



Predator-specific growth-selective predation on larval Japanese anchovy *Engraulis japonicus*

Akinori Takasuka^{1,*}, Ichiro Aoki², Yoshioki Oozeki¹

¹National Research Institute of Fisheries Science, Fisheries Research Agency, 2-12-4 Fukuura, Kanazawa, Yokohama, Kanagawa 236-8648, Japan

²Department of Aquatic Bioscience, Graduate School of Agricultural and Life Sciences, The University of Tokyo, 1-1-1 Yayoi, Bunkyo, Tokyo 113-8657, Japan

ABSTRACT: Predator-specific growth-selective predation on larval Japanese anchovy *Engraulis japonicus* was demonstrated by comparing growth rates between the larvae ingested by predators and the larvae from the corresponding original populations through otolith microstructure analysis, based on original data and reanalyzed data from previous studies. Ingested larvae from the stomachs of small pelagic predators (juvenile Japanese anchovy, round herring *Etrumeus teres*, jack mackerel *Trachurus japonicus* and white croaker *Pennahia argentatus*) had significantly lower growth rates than the larvae from the original populations in general. For large piscivorous predators (sea bass *Lateolabrax japonicus*, greater amberjack *Seriola dumerili* and skipjack tuna *Katsuwonus pelamis*), no measurable differences in the growth rates were observed between ingested larvae and larvae from the original populations. Small pelagic fish were therefore identified as growth-selective predators, whereas large piscivorous fish were identified as non-growth-selective predators. Exponential declines in the relative predation mortalities of larvae with higher growth rates suggest the potential for growth rate to exert a great effect on recruitment variability. However, the predator field would regulate selection for growth characteristics of survivors.

KEY WORDS: Growth-selective predation hypothesis · Growth rate · Otolith · Early life stage · Japanese anchovy · Relative predation mortality · Optimal foraging theory

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INTRODUCTION

Fish experience severe challenges to survival during their early life stages. Growth rates represent survival potential during these stages, playing a key role in survival dynamics. The paradigm that faster-growing individuals are more likely to survive has emerged through numerous studies (Meekan & Fortier 1996, Hare & Cowen 1997, Baumann et al. 2003, Takasuka et al. 2003, Takahashi & Watanabe 2004, Tanaka et al. 2006), and led to various field study designs (Shoji & Tanaka 2006, Takasuka & Aoki 2006, Robert et al. 2007, Takasuka et al. 2007), although there have been some conflicting observations (Litvak & Leggett 1992, Lankford et al. 2001, Munch & Conover 2003). Ander-

son (1988) concluded that the theory linking growth rate and mortality provides a rational framework, but that the relationship remains to be quantified. To clarify how and to what extent growth rates regulate survival, the functional mechanisms of the 'growth-survival' paradigm need to be scrutinized at finer scales (Hare & Cowen 1997, Searcy & Sponaugle 2001).

The growth-survival paradigm has been explained by size and time. The size-based concept, known as the bigger-is-better hypothesis (Miller et al. 1988), assumes survival advantages of larger somatic size of faster-growing individuals, although several studies concluded that bigger is not always better (Leggett & DeBlois 1994). The time-based idea is termed the

*Email: takasuka@affrc.go.jp

stage-duration hypothesis (Chambers & Leggett 1987, Houde 1987, 1989) and assumes that mortality rate decreases markedly with developmental stage. If a higher growth rate accelerates the timing of metamorphosis, faster-growing individuals will experience a much lower cumulative mortality rate during the larval stage. In these concepts, however, growth rates are translated into size or time and thus are indirectly linked to survival. Furthermore, no direct evidence has linked growth rate to predation, despite predation being recognized as the major source of mortality (Bailey & Houde 1989). These issues emerged because previous field tests focused solely on the characteristics of the survivors (references in Takasuka et al. 2003).

Takasuka et al. (2003) instead focused on the characteristics of larvae actually ingested by predators. Growth rates were compared between larval Japanese anchovy *Engraulis japonicus* from the stomachs of predators and the larvae from the original populations. As a consequence, the growth-selective predation hypothesis was proposed, which states that slower-growing individuals are more vulnerable to predation than their faster-growing conspecifics, even if they are of the same size. This hypothesis was also supported by the characteristics of the survivors (Takasuka et al. 2004a). However, it was suggested that the occurrence of growth-selective predation could differ among predatory species (Takasuka et al. 2003, 2004b). Predator specificity, if it exists, could markedly influence phenotypic selection and thus needs clarification if growth rates are to be used as a predictor of recruitment.

The present study shows predator-specific growth-selective predation on larval Japanese anchovy, based on original data and reanalyzed data from previous studies (Takasuka et al. 2003, 2004a,b). Through otolith microstructure analysis, growth rates and somatic sizes were compared between larvae from the stomachs of different predatory species and larvae from the original populations. Furthermore, changes in relative predation mortality with varying growth rates were estimated to quantify the potential role of growth-selective predation in survival dynamics.

MATERIALS AND METHODS

We conducted field collections of larval anchovy and predators in Sagami Bay, Japan, in 2001 and reanalyzed data from the previous studies by Takasuka et al. (2003, 2004b) (Table 1). Collection and quantitative methods from all studies were performed identically, unless otherwise noted.

Larval anchovy and their fish predators were captured simultaneously by the same tows of a commer-

cial trawl with a cod-end mesh size of 2.3 mm. The trawl was towed for 5 to 10 min several times after sunrise. Our same-tow sampling targeted dense larval shoals and predators attacking them in shallow (<10 m) areas. In Takasuka et al. (2003), sampling was conducted in Sagami Bay from 28 October to 4 November 2000 (Sample I) and on 23 November 2000 (Sample II). We added original samples collected in Sagami Bay from 1 to 9 July 2001 (Sample III), on 18 July 2001 (Sample IV) and from 6 to 8 November (Sample V) 2001. In Takasuka et al. (2004b), offshore sampling was conducted in the western North Pacific; larval and juvenile anchovy were captured by the same tow of a frame-type trawl with an 8 mm stretch mesh on 11 June 1997 (Sample VI), and larval anchovy and skipjack tuna *Katsuwonus pelamis* were captured concurrently using a neuston net with a mesh size of 0.45 mm and trolling lines, respectively, on 15 May 2000 (Sample VII). More details of sampling methods and location are described in the respective source papers.

Larval anchovy were captured simultaneously with the predators (original larvae) and were taken from the stomach contents of dissected predators (ingested larvae). Using the same-tow or concurrent sampling of larvae and predators, we assumed that the ingested larvae and original larvae originated from the same populations. The standard length (SL) of each original larva was measured directly, while that of each ingested larva was estimated from otolith sizes, except for individuals in an undigested condition. The extent of digestion of the ingested larvae was ranked as follows. Rank 1: fresh or having partial digestion of the integument; Rank 2: partial digestion of muscular tissue (< ca. 75% by sight); Rank 3: most of the muscular tissue digested.

Sagittal otoliths were extracted from both ingested larvae and original larvae. Maximum otolith radius (OR) and each daily growth increment width were measured to the nearest 0.1 μm along a measurement transect set from the nucleus to the outermost margin, with a transmitting light microscope equipped with a video camera connected to a computer and monitor. The relationships between SL and OR were expressed as allometric formulae for all samples of original larvae ($0.786 \leq r^2 \leq 0.930$, $p < 0.001$). The SL of each ingested larvae was estimated from its OR, based on the OR–SL relationships from the corresponding original larvae. This SL estimation procedure was previously validated to prevent serious biases in size and growth comparisons (Takasuka et al. 2003).

Daily growth-rate history was back-calculated at the individual level by the biological intercept method (Campana 1990, Campana & Jones 1992), based on an allometric formula determined for each larva. The SL

Table 1. *Engraulis japonicus*. Comparison of standard length (SL; mean \pm SD) and recent 5 d growth rate (GR; mean \pm SD) between larvae from stomach contents of each predatory fish species (ingested larvae) and from the original populations (original larvae). SL or fork length (FL) is indicated in parentheses for each predatory species. Numbers of individuals are indicated for predators (N), predators whose stomachs contained larvae (N'), ingested larvae in the stomachs (n), ingested larvae available for sagittal otolith microstructure analysis (n') and original larvae (n"). If the regression of growth rates on SL for the original larvae and differences in SL between the ingested larvae and original larvae were both significant, growth rates were compared within the overlapped range of SL between the 2 groups. Larger and Smaller: SL of the ingested larvae was larger/smaller than those of the original larvae; Higher and Lower: growth rates of the ingested larvae were higher/lower than those of the original larvae. Samples I and II were derived from Takasuka et al. (2003); Samples VI and VII were derived from Takasuka et al. (2004b). Samples III, IV and V represent original data described herein. *p < 0.05, **p < 0.01, ^aStudent's *t*-test, ^bWelch's *t*-test or ^cMann-Whitney's *U*-test

Sample (date of capture) Ingested larvae (by predator) or original larvae	Predator N (N')	Larvae			SL (mm) (range)	GR (mm d ⁻¹) (range)	Comparison	
		n	n'	n"			SL	GR
Sample I (28 Oct–4 Nov '00)								
Original larvae	–	–	–	120	20.3 \pm 3.3 (14.0–30.0)	0.44 \pm 0.11 (0.24–0.80)	–	–
Japanese anchovy (67–70 mm SL)	2 (2)	24	9	–	16.5 \pm 1.5 (14.8–19.5)	0.33 \pm 0.05 (0.26–0.44)	Smaller** ^b	Lower* ^a
Japanese jack mackerel (98–138 mm FL)	12 (1)	7	6	–	17.9 \pm 1.5 (15.8–19.9)	0.33 \pm 0.06 (0.24–0.40)	NS ^a	Lower* ^a
White croaker (123–128 mm SL)	2 (2)	15	13	–	21.3 \pm 2.6 (16.4–26.0)	0.37 \pm 0.06 (0.27–0.47)	NS ^a	Lower** ^b
Japanese sea bass (202–210 mm SL)	2 (2)	12	4	–	24.1 \pm 1.9 (21.4–25.7)	0.44 \pm 0.17 (0.19–0.55)	Larger** ^c	NS ^a
Sample II (23 Nov '00)								
Original larvae	–	–	–	120	21.8 \pm 1.9 (18.7–28.6)	0.33 \pm 0.07 (0.20–0.55)	–	–
Pacific round herring (134–148 mm SL)	3 (3)	60	40	–	21.6 \pm 2.3 (17.6–28.5)	0.28 \pm 0.04 (0.14–0.38)	NS ^a	Lower** ^b
Sample III (1–9 Jul '01)								
Original larvae	–	–	–	120	25.4 \pm 3.6 (15.6–33.2)	0.44 \pm 0.08 (0.27–0.74)	–	–
Japanese jack mackerel (93–167 mm FL)	15 (7)	21	16	–	25.2 \pm 5.2 (15.2–34.3)	0.39 \pm 0.08 (0.25–0.58)	NS ^b	Lower* ^a
Greater amberjack (135–199 mm FL)	2 (2)	28	15	–	25.5 \pm 2.3 (20.7–29.3)	0.41 \pm 0.07 (0.30–0.52)	NS ^a	NS ^a
Sample IV (18 Jul '01)								
Original larvae	–	–	–	120	24.7 \pm 3.5 (16.1–32.4)	0.42 \pm 0.08 (0.24–0.65)	–	–
Pacific round herring (71–86 mm SL)	5 (5)	53	30	–	19.8 \pm 2.5 (15.0–26.4)	0.42 \pm 0.08 (0.28–0.61)	Smaller** ^c	NS ^c
Japanese jack mackerel (114–198 mm FL)	4 (3)	33	27	–	23.7 \pm 3.3 (16.5–28.3)	0.39 \pm 0.08 (0.27–0.62)	NS ^a	Lower* ^a
Sample V (6–8 Nov '01)								
Original larvae	–	–	–	120	26.2 \pm 2.3 (20.4–31.4)	0.43 \pm 0.07 (0.29–0.62)	–	–
Pacific round herring (112–132 mm SL)	15 (15)	288	67	–	25.2 \pm 2.6 (19.6–32.0)	0.40 \pm 0.07 (0.28–0.59)	Smaller** ^a	Lower** ^a
Japanese jack mackerel (127–154 mm FL)	6 (3)	26	19	–	24.3 \pm 1.5 (22.0–27.0)	0.39 \pm 0.06 (0.31–0.53)	Smaller** ^a	Lower** ^a
Sample VI (11 Jun '97)								
Original larvae	–	–	–	100	18.9 \pm 3.1 (13.1–31.1)	0.57 \pm 0.12 (0.34–0.99)	–	–
Japanese anchovy (36–61 mm SL)	120 (31)	85	33	–	17.5 \pm 1.4 (13.6–20.2)	0.50 \pm 0.07 (0.38–0.63)	Smaller** ^c	Lower** ^b
Sample VII (15 May '00)								
Original larvae	–	–	–	47	22.0 \pm 3.1 (14.4–27.4)	0.48 \pm 0.08 (0.26–0.61)	–	–
Skipjack tuna (450–540 mm FL)	9 (7)	59	12	–	23.9 \pm 1.2 (22.2–26.2)	0.50 \pm 0.08 (0.35–0.64)	Larger* ^c	NS ^a
Total	197 (83)	711	291	747				

at the first ring deposition (i.e. biological intercept) was fixed at 5.6 mm. A recent 5 d mean growth rate (mm d^{-1}) directly before capture or predation was adopted as a proxy for survival potential, as recent growth rates reflect conditions that affect selective mortality (Oozeki et al. 2004, Takasuka et al. 2004b). To test size- and growth-selective predation mortalities, SL at the time of capture or predation and recent 5 d mean growth rates were compared between the ingested larvae and corresponding original larvae by Student's *t*-test, Welch's *t*-test or Mann-Whitney's *U*-test, depending on the results of tests of normality and homogeneity for each pair. If growth rates are related to somatic sizes, including the overall size range could lead to biases in growth comparisons under any significant size-selective predation. When growth rates were significantly related to SL for the original larvae and SL differed significantly between ingested and original larvae, we compared the growth rates of the original and ingested larvae whose SL range overlapped to reduce a possibility of such biases and discriminate size- and growth-selections.

The intensities of selection for size or growth rate were quantified by comparing the relative frequency distributions of estimated size or growth rate between the survivors and the original population (i.e. survival ratio) (Healey 1982, Hovenkamp 1992, Meekan & Fortier 1996). Since the present study focused on the characteristics of ingested larvae versus original larvae, we calculated the predation mortality ratio (PMR) as a proxy for relative predation mortality: $\text{PMR} = F_{\text{ingested}}/F_{\text{original}}$, where F_{ingested} and F_{original} are relative frequencies of each class of recent 5 d mean growth rate (interval: 0.05 mm d^{-1}) for the ingested larvae and original larvae, respectively.

RESULTS

Pacific round herring *Etrumeus teres*, Japanese jack mackerel *Trachurus japonicus*, white croaker *Argyrosomus argentatus*, Japanese sea bass *Lateolabrax japonicus*, greater amberjack *Seriola dumerili* and skipjack tuna *Katsuwonus pelamis* were found to be predators of larval anchovy (Table 1). Furthermore, juvenile Japanese anchovy also preyed on larvae of their own species. A total of 711 larval anchovy were collected from the stomach contents of 83 (of 197) individual predators; sagittal otoliths of 291 larvae were available for analysis. SL was estimated for 255 ingested larvae and directly measured for the remaining 36 ingested larvae. The ingested larvae were digested to varying degrees. For the 3 original samples (Samples III, IV and V), the ingested larvae with otoliths available were classified into Rank 1 ($n = 21$),

Rank 2 ($n = 104$) and Rank 3 ($n = 49$). No significant differences were found in growth rates among digestion ranks (where sample sizes allowed comparison), at least within each sample or within the ingested larvae from round herring of Sample V (ANOVA, $p > 0.05$). As such, we pooled the ingested larvae within each sample regardless of the extent of digestion.

The ingested larvae were compared with their corresponding original larvae in terms of SL for each predatory species (Table 1). The SL of the ingested larvae was significantly smaller than the original larvae for juvenile anchovy (Samples I and VI), round herring (Samples IV and V) and Japanese jack mackerel (Sample V). By contrast, the ingested larvae from the stomachs of sea bass and skipjack tuna had larger SL than the original larvae (Samples I and VII). No significant differences were found between ingested larvae and original larvae for round herring from Sample II, jack mackerel from Samples I, III and IV, white croaker from Sample I and greater amberjack from Sample III.

Recent 5 d mean growth rates were positively related with SL for the original larvae from Samples I, II, VI and VII (Fig. 1; linear regression analysis, $0.066 \leq r^2 \leq 0.295$, $p < 0.01$), but this was not the case with the original larvae from Samples III, IV and V ($0.001 \leq r^2 \leq 0.014$, $p > 0.05$). Thus, the original larvae whose SL range overlapped with the SL of the ingested larvae were used for growth comparisons for anchovy and sea bass from Sample I, juvenile anchovy from Sample VI and skipjack tuna from Sample VII. For Samples III, IV and V, size ranges were not considered in growth comparisons, even when SL differed between ingested larvae and original larvae.

The growth rates of the ingested larvae were generally lower than those of their corresponding original larvae when compared at the same SL (Fig. 1). Such same-size differences in growth rates were particularly evident for larvae with SL > 20 to 25 mm. The growth rates of the ingested larvae from juvenile anchovy (Samples I and VI), round herring (Samples II and V), jack mackerel (Samples I, III, IV and V) and white croaker (Sample I) were significantly lower than those of the corresponding original larvae ($p < 0.05$) (Table 1). No differences were found for the ingested larvae from round herring from Sample IV. There were also no significant differences in growth rates between ingested larvae and original larvae for sea bass (Sample I), greater amberjack (Sample III) and skipjack tuna (Sample VII) ($p > 0.05$).

PMR was calculated for the predatory species that exhibited significant growth-selective predation. In general, PMR declined exponentially with growth rate (Fig. 2). Based on the exponential functions fitted to the PMR versus growth rate, the decline in growth rates

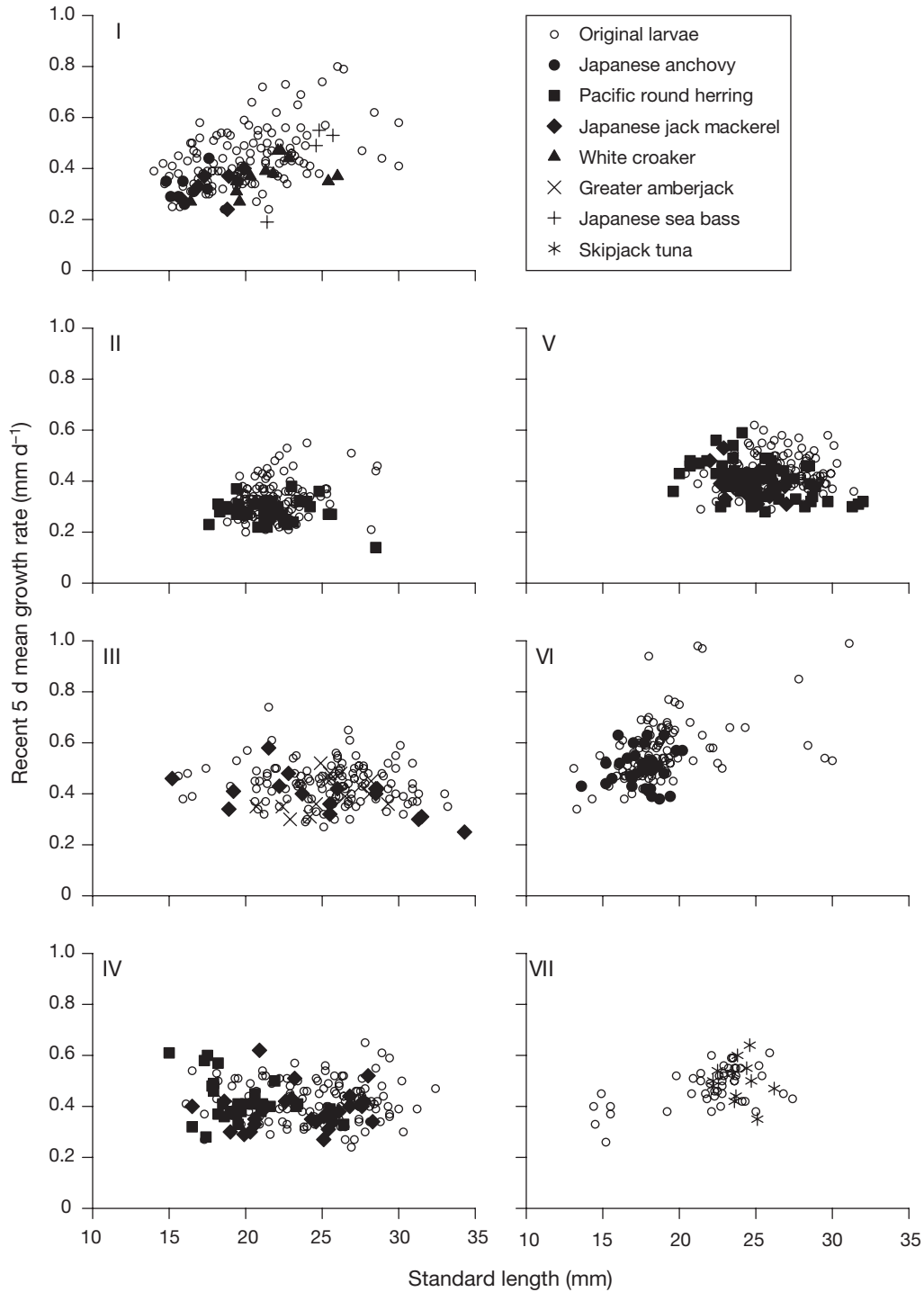


Fig. 1. *Engraulis japonicus*. Recent 5 d mean growth rate on standard length compared between original larvae and ingested larvae (represented by predatory species and original larvae). Sample profiles are summarized in Table 1

from 0.50 to 0.30 mm d⁻¹ corresponded to an increase in PMR from 0.21 to 3.43 for juvenile anchovy, jack mackerel and white croaker from Sample I, from 0.38 to 2.24 for jack mackerel from Sample IV and from 0.50 to 2.49 for round herring and jack mackerel from

Sample V. Similarly, as growth rates decreased from 0.40 to 0.20 mm d⁻¹ and from 0.70 to 0.40 mm d⁻¹, the PMR increased from 0.33 to 3.03 and from 0.33 to 2.28 for round herring from Sample II and juvenile anchovy from Sample VI, respectively.

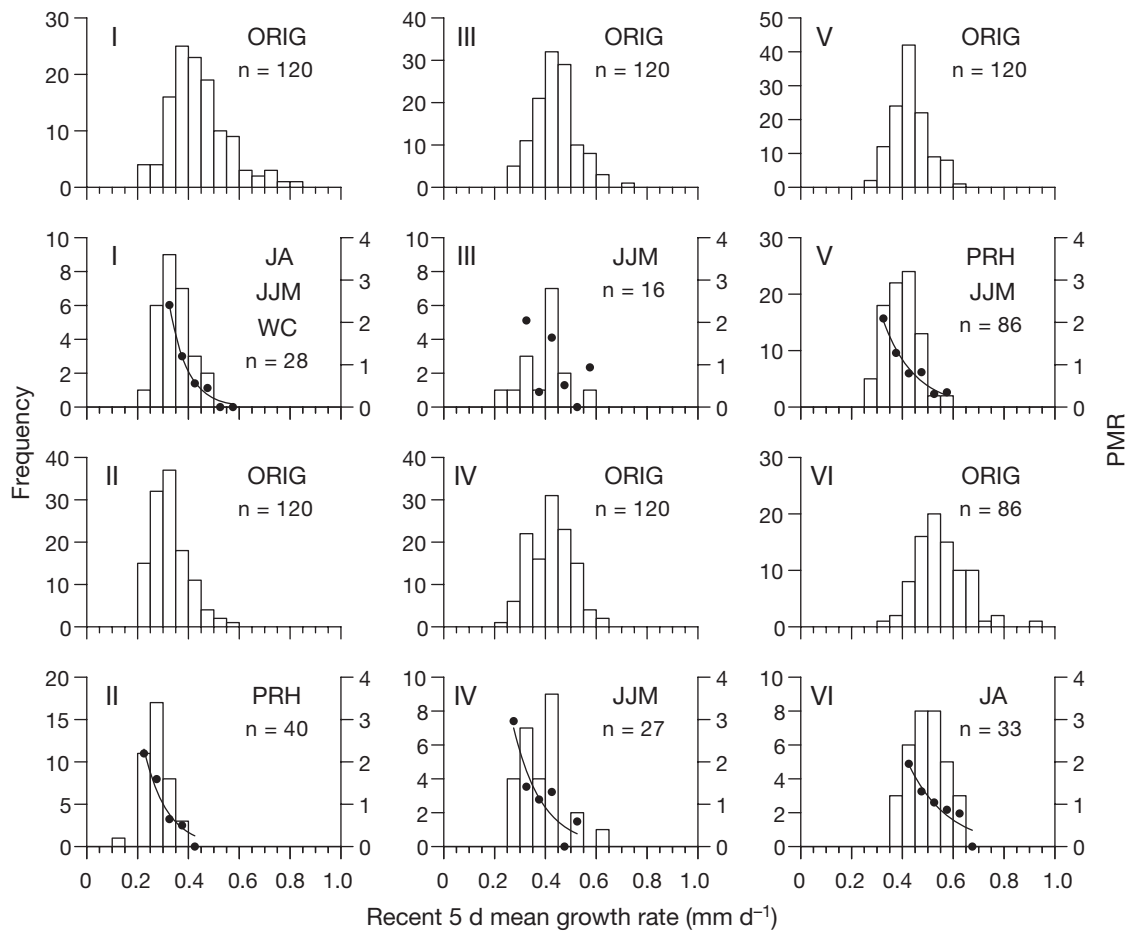


Fig. 2. *Engraulis japonicus*. Frequency distributions of recent 5 d mean growth rate compared between ingested larvae and original larvae in conjunction with predation mortality ratios (PMR) of the ingested larvae. Sample profiles are summarized in Table 1. ORIG: original larvae; JA, PRH, JJM and WC: ingested larvae from the stomachs of Japanese anchovy, Pacific round herring, Japanese jack mackerel and white croaker, respectively. Ingested larvae from different predatory species were pooled for Samples I and V. Functions of single exponential decay were fitted to the PRM values (but the infinities and the values at growth rate class with relative frequency of <0.05 for the original larvae were excluded). Sample I: $y = 234.5e^{-14.1x}$ ($r^2 = 0.988$, $p < 0.001$); Sample II: $y = 27.4e^{-11.0x}$ ($r^2 = 0.948$, $p = 0.013$); Sample III: not significant ($r^2 = 0.346$, $p = 0.244$); Sample IV: $y = 32.4e^{-8.9x}$ ($r^2 = 0.842$, $p = 0.021$); Sample V: $y = 27.6e^{-8.0x}$ ($r^2 = 0.962$, $p = 0.001$); Sample VI: $y = 30.3e^{-6.5x}$ ($r^2 = 0.884$, $p = 0.010$)

DISCUSSION

Size-selective predation on larval anchovy and its direction depended on predatory species. Size-selection favored larger larvae for juvenile anchovy, round herring and jack mackerel, and favored smaller larvae for sea bass and skipjack tuna—although in some samples, round herring and jack mackerel showed no size-selection. For the bigger-is-better mechanism to come into effect in the growth–survival paradigm, the assumption of a positive relationship between growth rate and somatic size must be satisfied. If all individuals hatched on the same date, this would be the case. However, in natural populations the individuals of different sizes, ages and growth rates are mixed. No clear relationship between growth rates and sizes was ob-

served for 3 of 7 original populations of larval anchovy, indicating that even if size-selection favors larger larvae, it does not always follow that faster-growing larvae have enhanced survivorship.

Predator-specific growth-selective predation was demonstrated through snapshots of prey–predator interactions between larval anchovy and various fish predators in field conditions. Slower-growing larvae were more vulnerable to predation than faster-growing conspecifics when they were attacked by juvenile anchovy, round herring, jack mackerel and white croaker. This growth-selective predation was observed for larvae of the same size and thus was independent of somatic size and stage duration. The link between growth rate and predation could be mediated by physiological condition and the ability for anti-predator

behaviors (Takasuka et al. 2003). In general, larval behavior is closely related to predation vulnerability (Fuiman & Magurran 1994, Fuiman et al. 2005). Physiological conditions can affect responses to predator attacks, escape activities (Chick & Van Den Avyle 2000, Gorud-Colvert & Sponaugle 2006) and positions in larval shoals (Skajaa et al. 2003). The characteristics-of-survivors approach also has indicated selective removal of individuals with poorer physiological conditions (Searcy & Sponaugle 2001, Hoey & McCormick 2004). Slower-growing larvae would have lower potential for anti-predator behaviors and may tend to be isolated from shoals, owing to deteriorated conditions. This inference also explains the possible shifts from random to growth-selective predation mortalities with larval size, since variation in the ability for anti-predator behaviors would increase as larvae develop (Skajaa et al. 2003).

Differences in predation mortality among different predator species or types have been shown in experimental studies (Bailey & Houde 1989, Chick & Van Den Avyle 2000); however, direct evidence has rarely been obtained in field conditions. The present study revealed that the presence of growth-selective predation on larval anchovy depended on predatory species. In general, juvenile anchovy, round herring, jack mackerel and white croaker ingested slower-growing larvae selectively and were therefore identified as growth-selective predators. In contrast, sea bass, greater amberjack and skipjack tuna ingested larvae almost randomly and were therefore identified as non-growth-selective predators. A distinction between these 2 predator groups lies in their sizes and, perhaps, feeding strategies. The growth-selective predators in this study comprise relatively small pelagic species whose stomachs contained zooplankton such as copepods as alternative prey (data not shown). In contrast, non-growth-selective predators comprise relatively large piscivorous predatory species whose stomachs contained almost exclusively fish larvae and juveniles. Probably because of the different attack performance of predators, faster-growing larvae may be able to escape from small pelagic predator attacks, but not from large piscivorous predators. However, future studies may need to clarify the more dynamic aspects of prey–predator interactions, as the size and feeding ecology of predators shift.

Both the size- and growth-selective predation mechanisms have a similar causal background, since size-selective mortality is also related to larval activity (Miller et al. 1988). Why do small pelagic predators nonetheless often select for growth rate rather than size? This could be theoretically addressed from the viewpoint of the optimal foraging theory with regard to of predators (Takasuka et al. 2003). The smaller the

larva a predator selects, the more easily the predator is able to capture the larva, but the gain of energy is less, since energy provided by the larva is an exponential function of larval size (Fig. 3: solid curves). In size-selective predation, net profitability for predators will approximate a dome-shaped function of larval size. However, by selecting a larva with a lower growth rate (irrespective of size), a predator minimizes its energy loss because the larva is easier to capture (due to its presumably poorer physiological condition) than a faster-growing larva of comparable size. In growth-selective predation, net profitability for predators will therefore be a monotone decreasing function of larval growth rate. Although the relative importance of size and growth rate has yet to be quantified, growth selection was more consistent than size selection within the size and growth ranges of the targeted populations. In reality, a predator does not consciously select a slower-growing larva; rather it incidentally ingests a slower-growing larva as a consequence of larval behaviors. However, the mechanism is rational for small pelagic predators. In contrast, large piscivorous predators

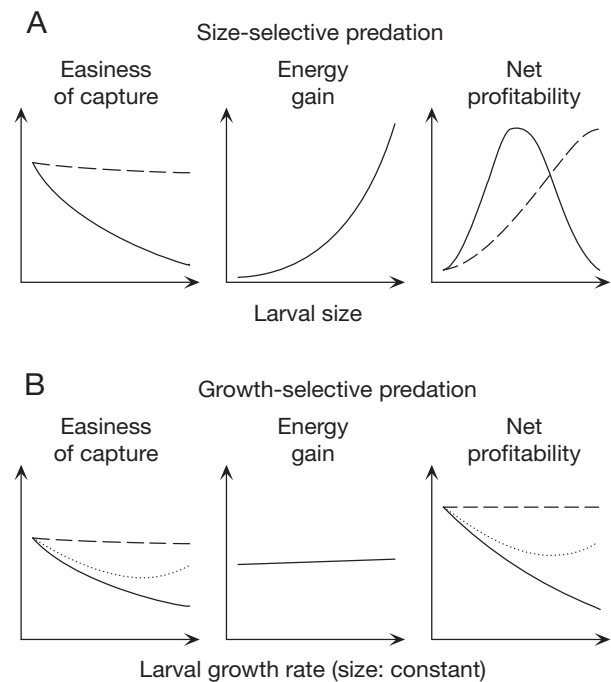


Fig. 3. *Engraulis japonicus*. Conceptual curves of fitness for predators based on the optimal foraging theory in (A) size-selective predation (only larval size considered) and (B) growth-selective predation (larval growth rate at the same size is considered). Solid and dashed curves indicate small pelagic predators and large piscivorous predators, respectively, from the present findings for the target populations of larval anchovy; dotted curves indicate an example of other possible patterns deduced from literature. Note that axes are not to be compared quantitatively within a panel or among panels

would not benefit from easiness of capture of a smaller or slower-growing larva because of their higher attack abilities, leading to non-growth-selection and, maybe, positive size-selection (Fig. 3: dashed curves). Note that predation vulnerability may become more complex if growth rates affect an encounter rate with predators (Bailey & Houde 1989). Also, if maximized growth rate increases predation susceptibility under an energy and growth trade-off against investment in anti-predator performance (Lankford et al. 2001, Munch & Conover 2003), the net profitability for small pelagic predators may deviate from a monotone decrease with growth rate (Fig. 3: dotted curves). In any case, the present field tests did not detect any disadvantage to faster-growing larvae.

At present, the stage-duration theory is most compelling to explain the effect of growth rate on survival probability. Houde (1987) showed that a more than 100-fold fluctuation in survival probabilities could result through cumulative effects of stage duration. In theory, the growth-selective predation mechanism is independent of and synergistic with size- and time-based mechanisms (Takasuka et al. 2003). The observed changes in PMR values with larval growth rates for the growth-selective predators showed that even subtle growth variations could lead to considerable fluctuations in relative predation mortality even through instantaneous events. Every encounter with a growth-selective predator will elevate mortality risk for slower-growing larvae. As such, growth-selective predation would serve as an amplifier in growth-survival processes during the early life stages in a predator field dominated by growth-selective predators; yet it would be less relevant in a predator field dominated by non-growth-selective predators. Growth rates potentially exert a far greater impact on recruitment variability through synergistic effects of multiple mechanisms than previously expected. However, the predator field would strongly regulate selection for growth characteristics of survivors, and serve as a key factor toward predicting the recruitment dynamics under the framework of the growth-survival paradigm.

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Editorial responsibility: Jon Hare (Contributing Editor), Narragansett, Rhode Island, USA

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