Dynamics of growth-based survival mechanisms in Japanese anchovy Engraulis japonicus larvae
Dynamics of growth-based survival mechanisms in Japanese anchovy Engraulis japonicus larvae

Akinori Takasuka, Ayumu Sakai, and Ichiro Aoki

A. Takasuka. National Research Institute of Fisheries Science, Japan Fisheries Research and Education Agency, 2-12-4 Fukuura, Kanazawa, Yokohama, Kanagawa 236-8648, Japan.

A. Sakai* and I. Aoki**. Department of Aquatic Bioscience, Graduate School of Agricultural and Life Sciences, The University of Tokyo, 1-1-1 Yayoi, Bunkyo, Tokyo 113-8657, Japan.

Corresponding author: Akinori Takasuka (e-mail: takasuka@affrc.go.jp).

*Present address: Maruha Nichiro Corporation, 3-2-20 Toyosu, Koto, Tokyo 135-8608, Japan.

**Present affiliation: Emeritus Professor, The University of Tokyo.
Abstract: Three growth-based survival mechanisms were tested for multiple cohorts of Japanese anchovy *Engraulis japonicus* larvae in Sagami Bay. Through otolith microstructure analysis, growth trajectories and histories of samples of the survivors were compared with those of the original populations to examine size- and growth-selective mortality to test the “bigger is better” and “growth-selective predation” mechanisms, respectively. The effects of growth rates on the timing of metamorphosis were examined to test the “stage duration” mechanism. The “bigger is better” and “growth-selective predation” mechanisms were detected to be effective in 2 and 6 of 8 seasonal cohorts, respectively. Results contrary to the “bigger is better” and “growth-selective predation” mechanisms were obtained from 3 and 2 of 8 cohorts, respectively. The “stage duration” mechanism was evaluated to be effective for both of 2 cohorts which were testable. Overall, none of the three mechanisms was universally appropriate for all of the cohorts. The relative contributions of the three mechanisms were dynamic, although the “growth-selective predation” mechanism was identified to be the major one in anchovy larvae in the study site.
Introduction

Highly variable growth and mortality rates characterize the early life stages of marine and freshwater fish species. These rates are tightly coupled in the framework of the “growth–survival” paradigm (“growth–mortality” hypothesis; Anderson 1988), which posits that larger and/or faster growing individuals have higher probabilities of survival than smaller and/or slower growing conspecifics. The “growth–survival” paradigm has been given much attention in studies on recruitment dynamics of fish and thus has been tested in numerous studies (e.g. Meekan and Fortier 1996; Hare and Cowen 1997; Searcy and Sponaugle 2001). This simple paradigm may not be universally valid, as experimental studies have sometimes reported contradictory evidence (Litvak and Leggett 1992; Lankford et al. 2001; Munch and Conover 2003); however, it has been largely supported for various species, particularly in field conditions (Sirois and Dodson 2000; Shoji and Tanaka 2006; Robert et al. 2007). Plaza and Ishida (2008) reviewed the tests of size- and growth-selective mortality of various taxonomic groups to support the generality of the paradigm. Overall, growth rates during the early life stages appear to be a potential predictor of recruitment dynamics, although this linkage has rarely been quantified mainly owing to the difficulty of estimating mortality rates in the field.

Growth rates exert both direct and indirect effects on survival probabilities under the theoretical framework of the “growth–survival” paradigm (Houde 2008; Leggett and Frank 2008). To date, three functional mechanisms linking growth rates to survival have been proposed by discriminating the effects of three growth-related factors—somatic size, stage duration, and growth rate per se (Hare and Cowen 1997; Searcy and Sponaugle 2001; Takasuka et al. 2004a). First, the “bigger is better” mechanism (Miller et al. 1988) assumes survival advantages of larger somatic size. Faster growing
individuals gain larger somatic sizes than slower growing conspecifics if they are of the same age, although it should be noted that the age structure is sometimes complex in natural populations. This size-based mechanism works when larger larvae have higher growth rates in the population and larvae experience negative size-selective mortality at the same time. Second, the “stage duration” mechanism (Chambers and Leggett 1987; Houde 1987) focuses on the effects of growth rates on the timing of metamorphosis. This time-based mechanism works when higher growth rates accelerate the timing of the metamorphosis from larval to juvenile stages and faster growing individuals experience a shorter duration of the high mortality larval stage. These two mechanisms link growth rates to survival indirectly in theory. Third, the “growth-selective predation” mechanism (Takasuka et al. 2003) links growth rates per se to survival directly. Slower growing individuals would be physiologically in a poor condition and thus have a lower potential to initiate anti-predator behaviors (Fuiman and Magurran 1994; Skajaa et al. 2003). The mechanism works when slower growing individuals are more vulnerable to predation mortality than faster growing conspecifics of the same somatic size. In this theory, growth rates have direct impacts on predation mortality, independent of somatic size or stage duration. The mechanism was proposed based on comparison of growth rates between larvae dissected from the stomachs of predatory fish and the larvae captured simultaneously with the predators through otolith microstructure analysis (Takasuka et al. 2003, 2004b, 2007a). This method of “characteristics of non-survivors versus original population” serves as a complementary approach to the traditional “characteristics of survivors versus original population” method. These three growth-based survival mechanisms were then tested based on the characteristics of the survivors versus the original population for a summer cohort of Japanese anchovy *Engraulis japonicus* larvae in Sagami Bay, Japan (Takasuka et al.)
The surviving larvae had smaller somatic sizes but higher growth rates than the mean values of the original population. This specific case from a summer cohort suggested that smaller but faster growing individuals could survive better than larger but slower growing conspecifics, supporting the “growth-selective predation” mechanism and not the “bigger is better” mechanism. In that study, the “stage duration” mechanism was not unequivocally supported. However, the relative contributions of the different mechanisms may differ spatially and temporally depending on the environmental conditions. In theory, the three growth-based survival mechanisms are independent of and potentially synergistic with one another (Takasuka et al. 2004a; Leggett and Frank 2008). Of interest is therefore dynamics of the different mechanisms, which may reflect early survival strategies of fish. Is the survival of larval fish regulated by a single mechanism or a combination of multiple mechanisms? Does a mechanism work on survival processes variably or invariably?

The present field study tested the three functional mechanisms of the “growth–survival” paradigm on the short-term survival processes of multiple cohorts of Japanese anchovy larvae in Sagami Bay, based on the characteristics of the survivors versus the original populations. Size- and growth-selective mortalities were examined to test the “bigger-is-better” and “growth-selective predation” mechanisms, respectively. Furthermore, growth effects on the timing of metamorphosis were examined to test the “stage duration” mechanism. Through multi-sample comparisons, we show evidence of dynamic and synergistic aspects of the three growth-based survival mechanisms.

Materials and methods

Field sampling
Japanese anchovy larvae are commercially exploited as a food resource in Japan. The coastal areas of Sagami Bay constitute a major commercial fishing ground for anchovy larvae, which was the target site of the present study (Fig. 1). The oceanographic features and recruitment processes of anchovy larvae in Sagami Bay (Mitani 1990) provide reasonable conditions that allow testing the growth-based survival mechanisms based on the characteristics of the survivors versus the original populations (Takasuka et al. 2004a). In waters around Sagami Bay, anchovy spawn throughout the year with the main season from spring to autumn. Spawning occurs mainly in offshore areas, and the eggs are concentrated mainly off Jyogashima Island (Fig. 1). Recruitment into the coastal areas is largely regulated by the counter-clockwise currents (eddies). The eggs and early larvae are passively transported into the coastal areas across the front formed by river runoff. Because of the intermittent current intensity, the timing of larval recruitment into the coastal areas is also intermittent and thus larval cohorts can be discriminated in the catches (Takasuka et al. 2004a). The larvae grow to at least 13 mm in standard length (SL) during the transport, and they are able to actively swim and forage near the bottom in shallow areas. Once the larvae recruit into the coastal areas, they are considered to remain there under favorable prey plankton availability and turbid waters for ca one month until they develop to the juvenile stage and emigrate from the coastal areas (Mitani 1990).

These processes provided circumstantial evidence to support the assumption that the same cohorts can be tracked by repeated samplings in the study site within a period of ca one month (Takasuka et al. 2004a). Hence, the older larvae captured at the sampling of a certain period (< ca one month) later than the previous sampling were regarded as the individuals which survived for that short period (survivors), and the younger larvae captured at the previous sampling were regarded as the individuals representative of the
population from which the survivors originated (original population), if their
back-calculated hatching dates fell within a certain common period.

Based on these backgrounds, anchovy larvae were captured repeatedly (at least twice)
at an approximate interval of 10 days (but ranging from ca one week to one month)
within a certain period by a commercial trawl in the coastal area near the mouths of
Sagami River and Hanamizu River in Sagami Bay during autumn 2003 to winter 2005
(January 2006) (Table 1, Fig. 1). The trawl with a cod-end mesh size of 2.3 mm targeted
anchovy larvae foraging just above the seafloor in the shallow areas (< 10 m depth) for 5
to 10 minutes several times right after sunrise. The larval samples were randomly
selected from the catches and were frozen at –20°C immediately after landing. The
sampling methods and laboratory procedures were consistent with those in Takasuka et
al. (2004a).

Growth analysis
SL of each larva was measured to the nearest 0.1 mm under a binocular microscope.
SL frequency distributions were described to observe shifts in mode of SL to ensure
successful cohort tracking. The samples in which SL modes shifted to a larger size with
sampling dates were adopted for growth analysis. Sagittal otoliths were dissected from
each larva and then mounted on a glass slide with enamel resin. Either the left or the
right otolith was used assuming symmetry of the bilateral otoliths. A series of otolith
measurements were conducted using an otolith measurement system (RATOC System
Engineering), which is composed of a transmitted light microscope with a video camera
connected to a computer and monitor. The maximum otolith radius (OR) and each daily
increment width were measured to the nearest 0.1 µm along the measurement transect,
which was set from the nucleus to the outermost posterior margin of the otolith.
The number of daily growth increments plus 3 was regarded as age in days (daily age), as the first increment is deposited 3 to 4 days after hatching (Tsuji and Aoyama 1984). Hatching date was determined by date of capture and daily age. SL and daily growth rate at each age were back-calculated by the biological intercept method (Campana 1990). As an allometric formula fits the relationships between OR and SL for anchovy larvae (Takasuka et al. 2008), it was determined separately for each larva with SL at the first growth increment deposition fixed at 5.6 mm (Fukuhara 1983) in the back-calculation.

Uncoupling between otolith and somatic size, if it occurs, could be a possible source of bias in the back-calculation (Campana 1990). However, OR and SL were confirmed to be highly correlated in the present samples: $R^2$ values of the allometric relationships ranged from 0.827 to 0.934 (data not shown). Accordingly, the present analysis adopted back-calculated SL and growth rate rather than raw OR and increment width (Takasuka et al. 2004a for details). The growth effect on the OR–SL relationship was found for anchovy and sardine larvae, but the correlations between OR and SL were high for these species in general (Takasuka et al. 2008).

Survivors and original populations

A total of 8 cohort samples (A–H) comprising at least 1 pair of survivors and original populations within each cohort sample were determined based on the sampling dates and hatching dates (Table 1, Fig. 2). Samplings carried out twice provide 1 pair of survivors and original populations within a cohort sample; 3 or more repeated samplings provide multiple pairs. The larvae captured at the first sampling were regarded as the original population, and the larvae captured at the second sampling were regard as the survivors originating from them. Similarly, the larvae captured at the third
and fourth samplings were regarded as the survivors originating from the cohort captured at the earlier samplings. The interval between the samplings of the survivors and the original populations corresponds to the survival period; the start of the survival period corresponds to the sampling date of the original populations. To ensure such a correspondence, the larvae that had hatching dates which fell within a common range among different sampling dates were extracted from the total samples so that the survivors and original populations have approximately the same mean hatching date within a pair (Table 1, Fig. 2).

For example, the cohort sample A, which was collected in autumn 2003, comprises the larvae captured on 25 Nov, 5 Dec and 15 Dec with 10-day intervals, which had hatching dates that fell within the common range of 16–29 Oct (14 days). The larvae captured on 25 Nov were used as the original population (OP); the larvae captured on 5 Dec were the survivors (SV-1) originating from OP; the larvae captured on 15 Dec were the survivors (SV-2) originating from OP and SV-1. The mean of hatching date was 22–25 Oct. for OP, SV-1, and SV-2. In this case, 3 pairs of survivor and original populations (SV-1 versus OP, SV-2 versus OP and SV-2 versus SV-1) were prepared. Note that the target survival period of SV-1 versus OP was also included in that of SV-2 versus OP.

Similarly, a total of 17 pairs of the survivor and original populations were prepared from the 8 cohort samples. Hatching date distributions were examined for the total samples comprising of a total of 2,974 individuals. A total of 2,077 individuals with SL from 16.1 to 41.7 mm and daily age from 23 to 98 days were adopted to constitute the samples of the survivors and the original populations (Table 1, Fig. 2).

**Mechanism tests**
Back-calculated daily SL versus calendar date (growth trajectory) and growth rate versus calendar date or daily age (growth and history) allow testing of the three functional mechanisms of the “growth–survival” paradigm. For each mechanism to be effective, several conditions need to be satisfied in theory, as follows. The “bigger is better”: (1) positive relationship between growth rate and somatic size within the population and (2) negative size-selective mortality; the “growth-selective predation”: (1) negative growth-selective mortality at the same somatic size and (2) predation as the direct source of mortality; the “stage duration”: (1) negative relationship between growth rate and larval stage duration and (2) higher mortality during larval stage than juvenile stage.

In general, the “bigger is better” mechanism has been tested based on the direction of size-selective mortality. In a strict sense, however, negative size-selective mortality is a necessary but not a sufficient condition for this mechanism to work under the theoretical framework of the “growth–survival” paradigm, because negative size-selective mortality does not produce any survival advantage if size is not linked to the growth rate. A positive relationship of size to growth rate should be true as far as all the individuals hatch at the same time and growth difference is kept; however, natural populations generally have a complex structure of various ages: faster-growing smaller larvae and slower-growing larger larvae may be mixed. The “growth-selective predation” is testable based on the direction of growth-selective mortality at the same size. Although it is not possible to identify the source of mortality by the present approach, we assumed that predation is the major source of mortality for the reasons detailed in the Discussion section.

Growth trajectories and histories of individual larvae can be pooled and arranged by either calendar date or daily age within a group when they are compared between the
groups of survivors and original populations. Date-based data represent temporal changes in growth characteristics, while age-based data represent stage-specific changes (Takasuka et al. 2004a for details). Selection (e.g. predation) occurs on variation in size and growth within the population at a given moment; in other words, size- and growth-selection occur as a snapshot of the population with real time. Therefore, the date-based growth trajectory and history were adopted to test the “bigger is better” and “growth-selective predation” mechanisms. On the contrary, the age-based growth history was adopted to test the “stage duration” mechanism (see below). If any selection occurs during the survival period, it would be reflected in the characteristics of the survivors versus the original populations. Since it is not possible to compare the characteristics during the survival period, SL at the start of the survival period (i.e. the time of sampling of the original population) and the last 3-day mean growth rate immediately before the start of the survival period were focused on in comparisons of the survivors with the original populations to test the “bigger is better” and “growth-selective predation” mechanisms, respectively. SL at the start of survival was back-calculated for the survivors, whereas it was SL at the time of capture for the original populations. The last 3-day mean growth rate was back-calculated for the survivors and original populations. In both cases, the timing for comparison (i.e. the start of survival) was consistent between the survivors and original populations in calendar date. The last 3-day mean growth rate was adopted as a proxy for survival potential at that time, since the last increments could reflect physiological conditions (e.g. Clemmesen and Doan 1996), which would determine the selection on growth rate. To test the “bigger is better” mechanism, relationship between SL and last 3-day mean growth rate was examined for the original populations by a linear regression analysis, and direction of size-selective mortality was examined by comparing the SL at
the start of survival between the survivors and the original populations. The mechanism was evaluated to be effective if the relationship between SL and 3-day mean growth rate was positive and if the size-selective mortality was directed negatively at the same time.

To test the “growth-selective predation” mechanism, the direction of growth-selective mortality was examined by comparing the last 3-day mean growth rate before the start of survival between the survivor and original populations. The mechanism was evaluated to be effective if the growth-selective mortality was directed negatively.

However, if any size-selection occurs simultaneously under any significant relationship between SL and growth rate for the original populations, growth-selection may be merely due to size-selection. In such a case, the growth rate was compared in the limited ranges of SL (at the start of survival) of the survivors and the original populations to test if selection occurred on growth rate per se. The individuals within the ranges of SL (at the start of survival) limited to 2–3 mm, in which SLs were not significantly different between the two groups, were extracted for this comparison. Growth rate and SL were compared between the two groups by Student’s t-test or Welch’s t-test, depending on the results of tests of homogeneity.

Presence/absence of guanine serves as an indicator of metamorphosis of anchovy larvae (Takahashi and Watanabe 2004). No individuals had guanine on the surface of the body or had morphologically reached the juvenile stage. Hence, the individuals with guanine deposition on the inside wall of the abdominal cavity were regarded as larvae undergoing the initial stages of metamorphosis. Back-calculated growth histories were compared between these metamorphosing larvae and non-metamorphosing larvae falling within the range of daily age overlapping between these two groups to test the effects of growth rates on the timing of metamorphosis. For this comparison, a multivariate analysis of variance (MANOVA) was applied to 5-day mean growth rates.
from hatching up to the minimum daily age of the metamorphosing larvae (i.e. mean growth rate during 6–10, 11–15,… days old for the MANOVA), using the age-based data rather than date-based data, since the analysis aims at the effects of growth rates on developmental changes. Mean growth rate from hatching up to the minimum daily age of the metamorphosing larvae, which was calculated by dividing SL at the minimum age of metamorphosing larvae minus SL at hatching of 2.9 mm (Fukuhara and Takao 1988) by the minimum age, was also compared between the two groups. The “stage duration” mechanism was evaluated to be effective if the metamorphosing larvae had higher growth rates than the non-metamorphosing larvae.

Results

Growth trajectory and history

The growth trajectories (Fig. 3) and histories (Fig. 4) showed different patterns of temporal changes in growth among the different cohort samples. Overall, however, the patterns were similar among the samples of survivors and original populations within each cohort sample. For example, sigmoid-like growth trajectories and shifts from slight to rapid decreases in growth rate around 10 Nov characterized the cohort sample D (autumn 2004): these patterns were consistent between the survivors and the original populations within that cohort. Although the difference in SL and growth rate within a cohort did not seem large, there were various relationships between the survivors and the original populations at the start of survival. The results of SL and growth rate relationships and comparisons of SLs and growth rates are summarized in Table 2.
The relationships between SL and last 3-day mean growth rates were variable for the original populations (Table 2, Fig. 5). The relationship was significantly positive for 7 of the 12 samples of original populations, whereas it was significantly negative for OP of the cohort sample D (autumn 2004) (linear regression analysis, \( p < 0.05 \)). On the contrary, no significant relationship was found for the remaining 4 samples of original populations.

**Size-selective mortality**

The directions of size-selective mortality were variable among the cohorts and even among different survival periods within the same cohort (Table 2). Although the ranges of SL at the start of survival largely overlapped between the survivors and the original populations, the distribution patterns of SL and growth rate in the scatterplots were more or less different between the survivors and the original populations, depending on the cohort sample (Fig. 5).

The SLs of the survivors were significantly larger than those of the original populations at the start of survival for 3 of 8 cohorts (4 of 17 pairs) (Student’s \( t \)-test or Welch’s \( t \)-test, \( p < 0.01 \)). Conversely, the SLs of the survivors were significantly smaller than those of the original populations for 3 of 8 cohorts (6 of 17 pairs) (\( p < 0.05 \)). No significant differences were found for 5 of 8 cohorts (7 of 17 pairs). Note that the results differed within the cohort samples B (spring 2004) and F (spring 2005-1), and thus these cohort samples were counted redundantly above. The results were consistent within pairs for which the start of the survival period was the same.

**Growth-selective mortality**

The directions of growth-selective mortality were also variable among and within the
cohorts (Table 2). The distribution patterns of SL and growth rate in the scatterplots
differed between the survivors and the original populations at the same SL despite their
substantial overlapping ranges of growth rate versus SL, depending on the cohort
sample (Fig. 5). The SL and growth rate relationships were significant and SLs differed
significantly between the survivors and the original populations for the samples with the
start of survival of 18 Apr '04 (B, spring 2004), 22 Nov '04 (D, autumn 2004), 8 Jan '05
(E, winter 2004), 9 Apr '05, and 18 Apr '05 (F, spring 2005-1); therefore, the
individuals within the limited SL range were extracted for these samples for growth
comparison.

The last 3-day mean growth rates before the start of survival were significantly higher
for the survivors than for the original populations for 6 of 8 cohorts (9 of 17 pairs)
(Student’s t-test or Welch’s t-test, p < 0.01). On the contrary, the growth rates of the
survivors were significantly lower than the original populations for 2 of 8 cohorts (2 of
17 pairs) (p < 0.05). No significant differences were found for 4 of 8 cohorts (7 of 17
pairs). As in the SL comparisons, the results differed among pairs within some cohort
samples, and the cohort samples were counted redundantly above. The different results
were found within the cohort samples A (autumn 2003), B (spring 2004), and F (spring
2005-1).

Growth effect on metamorphosis

Metamorphosing larvae occurred only in the cohorts collected in spring 2004 (cohort
sample B) and spring 2005 (cohort sample F). A total of 21 and 23 metamorphosing
larvae were found from the total samples collected on May 6, 2004 and May 10, 2005,
respectively. Note that these larval samples also included individuals whose SLs and
hatching dates were out of ranges of the samples of the survivors and the original
populations (Table 1, Fig. 2). The minimum ages of the metamorphosing larvae were 55
and 60 days for spring 2004 and spring 2005, respectively; the maximum ages of the
non-metamorphosing larvae were 70 and 81 days for spring 2004 and spring 2005,
respectively (Fig. 6). The individuals whose daily ages fell within the range of daily age
overlapping between these two groups (55–70 and 60–81 days for spring 2004 and
spring 2005, respectively) were extracted for growth comparison.

Comparison of 5-day mean growth rates showed that the metamorphosing larvae had
higher growth rates than the non-metamorphosing larvae during 6–30 days (MANOVA,
\( p < 0.01 \)) for spring 2004 and during 11–15, 21–25, and 46–50 days (\( p < 0.05 \)) for
spring 2005 although the relationship was reversed during 41–45 days (\( p = 0.039 \)) for
spring 2004 (Fig. 7). Mean growth rates from hatching up to 55 days were significantly
higher for the metamorphosing larvae (\( n = 7, \text{mean} \pm \text{SD} = 0.50 \pm 0.03 \text{mm day}^{-1} \)) than
for the non-metamorphosing larvae (\( n = 20, 0.43 \pm 0.02 \text{mm day}^{-1} \)) for spring 2004
(Student’s \( t \)-test, \( p < 0.001 \)). As well, mean growth rates up to 60 days were significantly
higher for the metamorphosing larvae (\( n = 19, 0.48 \pm 0.03 \text{mm day}^{-1} \)) than the
non-metamorphosing larvae (\( n = 27, 0.44 \pm 0.03 \text{mm day}^{-1} \)) for spring 2005 (\( p < 0.001 \)).

Three mechanisms

Results of the tests of the “bigger is better”, “growth-selective predation”, and “stage
duration” mechanisms are summarized in Table 3. For the cohort sample A (autumn
2003), neither “bigger is better” nor “growth-selective predation” was considered
effective for SV-1 and SV-2 versus OP, because no selection was observed (Table 2).
Only the “growth-selective predation” was considered effective for SV-2 versus SV-1,
as this pair showed negative growth-selective mortality but no size-selective mortality.
For B (spring 2004), SV-1 and SV-2 versus OP showed negative size-selective mortality
under the positive SL and growth rate relationship, which was considered contrary to
the “bigger is better”, while SV-1 versus OP showed negative growth-selective mortality,
indicating the “growth-selective predation” being effective. In contrast, SV-2 versus
SV-1 showed positive growth-selective predation, being contrary to the
“growth-selective predation”. For C (summer 2004), neither the “bigger is better” nor
the “growth-selective predation” was detected. D (autumn 2004) and E (winter 2004)
showed negative size-selective mortality. However, the “bigger is better” was effective
for E but not for D, since negative-size selective mortality under negative SL and
growth rate relationship was contrary to the “bigger is better”. The “growth-selective
predation” was effective for both D and E. Within F (spring 2005-1), the “bigger is
better” shifted from being contrary to being effective, as the size-selective mortality
shifted from being positive to being negative under the positive SL and growth rate
relationships for SV-1, SV-2 and SV-3 versus OP, and SV-2 and SV-3 versus SV-1,
whereas the “growth-selective predation” was consistently effective except for SV-1
versus OP. Then, both mechanisms became non-significant for SV-3 versus SV-2. For G
(spring 2005-2), the “bigger is better” was not significant because of the lack of SL and
growth rate relationship, whereas the “growth-selective predation” was effective. For H
(winter 2005), the “bigger is better” did not work without any size-selective mortality,
and the “growth-selective predation” was rejected by the positive growth-selective
mortality. The “stage duration” was considered effective for the cohort samples B and F,
based on the effects of growth rates on the timing of metamorphosis.

In summary, the “bigger is better” and “growth-selective predation” mechanisms
were detected to be effective in 2 and 6 of 8 cohorts (3 and 9 of 17 pairs of the survivors
and original populations), respectively, although different pairs showed different results
in some cohorts. The results contrary to the “bigger is better” and “growth-selective
“predation” mechanisms were obtained from 3 and 2 of 8 cohorts (6 and 2 of 17 pairs of the survivors and original populations), respectively. The “stage duration” mechanism was evaluated to be effective for both of the 2 cohorts which were testable.

Discussion

Three functional mechanisms of the “growth–survival” paradigm were shown to work simultaneously or separately in larval cohorts of Japanese anchovy in Sagami Bay. The first study of this population examining the three mechanisms (Takasuka et al. 2004a) detected the effect of the “growth-selective predation” mechanism only. However, the present work provides field evidence to demonstrate the independent and synergistic operation of these three mechanisms in the short-term survival processes of anchovy larvae in the study site through the tests of multiple cohorts. Although the actual processes of the different mechanisms may be sometimes interconnected or interactive in reality, a conceptual distinction in theory is necessary to understand how growth regulates survival dynamics (Hovenkamp 1992). In this context, the tests were conducted under a framework of clearly defined conditions of the operation of the mechanisms.

Correspondence between the survivors and the original populations is an essential assumption in the “characteristics of the survivors versus original populations” method (Meekan and Fortier 1996). In the study site, this assumption was well supported by circumstantial evidence in terms of the oceanographic features and larval recruitment processes. Also, the survivors and the original populations were extracted to have approximately the same mean hatching date. Moreover, the patterns of growth trajectories and histories were similar within a cohort sample. Among the conditions for
the mechanisms to be evaluated, two conditions remain to be tested directly: predation as the direct source of mortality for the “growth-selective predation” mechanism and higher mortality during the larval stage than the juvenile stage for the “stage duration” mechanism. However, we regarded these conditions as basic premises, as follows. The present samples were considered to pass stages right after hatching when starvation can be critical. The study site is a feeding ground where food availability is relatively high for anchovy larvae. Moreover, the “growth-selective predation” was directly demonstrated by sampling anchovy larvae and predators by the same tows in the same study site in previous studies (Takasuka et al. 2003, 2007a). Hence, predation was assumed to be the direct source of mortality in the study site. As to stage-related mortality, mortality rate dramatically decreases with developmental stage in general (Houde 1987). This would also be true for anchovy in Sagami Bay partly because juveniles were rare in the gut contents of predatory fish there (Takasuka et al. 2003). Based on these assumptions, the “bigger is better” and “growth-selective predation” mechanisms were tested based on the key conditions relevant to somatic size and growth rate. The results of the operation of the mechanisms (effective, contrary, or non-significant) differed among cohorts, seasons and years with a great variability from a viewpoint of the combinations of the mechanisms. The “bigger is better” mechanism worked in favor of the survivorship of larger somatic size for 2 of the 8 cohorts, but it worked conversely more frequently. In a specific case, even with the negative size-selective mortality, the selection did not favor the survivorship of larger larvae because of the negative size and growth rate relationship in the cohort of autumn 2004. Another point of note was the changes of the operation of the mechanisms even within the same seasonal cohort, as in the cohorts of spring 2004 (from being contrary to being non-significant) and spring 2005-1 (from being contrary to being effective). In contrast,
the “growth-selective predation” mechanism was detected to be effective more frequently and if not effective the mechanism was non-significant except for 2 contrary cases. The trends of being effective, contrary or non-significant were relatively consistent within the same cohort. The significance of the “growth-selective predation” mechanism relative to the “bigger is better” can be theoretically explained by the optimal foraging theory of predators (Takasuka et al. 2003, 2007a). The present work provides a practical example to support the operation of the mechanisms through a multiple cohort comparison.

The “stage duration” mechanism could only be tested on 2 cohorts. Both cases demonstrated the accelerating effects of growth rates with the timing of metamorphosis, providing positive evidence for the operation of this mechanism. The “stage duration” mechanism was effective even when the other 2 mechanisms were not effective or contrary. In such a case, the “stage duration” mechanism could exert counter effects on survivorship against the other two mechanisms. Unlike the other two mechanisms, the “stage duration” mechanism deals with the cumulative effects of variability of the mortality rate. Therefore, if this mechanism works simultaneously with the others, the effects of those other mechanisms on survival probability throughout the larval stage would be multiplied. However, the “stage duration” mechanism would not be universal either, when the case of a summer cohort in 2001 of a previous study (Takasuka et al. 2004a) is also considered (Table 3). Therefore, each mechanism was detected to be effective at least in some cases, but none of these 3 mechanisms was universally applicable over all of the cohorts available for analysis.

The contributions of the different growth-based factors to the survivorship have been a focal point in understanding the selective recruitment dynamics. Some studies highlighted strong effects of size-selective mortality (Meekan et al. 2006; Perez and
Munch 2010), and others focused on stage duration effects (Hovenkamp 1992) and physiological conditions (Searcy and Sponaugle 2001). However, the results tended to be consistent within the species, populations, or seasonal cohorts. For example, the synergistic and consistent operation of multiple mechanisms has been shown for Japanese sardine *Sardinops melanostictus* larvae (Plaza and Ishida 2008). The variability and dynamics of the operation of the three mechanisms shown in the present study is in contrast to these examples. Such differences may reflect differential survival strategies among different populations, species or taxonomical groups, as well as differences in environments among different systems, which would be a subject of a cross-sectional review in the future.

The present work examined short-term survival processes by collecting samples repeatedly with an interval of *ca* 10 days. However, the sampling interval was variable to some extent, and multi-pairing of the survivors and the original populations led to various survival periods. If the target survival period is too short, the mechanism may not be detected even when it actually operates, while the longer target period may allow the mechanism to be detected easier. That is, the target survival period could affect detection of the mechanisms. However, no consistent trend was observed between the results of the mechanism tests and survival periods (Table 3). The observed variety of mechanism detection should not be mainly attributed to the variation of survival period.

Now, what factors affect the dynamics of the mechanisms? Although the dynamics would be a composite of multiple factors, we speculate that it would be largely determined by the compound effects of two factors. First, predator field, that is, the temporal changes in predator abundance and composition which larvae encounter, would be responsible for the dynamics of the mechanisms. In general, prey size selection could differ among predatory species (Scharf et al. 2000). In prey–predator
interactions, encounter rate, susceptibility, and thus net vulnerability were expressed as a function of prey–predator size ratio and the patterns differ among predator types (Bailey and Houde 1989). In fact, predator specific “growth-selective predation” has been demonstrated for anchovy larvae in previous studies based on the “characteristics of non-survivors versus original populations” (Takasuka et al. 2007a; Robert et al. 2010). Small pelagic fish (juvenile anchovy, round herring *Etrumeus teres*, jack mackerel *Trachurus japonicus* and white croaker *Pennahia argentatus*) were identified as growth-selective predators, whereas piscivorous fish (sea bass *Lateolabrax japonicus*, greater amberjack *Seriola dumerili*, skipjack tuna *Katsuwonus pelamis*, chub mackerel and spotted mackerel *Scomber* spp.) were identified as non-growth-selective predators. Comparative analyses to generate the mechanisms of selective mortality need to consider trophic interactions in local food webs (Pepin 2016).

Second, growth level and variability at the population (cohort) level are likely to affect the operation of the mechanisms, in conjunction with the predator field. Growth rate is a function of external factors (e.g. temperature and food) as well as internal factors (e.g. size and age) (Pepin 1991; Heath 1992; Robert et al. 2009). Further, growth rate and feeding success are correlated; thus instantaneous growth rate is affected by past growth histories (Robert et al. 2014; Pepin et al. 2015). Environmental effects on growth rates have been examined for Japanese anchovy larvae (Takasuka and Aoki 2006; Takasuka et al. 2007b; Takahashi et al. 2009). In the present study, growth level and variability fluctuated substantially among the cohorts (Table 2, Fig. 5). Folkvord (2005) established the size- and temperature-dependent growth models to evaluate relative growth performance of different populations of larval Atlantic cod *Gadus morhua*. For anchovy larvae, a dome-shaped function of the recent 3-day mean growth rate to sea surface temperature was obtained from 34 samples comprising 2,041 samples.
individuals collected broadly in the western North Pacific (Takasuka et al. 2007): $y = -2.302 + 0.255 \times - 0.006 \times ^2$ ($n = 34$, $r^2 = 0.507$, $p < 0.001$). Based on the last 3-day mean growth rates at the start of survival (Table 2) coupled with the 3-day mean sea surface temperature, the residuals of the growth rate from the growth–temperature function were calculated. The residuals ranged from −0.09 to 0.38 under 14.2–22.3°C. This calculation suggests that the present study tested the selections occurring for the cohorts exhibiting relatively high growth performance for this species.

In these contexts, however, we should be careful with the intrinsic issue of growth selection. The populations comprising slower growing individuals at the earlier stages, if they are then exposed to intensive selection on growth rates and slower growing individuals are removed, could exhibit higher growth level and lower growth variability at the later stages. Robert et al. (2007) discriminated the effects of fast growth and the selection for fast growth to demonstrate that a strong recruitment of Atlantic mackerel *Scomber scombrus* occurred only when larval growth rates are high and predation pressure is weak. To disentangle this issue for anchovy larvae in Sagami Bay or elsewhere, future studies will be required to examine the relationships among growth level and variability, intensity of size- and growth-selection, predator field, and survival success. Such a study framework would lead to a key step toward predicting the fish recruitment dynamics based on the growth–survival relationships during their early life stages.

In conclusion, the three different growth-based mechanisms actually regulated the short-term survival processes independently and synergistically. The relative contributions of the three mechanisms were nonstationary even in the same species within a certain region, although the “growth-selective predation” mechanism was identified to be the major one regulating survival in anchovy larvae in the study site.
The present study raises a question to the simple “growth–survival” paradigm: the relationship between growth and survival appears to be much more variable and dynamic than previously recognized. Further studies on the relationships among the mechanisms, growth level, intensity of growth selection, and predator field in terms of their annual and seasonal changes would contribute to understanding the survival mechanisms during the early life stages of pelagic fish.

Acknowledgements

The authors appreciate the critical and constructive comments on the earlier contents by T. Yamakawa and Y. Watanabe. Field samplings and data collections were supported by I. Mitani, C. Fukawa, Y. Fukawa, and H. Nakategawa. The samples during the fishing-closed season were supplemented by Y. Watanabe. Laboratory procedures were helped by H. Tanaka, T. Kaneko, and H. Arai.

References

Chambers, R.C., and Leggett, W.C. 1987. Size and age at metamorphosis in marine fishes: an analysis of laboratory-reared winter flounder (Pseudopleuronectes...
1 *americanus*) with a review of variation in other species. Can. J. Fish. Aquat. Sci. 2
2 Clemmesen, C., and Doan, T. 1996. Does otolith structure reflect the nutritional
3 condition of a fish larva? Comparison of otolith structure and biochemical
6 Folkvord, A. 2005. Comparison of size-at-age of larval Atlantic cod (*Gadus morhua*)
7 from different populations based on size- and temperature-dependent growth models.
11 Fukuhara, O. 1983. Development and growth of laboratory reared *Engraulis japonica*
14 Fukuhara, O., and Takao, K. 1988. Growth and larval behaviour of *Engraulis japonica*
18 planktonic larvae of *Pomatomus saltatrix* (Pisces: Pomatomidae). Ecology 78(8):


1 Robert, D., Takasuka, A., Nakatsuka, S., Kubota, H., Oozeki, Y., Nishida, H., and
2 Fortier, L. 2010. Predation dynamics of mackerel on larval and juvenile anchovy: is
4


10 of marine fish predators: interspecific variation and effects of ontogeny and body size

13 avoidance in cod larvae (Gadus morhua L.); trade-offs between hunger and predation
14 risk. In The Big Fish Bang: Proceedings of the 26th Annual Larval Fish Conference.
15 Edited by H.I. Browman and A.B. Skiftesvik. The Institute of Marine Research,
16 Bergen, Norway, pp. 105–121.

17 Shoji, J., and Tanaka, M. 2006. Growth-selective survival in piscivorous larvae of
18 Japanese Spanish mackerel Scomberomorus niphonius: early selection and

20 Sirois, P., and Dodson, J.J. 2000. Critical periods and growth-dependent survival of


Table 1. *Engraulis japonicus*. Profiles of the 8 cohort samples of Japanese anchovy larvae collected in Sagami Bay during autumn 2003 to winter 2005 (January 2006).

Note: Each cohort sample comprises at least 1 pair of survivor (SV) and original populations (OP). Within a cohort sample, SV, SV-1, SV-2, and SV-3 are the survivors originating from OP; SV-2 and SV-3 are also the survivors originating from SV-1; SV-3 are also the survivors originating from SV-2. Hatching date range and period are shown for each cohort sample; date of capture, sampling interval, sample size, standard length (SL), age in days and mean hatching date are shown for each category group of survivors and original populations.

Individuals collected on 6 Feb and 15 Feb '05 were pooled into a sample of survivors (SV) because of the small sample sizes. Individuals collected on 30 Apr and 10 May '05 were divided into 2 cohort samples (30 Apr: SV-2 of F and OP of G; 10 May: SV-3 of F and SV of G) because of the broad range of hatching dates.
<table>
<thead>
<tr>
<th>Sample</th>
<th>Cohort</th>
<th>Hatching date</th>
<th>Category</th>
<th>Date of capture</th>
<th>Interval (d)</th>
<th>n</th>
<th>SL (mm)</th>
<th>Age (d)</th>
<th>Hatching date</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Range</td>
<td>Mean</td>
<td>Range</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Mean</td>
<td></td>
<td>Mean</td>
</tr>
<tr>
<td>A</td>
<td>Autumn 2003</td>
<td>16–29 Oct '03</td>
<td>14 OP</td>
<td>25 Nov '03</td>
<td>–</td>
<td>102</td>
<td>18.0–23.9</td>
<td>20.5</td>
<td>29–41</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>22–23 Oct '03</td>
<td>35</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>SV-1</td>
<td>5 Dec '03</td>
<td>10</td>
<td>18.9–28.0</td>
<td>23.6</td>
<td>37–50</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>23–24 Oct '03</td>
<td>43</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>SV-2</td>
<td>15 Dec '03</td>
<td>10</td>
<td>21.9–30.9</td>
<td>26.3</td>
<td>47–60</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>24–25 Oct '03</td>
<td>52</td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>Spring 2004</td>
<td>9–21 Mar '04</td>
<td>13 OP</td>
<td>18 Apr '04</td>
<td>–</td>
<td>90</td>
<td>16.3–27.0</td>
<td>20.4</td>
<td>28–40</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>13–14 Mar '04</td>
<td>36</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>SV-1</td>
<td>30 Apr '04</td>
<td>12</td>
<td>21.1–30.0</td>
<td>24.5</td>
<td>40–52</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>15–16 Mar '04</td>
<td>45</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>SV-2</td>
<td>6 May '04</td>
<td>6</td>
<td>21.5–31.3</td>
<td>26.2</td>
<td>46–58</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>15–16 Mar '04</td>
<td>51</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>Summer 2004</td>
<td>23 May–11 Jun '04</td>
<td>20 OP</td>
<td>15 Jul '04</td>
<td>–</td>
<td>112</td>
<td>18.9–30.7</td>
<td>24.5</td>
<td>34–53</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2–3 Jun '04</td>
<td>42</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>SV</td>
<td>10 Jul '04</td>
<td>11</td>
<td>33.0–41.7</td>
<td>37.2</td>
<td>86–98</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>14–15 Nov '04</td>
<td>92</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>20–21 Oct '04</td>
<td>33</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>SV</td>
<td>29 Nov '04</td>
<td>7</td>
<td>19.9–29.1</td>
<td>24.7</td>
<td>31–48</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>21–22 Oct '04</td>
<td>39</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>13–14 Nov '04</td>
<td>55</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>SV</td>
<td>6 Feb '05</td>
<td>29</td>
<td>30.3–36.9</td>
<td>33.7</td>
<td>77–89</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>14–15 Nov '04</td>
<td>84</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>SV</td>
<td>15 Feb '05</td>
<td>9</td>
<td>33.0–41.7</td>
<td>37.2</td>
<td>86–98</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>14–15 Nov '04</td>
<td>92</td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>Spring 2005-1</td>
<td>1–14 Mar '05</td>
<td>14 OP</td>
<td>9 Apr '05</td>
<td>–</td>
<td>108</td>
<td>17.1–26.4</td>
<td>21.0</td>
<td>26–39</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>6–7 Mar '05</td>
<td>34</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>SV-1</td>
<td>18 Apr '05</td>
<td>9</td>
<td>18.2–29.2</td>
<td>22.3</td>
<td>35–48</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>9–10 Mar '05</td>
<td>40</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>SV-2</td>
<td>30 Apr '05</td>
<td>12</td>
<td>21.7–35.3</td>
<td>27.9</td>
<td>47–60</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>9–10 Mar '05</td>
<td>52</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>SV-3</td>
<td>10 May '05</td>
<td>10</td>
<td>27.0–35.7</td>
<td>31.0</td>
<td>57–70</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>9–10 Mar '05</td>
<td>62</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>20–21 Mar '05</td>
<td>40</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>SV</td>
<td>10 May '05</td>
<td>10</td>
<td>23.6–31.7</td>
<td>27.4</td>
<td>40–56</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>23–24 Mar '05</td>
<td>48</td>
<td></td>
</tr>
<tr>
<td>H</td>
<td>Winter 2005</td>
<td>6–21 Nov '05</td>
<td>16 OP</td>
<td>10 Jan '06</td>
<td>–</td>
<td>114</td>
<td>21.6–31.5</td>
<td>26.7</td>
<td>50–65</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>13–14 Nov '05</td>
<td>57</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>SV</td>
<td>27 Jan '06</td>
<td>17</td>
<td>24.4–35.0</td>
<td>30.6</td>
<td>67–82</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>13–14 Nov '05</td>
<td>74</td>
<td></td>
</tr>
</tbody>
</table>
Table 2. *Engraulis japonicus*. Summary of the tests of the conditions for the “bigger is better” and “growth-selective predation” mechanisms.

Note: Directions of relationship between standard length (SL) at the start of the survival period and the last 3-day mean growth rate (GR) immediately before the start of the survival period were examined for the original populations (SL–GR). SL at the start of survival and GR right before the start of survival were compared between the survivors and the original populations. Larger/Smaller: SLs of the survivors were larger/smaller than those of the original populations; Higher/Lower: GRs of the survivors were higher/lower than those of the original populations; NS: not significant. Shaded areas indicate the SL ranges adopted for GR comparison. When the SL–GR relationship was significant and SLs significantly differed between the survivors and the original populations, the SL ranges were limited to 2–3 mm, in which their SLs did not significantly differ.

*p* < 0.05, **p** < 0.01, ***p*** < 0.001; *a* Individuals collected on 2 different days were pooled; *b* Student’s *t*-test, *c* Welch’s *t*-test.
Sample Cohort | Start of survival | Category | Population | Survival period (d) | SL–GR | SL (mm) Mean ± SD | GR (mm day$^{-1}$) Mean ± SD | SL range for GR comparison
---|---|---|---|---|---|---|---|---
A Autumn 2003 | 25 Nov '03 | OP Original | – Positive | * | 20.5 ± 1.3 | – | 0.31 ± 0.06 | All
SV-1 Survivors | 10 | – | 20.9 ± 1.8 | NS$^a$ | | 0.33 ± 0.07 | NS$^a$ | All
SV-2 Survivors | 20 | – | 20.4 ± 1.6 | NS$^b$ | | 0.33 ± 0.06 | NS$^b$ | All
5 Dec '03 | SV-1 Original | – NS | 23.6 ± 1.9 | – | 0.28 ± 0.06 | – | All
SV-2 Survivors | 10 | – | 23.5 ± 1.6 | NS$^c$ | | 0.33 ± 0.06 | Higher$^c$ | All
B Spring 2004 | 18 Apr ’04 | OP Original | – Positive *** | | 20.4 ± 2.1 | – | 0.41 ± 0.06 | 18–20
SV-1 Survivors | 12 | – | 19.3 ± 1.7 | Smaller$^b$ *** | | 0.45 ± 0.07 | Higher$^b$ ** | 18–20
SV-2 Survivors | 18 | – | 19.5 ± 2.3 | Smaller$^b$ ** | | 0.44 ± 0.08 | NS$^b$ | 18–20
30 Apr '04 | SV-1 Original | – Positive ** | 24.5 ± 1.7 | – | 0.42 ± 0.08 | – | All
SV-2 Survivors | 6 | – | 24.1 ± 2.1 | NS$^b$ | | 0.37 ± 0.08 | Lower$^b$ *** | All
C Summer 2004 | 4 Jul ’04 | OP Original | – NS | | 20.7 ± 2.1 | – | 0.40 ± 0.08 | – | All
SV Survivors | 11 | – | 20.5 ± 2.7 | NS$^a$ | | 0.41 ± 0.07 | NS$^a$ | All
D Autumn 2004 | 22 Nov ‘04 | OP Original | – Negative ** | | 21.8 ± 1.2 | – | 0.39 ± 0.07 | 20–23
SV Survivors | 7 | – | 22.3 ± 1.8 | Larger$^c$ ** | | 0.43 ± 0.08 | Higher$^c$ ** | 20–23
E Winter 2004 | 8 Jan ’05 | OP Original | – Positive * | | 25.9 ± 1.8 | – | 0.23 ± 0.04 | 25–28
SV Survivors | 29–38$^a$ | – | 27.5 ± 1.5 | Larger$^c$ *** | | 0.26 ± 0.05 | Higher$^c$ ** | 25–28
F Spring 2005-1 | 9 Apr ’05 | OP Original | – Positive ** | | 21.0 ± 1.6 | – | 0.37 ± 0.08 | 20–22
SV-1 Survivors | 9 | – | 19.4 ± 1.6 | Smaller$^b$ *** | | 0.38 ± 0.08 | NS$^b$ | 20–22
SV-2 Survivors | 21 | – | 20.4 ± 2.2 | Smaller$^b$ * | | 0.45 ± 0.09 | Higher$^b$ *** | 20–22
SV-3 Survivors | 31 | – | 20.1 ± 2.6 | Smaller$^b$ * | | 0.49 ± 0.12 | Higher$^b$ ** | 20–22
18 Apr ’05 | SV-1 Original | – Positive *** | 22.3 ± 1.7 | – | 0.31 ± 0.05 | – | 21–23
SV-2 Survivors | 12 | – | 23.9 ± 2.2 | Larger$^c$ *** | | 0.39 ± 0.07 | Higher$^c$ *** | 21–23
SV-3 Survivors | 22 | – | 23.9 ± 2.4 | Larger$^c$ *** | | 0.42 ± 0.06 | Higher$^c$ *** | 21–23
30 Apr ’05 | SV-2 Original | – NS | 27.9 ± 2.2 | – | 0.31 ± 0.05 | – | All
SV-3 Survivors | 10 | – | 28.2 ± 2.2 | NS$^b$ | | 0.33 ± 0.07 | NS$^b$ | All
G Spring 2005-2 | 30 Apr ’05 | OP Original | – NS | | 24.6 ± 2.7 | – | 0.36 ± 0.06 | – | All
SV Survivors | 10 | – | 24.0 ± 1.8 | Smaller$^c$ * | | 0.41 ± 0.10 | Higher$^c$ *** | All
H Winter 2005 | 10 Jan ’06 | OP Original | – Positive ** | | 26.7 ± 2.2 | – | 0.28 ± 0.05 | – | All
SV Survivors | 17 | – | 26.8 ± 1.5 | NS$^b$ | | 0.26 ± 0.08 | Lower$^c$ * | All

### Notes
- **: p < 0.05
- ***: p < 0.001
- NS: Not significant
- Higher: GR for survivors is higher than original
- Lower: GR for survivors is lower than original

### SL–GR Comparison
- OP: Original period
- SV: Survivors
- SL (mm): Standard length
- Mean ± SD: Mean ± standard deviation
- GR (mm day$^{-1}$): Growth rate
Table 3. *Engraulis japonicus*. Summary of the test results of the “bigger is better”,
“growth-selective predation”, and “stage duration” mechanisms for the short-term
survival processes of multiple cohorts of anchovy larvae in Sagami Bay.

Note: “Effective” indicates that the mechanism was detected to be effective;
“Contrary” indicates that the mechanism was detected to be contrary; “NS” indicates
that the mechanism was non-significant. The test results of the “stage duration”
mechanism were available only for cohort samples B (spring 2004) and F (spring
2005-1) irrespective of pair of survivors and original populations and survival period.

*Results of Takasuka et al. (2004a) for reference; Individuals collected on 2 different
days were pooled.*
<table>
<thead>
<tr>
<th>Sample</th>
<th>Cohort</th>
<th>Season and year</th>
<th>Pair</th>
<th>Survival period (d)</th>
<th>Bigger is better</th>
<th>Growth-selective predation</th>
<th>Stage duration</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>OP SV-1</td>
<td>Autumn 2003</td>
<td>10</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>OP SV-2</td>
<td></td>
<td>20</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>–</td>
</tr>
<tr>
<td>B</td>
<td>OP SV-1</td>
<td>Spring 2004</td>
<td>12</td>
<td>Contrary</td>
<td>Effective</td>
<td>Effective</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>OP SV-2</td>
<td></td>
<td>18</td>
<td>Contrary</td>
<td>NS</td>
<td>Effective</td>
<td>–</td>
</tr>
<tr>
<td>C</td>
<td>OP SV</td>
<td>Summer 2004</td>
<td>11</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>–</td>
</tr>
<tr>
<td>D</td>
<td>OP SV</td>
<td>Autumn 2004</td>
<td>7</td>
<td>Contrary</td>
<td>Effective</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>E</td>
<td>OP SV</td>
<td>Winter 2004</td>
<td>6</td>
<td>NS</td>
<td>Contrary</td>
<td>Effective</td>
<td>–</td>
</tr>
<tr>
<td>F</td>
<td>OP SV-1</td>
<td>Spring 2005-1</td>
<td>9</td>
<td>Contrary</td>
<td>NS</td>
<td>Effective</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>OP SV-2</td>
<td></td>
<td>21</td>
<td>Contrary</td>
<td>Effective</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>OP SV-3</td>
<td></td>
<td>31</td>
<td>Contrary</td>
<td>Effective</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>SV-1 SV-2</td>
<td></td>
<td>12</td>
<td>Effective</td>
<td>Effective</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>SV-1 SV-3</td>
<td></td>
<td>22</td>
<td>Effective</td>
<td>Effective</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>SV-2 SV-3</td>
<td></td>
<td>10</td>
<td>NS</td>
<td>NS</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>G</td>
<td>OP SV</td>
<td>Spring 2005-2</td>
<td>10</td>
<td>NS</td>
<td>Effective</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>H</td>
<td>OP SV</td>
<td>Winter 2005</td>
<td>17</td>
<td>NS</td>
<td>Contrary</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>I</td>
<td>OP SV</td>
<td>Summer 2001</td>
<td>13–17</td>
<td>NS</td>
<td>Effective</td>
<td>NS</td>
<td>–</td>
</tr>
</tbody>
</table>
Figure legends

Fig. 1. Sampling area for Japanese anchovy *Engraulis japonicus* larvae in the coastal fishing ground (study site) in Sagami Bay, Japan (modified from Takasuka et al. 2004a). Schematic pattern of the current (eddy) indicated by the curved arrow.

Fig. 2. Hatching date distributions of Japanese anchovy *Engraulis japonicus* larvae collected in Sagami Bay during autumn 2003 to winter 2005 (January 2006). Date of capture, cohort sample (A–H), and sample size are indicated in each panel. The individuals whose hatching dates fell within a common range among different sampling dates within a certain period were extracted from the body samples (A–H) for comparison of growth rates (shaded areas; sample size in parenthesis; Table 1). The individuals collected on 6 and 15 Feb ’05 were pooled because of the small sample size; the individuals collected on 30 Apr and 10 May ’05 were divided into 2 cohort samples (F and G; divided by grey vertical lines) because of the broad range of hatching dates.

Fig. 3. Growth trajectories of the survivors versus the original populations of Japanese anchovy *Engraulis japonicus* larvae collected in Sagami Bay. Standard length at each daily age is arranged by calendar date (i.e. real time rather than age). Cohort samples (A–H; season and year) are indicated in each panel. Shaded areas indicate the target survival periods. Bold vertical lines indicate dates of capture. See Table 1 for detailed profiles of the survivors (SV, SV-1, SV-2, and SV-3) and the original populations (OP, SV-1, and SV-2) of the cohort samples.

Fig. 4. Growth histories of the survivors versus the original populations of Japanese...
anchovy *Engraulis japonicus* larvae collected in Sagami Bay. Daily growth rate is arranged by calendar date (i.e. real time rather than age). Cohort samples (A–H; season and year) are indicated in each panel. Shaded areas indicate the target survival periods. Bold vertical lines indicate dates of capture. See Table 1 for detailed profiles of the survivors (SV, SV-1, SV-2, and SV-3) and the original populations (OP, SV-1, and SV-2) of cohort samples.

**Fig. 5.** Relationships between standard length and 3-day mean growth rate at the start of the survival period for the survivors versus the original populations of Japanese anchovy *Engraulis japonicus* larvae collected in Sagami Bay. See Table 2 for correspondence between the survivors and the original populations. Cohort sample (A–H) and the date of the start of the survival period are indicated in each panel. A linear regression of growth rate on size is shown for the original populations when it was significant. A, 25 Nov '03, OP: $y = 0.110 + 0.010 x$ ($n = 102, r^2 = 0.050, p = 0.023$); B, 18 Apr '04, OP: $y = 0.121 + 0.015 x$ ($n = 90, r^2 = 0.160, p < 0.001$); B, 30 Apr '04, SV-1: $y = 0.096 + 0.013 x$ ($n = 104, r^2 = 0.079, p = 0.004$); D, 22 Nov '04, OP: $y = 0.706 – 0.014 x$ ($n = 148, r^2 = 0.064, p = 0.002$); E, 8 Jan '05, OP: $y = 0.104 + 0.005 x$ ($n = 101, r^2 = 0.054, p = 0.019$); F, 9 Apr '05, OP: $y = 0.089 + 0.012 x$ ($n = 108, r^2 = 0.063, p = 0.009$); F, 18 Apr '05, SV-1: $y = 0.082 + 0.010 x$ ($n = 146, r^2 = 0.108, p < 0.001$); H, 10 Jan '06, OP: $y = 0.110 + 0.006 x$ ($n = 114, r^2 = 0.088, p = 0.001$). Shaded areas indicate ranges of standard length for comparison of growth rate.

**Fig. 6.** Relationships between daily age and standard length of the metamorphosing larvae versus non-metamorphosing larvae of Japanese anchovy *Engraulis japonicus* collected in Sagami Bay in spring 2004 (cohort sample B) and spring 2005 (cohort sample F).
sample F). Shaded areas indicate ranges of daily age overlapping between the metamorphosing and non-metamorphosing larvae.

**Fig. 7.** Growth histories of the metamorphosing larvae versus non-metamorphosing larvae of Japanese anchovy *Engraulis japonicus* collected in Sagami Bay in spring 2004 (cohort sample B) and spring 2005 (cohort sample F). Daily growth rate data are arranged by daily age (i.e. development rather than real time). Cohort is indicated in each panel. Note that statistical comparisons were made by 5-day mean growth rates.
Fig. 1
Fig. 2
Fig. 2 (continued)
Fig. 3
Fig. 4
Fig. 5
Fig. 5 (continued)
Fig. 6
Fig. 7