversed, roughly corresponded to size at recruitment into the shirasu fishing ground (i.e. ca. 13 mm; see above). In Sagami Bay, the current intensity regulates the recruitment into the shirasu fishing ground (Mitani 1988a, 1990). Thus, we can speculate that the larvae had yet to reach the shirasu fishing ground and had been passively transported by the current for the duration of the lower growth rates of the survivors (i.e. before ca. 20 June). The 'growth-selective predation' would become effective with larval development (Takasuka 2003). Therefore, lowered

growth rates might not affect vulnerability to predation during the earlier developmental stages.

The results are against the 'bigger is better' hypothesis, but support the 'growth-selective predation' hypothesis. In conclusion, faster growing individuals gained survivorship, even if they were smaller than slower growing conspecifics, and this phenomenon was probably mediated by predation. This may extend the 'growth selective predation' hypothesis that slower growing individuals are more vulnerable to predation than faster growing individuals, even if they are the same size, at a given moment in the sea.

### 'Stage duration' hypothesis

For the 'stage duration' mechanism to come into effect in the regulation of larval survival, 2 essential requirements must be satisfied: (1) high mortality stages must exist for some time period, and (2) growth rates must determine the duration of such stages. In general, the larval stage is a high mortality stage for pelagic fish. In the juvenile stage, the predator field and predation pressure remain unclear, since Japanese anchovy emigrate from the shirasu fishing ground after completing their metamorphosis (Mitani 1988a). However, smaller pelagic predators, such as Japanese jack mackerel *Trachurus japonicus* and Japanese sardine *Sardinops melanostictus*, which are the dominant species in Sagami Bay, are expected to be excluded from the predator field of juvenile anchovy (Takasuka 2003). Thus, larvae will suffer higher predation mortality rates than juveniles, and variation in larval stage duration should greatly influence survival.

Fig. 5 suggests that before metamorphosis can begin, the individual could grow to at least 26 mm (SL) or reach an age of 40 d. Meanwhile, non-metamorphosing larvae of ca. 30 mm SL or ca. 50 d old were observed. Assuming a constant duration of metamorphosis, a delay in the start of metamorphosis will equal a delay of the development to the juvenile stage. Assuming that the average age at the start of metamorphosis is 45 d, a variation of 10 d in the development into the juvenile stage will lead to a variation of more than 20% in larval stage duration. This would be significant considering the time-integrated cumulative probabilities of mortality.

However, the daily growth rate histories were consistently similar between the metamorphosing larvae and non-metamorphosing larvae, except for the period immediately after hatching (Fig. 6). The growth rates before recruitment into the shirasu fishing ground perhaps affected the timing of metamorphosis; however, we failed to detect a clear relationship between growth rates and the timing of metamorphosis as a whole. The

results do not deny the theory of the 'stage duration' hypothesis, but they do imply that the growth–survival relationship was not explained by the 'stage duration' concept, at least for the larvae used in this study. We concluded that the larval stage duration per se would influence survival, but that the 'stage duration' mechanism is unlikely to conclusively regulate recruitment dynamics in the shirasu fishing ground.

### Growth-related survival mechanisms of pelagic fish

The present study supported the 'growth-selective predation' hypothesis but not the 'bigger is better' hypothesis. Furthermore, the 'stage duration' hypothesis was not unequivocally supported. However, the relative contributions of these 3 growth-related mechanisms may differ according to taxonomical groups, species, stages and regions. The relationship between growth rates and larval duration (metamorphosis) has been a focus of study especially for a variety of coral reef fishes (Victor 1986, McCormick 1999, Searcy & Sponaugle 2000, 2001, Victor & Wellington 2000, McCormick et al. 2002, Shima & Findlay 2002, Wilson & Meekan 2002) as well as flatfishes (Chambers & Leggett 1987, Chambers et al. 1988, Hovenkamp 1992, Bertram et al. 1997). These species are characterized by settlement through metamorphosis. Also, larval duration corresponds to planktonic phase. Therefore, the 'stage duration' mechanism might potentially determine survival. Interestingly, a protracted planktonic larval duration would lead to not only the disadvantages of higher mortality rates, but also the advantages of successful recruitment to a preferable nursery ground, since it can strongly influence the biogeography and community structure of the species via passive transport (Doherty 1991, Victor & Wellington 2000, Shima & Findlay 2002).

On the other hand, a protracted larval duration would almost unidirectionally negatively affect the survival of pelagic fish species such as Japanese anchovy. Although metamorphosis generally includes major changes that are morphological (Youson 1988), physiological (Balon 1984) and ecological (Bergman et al. 1988, Thorisson 1994), pelagic fish will undergo gradual rather than sudden changes. Thus, mortality rates and ecological features of pelagic fish can be more continuous through metamorphosis, compared with species that settle through metamorphosis. In addition, pelagic fish generally increase their swimming ability and come to form shoals during the post-larval stage (Matsuura & Hewitt 1995). Therefore, 'growth-selective predation' would have a more significant role in the recruitment dynamics of pelagic fish species than would the 'stage duration' mechanism.

Such differences in the relative importance of the growth-related mechanisms may reflect differences in the survival strategies.

*Acknowledgements.* We greatly appreciate the work of Drs. Y. Watanabe, T. Sugimoto (Ocean Research Institute, The University of Tokyo), T. Yamakawa and M. Sano (Graduate School of Agricultural and Life Sciences, The University of Tokyo) for their critical and constructive comments on an earlier draft. We thank C. Fukawa and Y. Fukawa for their support in field sampling with the shirasu fishing boat 'Yoshieimaru'. Also, we express sincere thanks to 4 anonymous referees for their detailed reviews and comments, which clearly polished up our manuscript.

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Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: March 20, 2003; Accepted: December 9, 2003  
Proofs received from author(s): March 22, 2004