

Evidence of growth-selective predation on larval Japanese anchovy *Engraulis japonicus* in Sagami Bay

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ABSTRACT: Growth-selective predation mortality was demonstrated for postlarval Japanese anchovy *Engraulis japonicus* in field research. The larval anchovy and their predatory fish were simultaneously captured by a trawl in Sagami Bay during October to November 2000. The growth rates analyzed by otolith microstructure were compared between the larvae from the stomach contents of the predators (prey larvae) and those from the population of origin (surviving larvae). The mean growth rates of the prey larvae collected on 28 October and 2 to 4 November (mean \pm SD: 0.57 ± 0.07 mm d⁻¹) and on 23 November (0.50 ± 0.06 mm d⁻¹) were significantly lower than those of the corresponding surviving larvae (0.63 ± 0.07 and 0.54 ± 0.06 mm d⁻¹, respectively). Such significant differences were not explained by size-selective predation, but were due to variations in the mean growth rates at the same larval size (i.e. non-size-related). The mean growth rates of the prey larvae were different among predatory species (barracuda *Sphyraena pinguis*, Japanese sea bass *Lateolabrax japonicus*, white croaker *Pennahia argentatus*, Japanese jack mackerel *Trachurus japonicus*, Pacific round herring *Etrumeus teres* and juvenile anchovy). Comparisons of back-calculated daily growth rates showed that the decrease in growth rates of the prey larvae were consistent from directly after hatching up to predation. The larvae with lower growth rates were more vulnerable to predation, owing to the cumulative decline in growth rates from hatching to each encounter with predators, compared to the larvae with higher growth rates, even if they were the same size, at a given moment in the sea. Therefore, the level of growth rates itself had direct impact on vulnerability to predation for larval anchovy, independently of both size (size-selective mortality) and time (stage duration). In addition, such impacts could be predator specific. We propose the 'growth-selective predation' hypothesis (mechanism), which is theoretically independent of and synergistic with the existing hypotheses based on size and time under the general 'growth-mortality' concept for the survival process during the early life history of marine pelagic fish.

KEY WORDS: Growth rate · Vulnerability to predation · Otolith microstructure analysis · Larvae · Japanese anchovy · Sagami Bay · Growth-selective predation

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INTRODUCTION

Pelagic fish have high mortality during early life history stages in general. This high mortality is attributed to predation, starvation, physical transport and sublethal factors, although the relative roles of these as determinants of recruitment remain unresolved (Anderson 1988, Bailey & Houde 1989, Leggett & DeBlois 1994). To better understand the mechanisms

underlying the population fluctuations of pelagic fish, both biotic and abiotic factors have been examined and subsequently, a variety of hypotheses have been proposed. The relationship between growth rate and survival has been a focal point, as small variations in growth rates during early life history stages could lead to dramatic fluctuations in recruitment (Houde 1987, 1989). Consequently, many studies have suggested that lower growth rates during the larval and juvenile

stages could result in higher mortality (Healey 1982, Post & Prankevicus 1987, West & Larkin 1987, Miller et al. 1988, Hovenkamp 1992, Rice et al. 1993, Campana 1996, Meekan & Fortier 1996, Wilson & Meekan 2002). A paradigm emerged that larger and/or faster growing individuals will survive better.

The 'growth-mortality' hypothesis (Anderson 1988) has been particularly used to explain recruitment dynamics. Hare & Cowen (1997) grouped 3 functional mechanisms (hypotheses)—'bigger is better', 'growth rate' and 'stage duration'—into this general concept. In the 'bigger is better' hypothesis, it was postulated that larger individuals are less vulnerable to mortality than smaller individuals and that at a given age will have a higher probability of survival (see Miller et al. 1988). Although there is evidence that larger individuals have experienced higher mortality (Fuiman 1989, Litvak & Leggett 1992, Pepin et al. 1992, Leggett & DeBlois 1994, Gleason & Bengtson 1996a,b), the theory could be correct under certain conditions, such as strongly negative size selection by predators and the declining number of potential predators as prey size increases. Similarly, the 'growth rate' concept is also based on the assumption that mortality is negatively size dependent (Hare & Cowen 1997). If so, faster growing larvae should experience shorter high mortality periods (Ware 1975, Shepherd & Cushing 1980). The idea focusing on age at metamorphosis is the 'stage duration', in which faster growing larvae are considered to have a higher probability of survival by means of shortening the high mortality larval stage and developing into the juvenile stage faster (Chambers & Leggett 1987, Houde 1987).

Within certain limitations, these hypotheses serve to explain the growth-survival relationship. However, they are based on 2 theories: size (negative size-dependent mortality) and time (stage duration). Size is an outcome of growth, and mortality due to protracted stage duration (time) is dependent on integrated cumulative probabilities of lethal events throughout high mortality stages. Therefore, the relationship between growth and survival remains indirect, at least from 2 viewpoints; firstly that the existence of non-size-related effects has rarely been considered, nor incorporated into the theoretical framework; secondly, that what is happening at a given moment in the sea is always speculative.

In the early studies, mortality due to starvation linked with food supply and feeding success was regarded as the determinant of recruitment success according to the 'critical period' (Hjort 1914), 'match-mismatch' (Cushing 1975, 1990) and 'ocean stability' (Lasker 1975, 1978) hypotheses. Recent studies, however, have not conclusively linked starvation with year-class strength (Anderson 1988, Leggett & DeBlois 1994). Alternatively, predation pressure has been indicated as the primary and direct source of mortality for larval and juvenile

stages (Bailey & Houde 1989), although starvation and predation are not exclusive, rather interactive factors as many authors have noted (e.g. Cushing 1990, 1995, Leggett & DeBlois 1994). In accordance with this, predation has also been regarded as the major cause of mortality in the 'growth-mortality' hypothesis, although this integrates the processes of food supply and predation in the theory (Anderson 1988). Nonetheless, no evidence has yet been obtained to support the predation part of the 'growth-mortality' hypothesis in field conditions. Is a slower growing individual actually removed by predation in the sea?

Most previous studies on vulnerability to predation were conducted under laboratory and enclosure conditions, partly because the direct study of predation at sea is difficult. For example, the rapid digestion of prey fish and the patchy distributions of various predators contribute to this difficulty (Anderson 1988). Moreover, prey-predator interactions in the limited space of tanks and enclosures are not always applicable to the natural population in field conditions (Heath 1992). Even in a mesocosm study, poor ecological realism was reported (Kraufvelin 1999). Thus, *in situ* demonstrations are desirable in the real field.

Sagami Bay, Japan, is one of the biggest fishing grounds for Japanese anchovy *Engraulis japonicus* post-larvae 'shirasu'. Anchovy females spawn throughout the year, the main spawning season being from March to October. The eggs are transported by the Kuroshio Countercurrent and then become concentrated at the front formed by river runoff (Lindsay et al. 1998). The larvae then enter the coastal fishing ground to be the target of 'shirasu' fisheries (Mitani 1988). Some potentially predatory species are incidentally caught by commercial 'shirasu' trawl, indicating that those species forage larval anchovy, which consequently would suffer predation mortality. This situation appeared to satisfy our requirements for a field study on predation mortality of larval anchovy in relation to growth rates.

In the present study, we directly examined the growth rates of the larval Japanese anchovy from the stomach contents of their predatory fish by otolith microstructure analysis, and compared their growth rates with those of larvae from the population of origin, simultaneously captured in Sagami Bay. The principal aim was to demonstrate the existence of growth-selective predation mortality for larval anchovy in field conditions. This included testing the hypothesis that slower growing larvae are more vulnerable to predation mortality at a given moment in the field, and comparing larvae of the same size to investigate the existence of non-size-related mortality, regardless of size selection by predators. In addition, daily growth rates were back-calculated and the period and stages responsible for the differences in growth rates examined.

MATERIALS AND METHODS

Field sampling. Japanese anchovy postlarvae and their potentially predatory fish were simultaneously captured by the same tows of a commercial 'shirasu' trawl with a mesh size (cod end) of 2.3 mm in Sagami Bay during October and November 2000. The net was towed for 5 to 10 min several times in the first few hours after sunrise, at an approximate depth of 10 m maximum, targeting postlarvae foraging just above the seabed during the daytime (Mitani 1988). The larval anchovy, which were randomly selected from the daily catch, and all the potentially predatory fish were immediately frozen at -20°C .

Larvae from the stomach contents of their predatory fish. After the standard length (SL) or fork length (FL) of each predatory fish was measured to the nearest 0.1 mm, the stomach was dissected and then weighted to the nearest 0.01 g. The stomach contents were examined under a binocular microscope and sorted for larval anchovy, which were then weighted to the nearest 0.01 g in pool per stomach. The percent contribution of anchovy larvae to the whole stomach by wet weight (anchovy weight contribution, AWC) was calculated for each predatory fish.

Concurrently with dissection, the positions of the larvae in the stomachs were classified into front, middle and back parts of the stomach (F, M and B, respectively). The larvae were ranked, from A to F, according to the extent of digestion, as follows. A: considered to be in fresh condition; B: integument has been digested; C: a portion of muscular tissue has been digested; D: more than half of the muscular tissue has been digested; E: almost all of the muscular tissue has been digested; F: only a set of vertebrae or eyeballs remain. Then, SLs of the larvae were measured, where possible.

The larvae dissected from the stomach contents of their predators must be the larvae actually ingested by the predators (prey larvae). The larvae captured simultaneously with the predators were regarded as the temporarily surviving larvae from the population of origin (surviving larvae) for comparison.

Growth rates by otolith microstructure analysis. After SL measurements had been made to the nearest 0.1 mm, sagittal otoliths were dissected from individual larvae under a binocular microscope. The otoliths were mounted on a slide glass with euparal for subsequent growth analysis. Either the left or right otolith was used for analysis assuming they were symmetrical (Wang & Tzeng 1999). For a series of otolith measurements, the otolith measurement system (Ratoc System Engineering) was used, which was composed of a transmitted light microscope and video camera connected to a monitor and computer. Along a measurement transect set from the nucleus to the outermost margin, maximum otolith

radius (OR) and each daily growth increment width were measured to the nearest 0.1 μm . Tsuji & Aoyama (1984) reported that Japanese anchovy completed yolk absorption at 2 to 3 d after hatching, and that the first daily growth increment was deposited at the start of external feeding (3 to 4 d) at a temperature of 20°C . Therefore, daily ages were determined as the number of daily growth increments plus 3. Hatching dates were calculated from the daily ages and dates of capture. SLs of 2.9 mm at hatching (Fukuhara & Takao 1988) and 5.6 mm at completion of yolk absorption (Fukuhara 1983) were adopted. Then, individual mean growth rates from hatching to capture or predation were calculated by dividing SL minus 2.9 by the daily ages (Aoki & Miyashita 2000). SL and daily growth rate at each daily age were back-calculated for individual larvae by the biological intercept method (Campana 1990, Campana & Jones 1992, Watanabe & Kuroki 1997) with SL at the first ring deposition fixed at 5.6 mm, after determining an allometric relationship between OR and SL for each larva (see 'Results'). Otolith preparation, measurements and growth analyses were conducted in the same way for the prey larvae and surviving larvae.

SL restoration for prey larvae. SL measurement of the semi-digested larvae in the stomachs was often impossible to carry out, or unreliable. In such cases, SLs were restored from measured OR data by using the OR-SL relationship of the larvae from the population of origin. The SL restoration could, however, lead to bias due to its monistic restoration process, if somatic growth rates affected the OR-SL relationship (see 'Discussion'). To examine the effects of growth rates on the OR-SL relationship, the surviving larvae were classified into 3 groups according to the level of mean growth rates (Group H: high-order one-third; Group M: middle-order one-third; Group L: low-order one-third). Then, an analysis of covariance (ANCOVA) was applied to test the effects of groups on ln-transformed SL with ln-transformed OR as a covariate. For additional validation, SL restoration was also applied to the prey larvae with measured SLs available and then restored estimates were compared with actual measurements by a Student's *t*-test.

Comparative analysis. The mean growth rates from hatching to capture or predation, the 5 d mean growth rates (mean growth rates every 5 d), and the recent mean growth rates from 3, 7 and 14 d before capture or predation were compared between the prey larvae and surviving larvae by means of a Student's *t*-test. SLs were also compared between them with a Student's *t*-test, and size selectivity of the predators was described to examine whether the differences in growth rates were due to size-selective predation or not. To examine the differences in the mean growth rates among positions and digestion ranks of the larvae in the stom-

achs and among predatory species, a 1-way analysis of variance (ANOVA) was used. An ANCOVA was applied for ln SLs using ln OR as a covariate, in order to find out the differences in OR-SL relationships. Comparisons of the mean growth rates at the same size between the prey larvae and surviving larvae were also conducted by ANCOVA, with SL as a covariate.

RESULTS

Predatory fish and prey larvae

In total, the stomach contents of 8 potentially predatory species and 65 fish were examined (Table 1). A total of 337 larvae were dissected from 7 species and 35 individuals (Table 2). Although the number of larvae and the value of AWC (%) varied to some extent, larval anchovy were the predominant component of the stomach contents of these predatory fish and were considered to constitute a major energy source for them. Sagittal otoliths were obtained from 155 larvae in total. SLs of 72 larvae were measured for growth analysis; SLs of the remaining 83 larvae were restored from measured OR data prior to growth analysis.

Hatching date distribution

According to dates of capture and hatching date distributions, the prey larvae and surviving larvae were divided into 3 and 2 groups (P_0 , P_1 , P_2 and S_1 , S_2 , respectively) (Fig. 1). The prey larvae collected on 4 and 5 October were pooled into P_0 . P_1 was the prey larvae on 28 October and 2 to 4 November. The surviving larvae captured on 28 October and 3 November were pooled

into S_1 , which corresponded to P_1 . The prey larvae P_2 and its corresponding surviving larvae S_2 were collected on the same day, 23 November. The peak of S_1 hatching dates was early in October, while that of S_2 was after the middle of October. The bulk of the P_0 hatching dates were not included in the range of S_1 , and the mean hatching date of P_0 was ca. 1 mo before that of S_1 .

Positions and digestion ranks in the stomachs

The number of larvae was not highly partial both among the positions (Table 3) and digestion ranks except for the relative rarity of digestion rank A (Table 4). There were no significant differences in the mean growth rates of the prey larvae among the positions in the stomachs (ANOVA, $p > 0.05$). Comparisons among the digestion ranks (A–B, C–D and E–F) also showed no significant differences (ANOVA, $p > 0.05$) except slightly lower growth rates of A–B larvae for P_0 ($0.01 < p < 0.05$).

SL restoration for prey larvae

An allometric formula was well fitted for the relationship between OR and SL of the surviving larvae. Since the slopes of ln SL against ln OR were different between S_1 and S_2 ($p < 0.001$), the OR-SL relationship of the corresponding surviving larvae was used separately for restoration of SL of the prey larvae (Fig. 2). The formula obtained from S_1 was also used for SL restoration for P_0 , which had no corresponding surviving larvae, as a matter of convenience.

Application of ANCOVAs showed significant differences in ln SL among the 3 groups (H, M and L)

Table 1. Samples and date of capture of larvae and their potentially predatory species collected in Sagami Bay during October to November 2000

Fish species	Date of capture (2000)								Total
	4 Oct	5 Oct	28 Oct	2 Nov	3 Nov	4 Nov	9 Nov	23 Nov	
Larvae									
<i>Engraulis japonicus</i> ^a			60		60			120	240
Predator									
<i>Sphyraena pinguis</i>	5	2	1	1	2			3	14
<i>Lateolabrax japonicus</i>	1					2			3
<i>Pennahia argentatus</i>	4					2			6
<i>Trachurus japonicus</i>	17	2		7	4	1			31
<i>Etrumeus teres</i>			3					3	6
<i>Sillago japonica</i>		1							1
<i>Chelidonichthys spinosus</i>					1		1		2
<i>Engraulis japonicus</i> ^b			2						2
Total for predator	27	5	6	8	7	5	1	6	65

^aLarvae collected from the population of origin

^bJuveniles dissected from the stomach contents of *S. pinguis*; only individuals showing cannibalism

Table 2. Stomach content analysis of the different predatory species. n: number of predators examined; n': number of predators preying on larvae; length: fork length for *Trachurus japonicus* and standard length for the other species; AWC: anchovy weight contribution to the whole stomach of predator. Range and mean data calculated for all individuals examined (n); AWC and number in the stomachs also included data for juveniles as stage distinction for the prey individuals proved difficult

Predatory fish species	n	n'	Length (mm)		AWC (%)		Number of larvae in the stomachs			Otolith analyzed
			Range	Mean	Range	Mean	Range	Mean	Total	
<i>Sphyraena pinguis</i>	14	9	155.1–255.5	202.2	0–94.5	29.8	0–28	5.7	80	17
<i>Lateolabrax japonicus</i>	3	3	179.7–209.7	197.1	5.8–52.5	24.8	3–43	18.3	55	27
<i>Pennahia argentatus</i>	6	4	115.1–128.2	120.7	0–50.0	24.2	0–12	3.3	20	18
<i>Trachurus japonicus</i>	31	13	89.7–137.6	113.8	0–72.7	17.6	0–27	3.1	96	44
<i>Etrumeus teres</i>	6	3	119.3–147.5	134.1	0–31.7	12.5	0–30	10.0	60	40
<i>Sillago japonica</i>	1	1	–	158.0	–	30.5	–	2.0	2	0
<i>Chelidonichthys spinosus</i>	2	0	199.7–203.4	201.6	–	0.0	–	0.0	0	0
<i>Engraulis japonicus</i> ^a	2	2	67.4–69.5	68.5	–	45.5	11–13	12.0	24	9
Total	65	35							337	155

^aJuveniles dissected from the stomach contents of *S. pinguis*; only individuals showing cannibalism

divided by the level of mean growth rates, with ln OR as a covariate (Fig. 3). The lowest growth group had larger otoliths than the other 2 groups for S_1 ($p < 0.01$), and the highest growth group had smaller otoliths than the others for S_2 ($p < 0.05$). Comparison between estimates and measurements revealed that SLs restored from OR data were not significantly different from measured SLs for the prey larvae with actual measurements available (Student's t -test, $p > 0.05$; $n = 72$).

Comparison of growth rates and SLs between prey larvae and surviving larvae

Frequency distributions of the mean growth rates of the prey larvae (P_0 , P_1 and P_2) and surviving larvae (S_1 and S_2) are shown in Fig. 4. The mean growth rates were 0.57 ± 0.07 (mean \pm SD) mm d^{-1} for P_1 and 0.50 ± 0.06 mm d^{-1} for P_2 , which were significantly lower than 0.63 ± 0.07 mm d^{-1} for S_1 and 0.54 ± 0.06 mm d^{-1} for S_2 , respectively (Student's t -test, $p < 0.001$), although there were no significant differences between P_0 (0.64 ± 0.08 mm d^{-1}) and S_1 ($p > 0.05$). As was the case in OR-SL relationships (Fig. 2), there were significant differences in the mean growth rates between the 2 surviving samples ($p < 0.001$); S_2 had considerably lower growth rates.

On the other hand, no significant differences in the larval SLs were found between P_1 and S_1 (19.6 ± 3.3 and 20.3 ± 3.3 mm, respectively; Student's t -test, $p > 0.05$), or between P_2 and S_2 (21.9 ± 2.6 and 21.7 ± 1.9 mm, respectively; $p > 0.05$) as shown in Fig. 5 (prey juvenile anchovy > 40 mm SL were excluded from comparisons). However, the sizes of the prey larvae differed slightly among predatory species. Although most of the prey larvae were in the size range of the surviving larvae (14 to 30 mm SL), barracuda *Sphyraena pinguis* and Japanese sea bass *Lateolabrax japonicus* tended to prey on larvae across a wider range of SL, and are capable of capturing larger larvae than the other species. The bar-

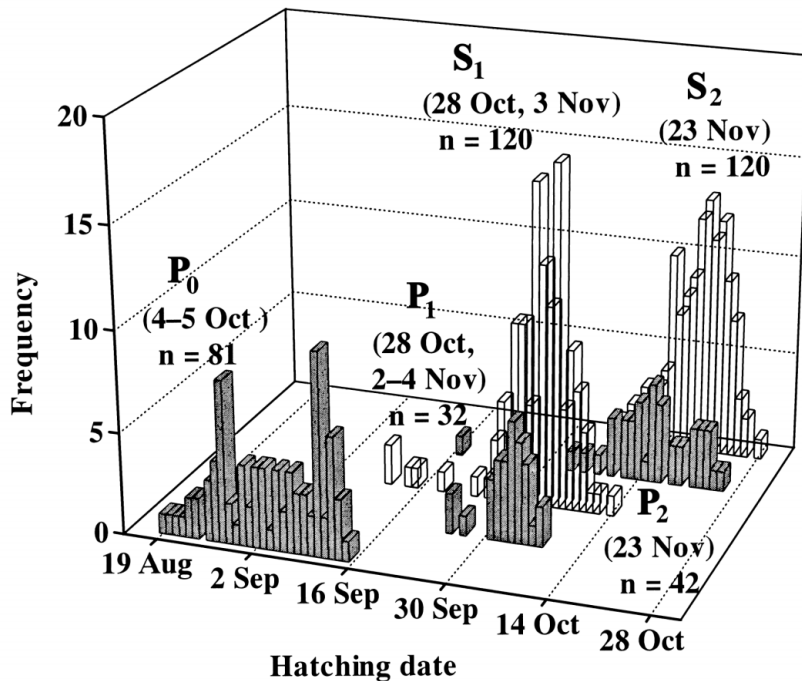


Fig. 1. Hatching date distributions of the prey larvae (solid: P_0 , P_1 and P_2) and surviving larvae (open: S_1 and S_2). Dates of capture indicated in parentheses

Table 3. Comparison of occurrence and mean growth rates of the prey larvae (P_0 , P_1 and P_2) among the positions in the stomachs of predators. n: occurrence of larvae; n': number of larvae with growth rate data available; GR: the mean growth rates (mean \pm SD); Significance: p-value in the comparison of mean growth rates by ANOVA; F, M and B: front, middle and back parts of the stomach, respectively

Position in stomach:	P_0		P_1		P_2	
	F	B	F	M	F	M
n	55	86	17	23	19	14
n'	31	22	13	13	13	12
GR (mm d ⁻¹)	0.63 \pm 0.08	0.63 \pm 0.07	0.60 \pm 0.06	0.57 \pm 0.07	0.49 \pm 0.05	0.50 \pm 0.07
Significance	p = 0.91		p = 0.08		p = 0.74	

Table 4. Comparison of occurrence and mean growth rates of the prey larvae (P_0 , P_1 and P_2) among the digestion ranks in the stomachs of predators. n: occurrence of larvae; n': number of larvae with growth rate data available; GR: the mean growth rates (mean \pm SD); significance: p-value in the comparison of mean growth rates by ANOVA; A: considered to be in fresh condition; B: integument has been digested; C: a portion of muscular tissue has been digested; D: more than half of the muscular tissue has been digested; E: almost all of the muscular tissue has been digested; F: only a set of vertebrae or eyeballs remain

Digestion rank:	P_0		P_1		P_2	
	A,B	E,F	A,B	C,D	A,B	C,D
n	3,27	53,23	0,6	8,8	0,1	12,19
n'	20	8	3	15	1	25
GR (mm d ⁻¹)	0.60 \pm 0.07	0.66 \pm 0.09	0.57 \pm 0.02	0.60 \pm 0.08	–	0.50 \pm 0.07
Significance	p = 0.03		p = 0.11		p = 0.81	

racuda stomachs also contained 3 juvenile anchovy (40 to 70 mm). Juvenile anchovy were excluded from otolith examination and 2 of them were analyzed as a predatory species because of their cannibalism. In contrast to barracuda and Japanese sea bass, these juvenile anchovy indicated size-selective predation on smaller larvae.

Comparisons of the mean growth rates by ANCOVAs with SL as a covariate still showed that the growth rates of the prey larvae were clearly lower than those of the corresponding surviving larvae even if compared at the same size (Fig. 6). The mean growth rates were positively correlated with larval SLs for both P_1 and S_1 , and the intercepts in the linear relationships differed significantly ($p < 0.001$). Between P_2 and S_2 , there were significant differences in the regression slopes of growth rates on SLs ($p < 0.001$), showing that the prey larvae had lower growth rates within the range of SLs analyzed.

Comparison of growth rates of prey larvae among predatory species

Differences in the mean growth rates of the prey larvae were found among predatory species in 3 samples (P_0 , P_1 and P_2) (ANOVA, $p < 0.01$). Although the relative levels of mean growth rates of the prey larvae among predatory species fluctuated among samples, barracuda generally preyed on the larvae with higher growth rates (Fig. 7). On the other hand, lower growth rates were characteristic of the larvae from white croaker *Argyrosomus argentatus*, Pacific round herring *Etrumeus teres* and juvenile anchovy, which were the predators smaller than barracuda (Table 1).

Back-calculated daily growth rates

Overall, daily growth rates of the prey larvae pooled by daily age were consistently slightly lower than those of the surviving larvae from 5 d after hatching (Fig. 8a). In comparisons of 5 d mean growth rates, statistically significant differences from the surviving larvae were found at 5 to 10 and 21 to 25 daily ages for P_1 and 5 to 15 for P_2 (Student's *t*-test, $p < 0.01$). Moreover, in data pooled by the days before capture or predation, consistent lower growth rates of the prey larvae were more distinct (Fig. 8b), and significant differences were found from at least 2 wk before predation ($p < 0.01$).

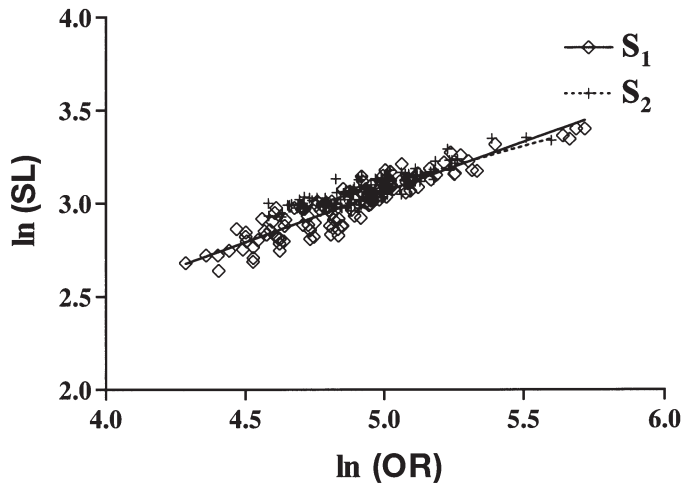


Fig. 2. Relationships between maximum otolith radius (OR) and standard length (SL) of the surviving larvae (S_1 and S_2). S_1 : $\ln SL = 0.539 \ln OR + 0.367$ ($r^2 = 0.854$, $n = 120$); S_2 : $\ln SL = 0.418 \ln OR + 1.009$ ($r^2 = 0.786$, $n = 120$). Regressions of $\ln SL$ on $\ln OR$ were compared between S_1 and S_2 . The relationships for S_1 and S_2 were used for restoration of SL from measured OR data for the prey larvae, P_1 (also P_0) and P_2 , respectively

DISCUSSION

Sampling method and predation in the net

An essential assumption in comparative studies between survivors and survivors plus non-survivors (non-survivors and temporary survivors in the present study) in the sea is that they originated from the same population or cohort (Meekan & Fortier 1996), usually not easily proved (but see Tsukamoto et al. 1989, Yamashita et al. 1994). We satisfied this assumption by simultaneously capturing both larvae and the predators foraging them; however, in doing so, we may have generated another problem to be solved. Predation in the net, if indeed it happened, could lead to bias in field studies on the feeding ecology of fish (Purcell 1985, Bailey et al. 1993). Apart from the uniformity in the numbers of larvae among the positions in the stomachs and the wide range of digestion extent with larvae in fresh condition occurring only rarely in the stomachs, this study found no highly significant differences in the growth rates among the positions or among the digestion ranks (Tables 3 & 4). Therefore, we assumed that the predators continually preyed on larval anchovy from the same population in terms of growth rates by the time of capture, and that our results were not affected by predation due to exceptionally high larval density in the net.

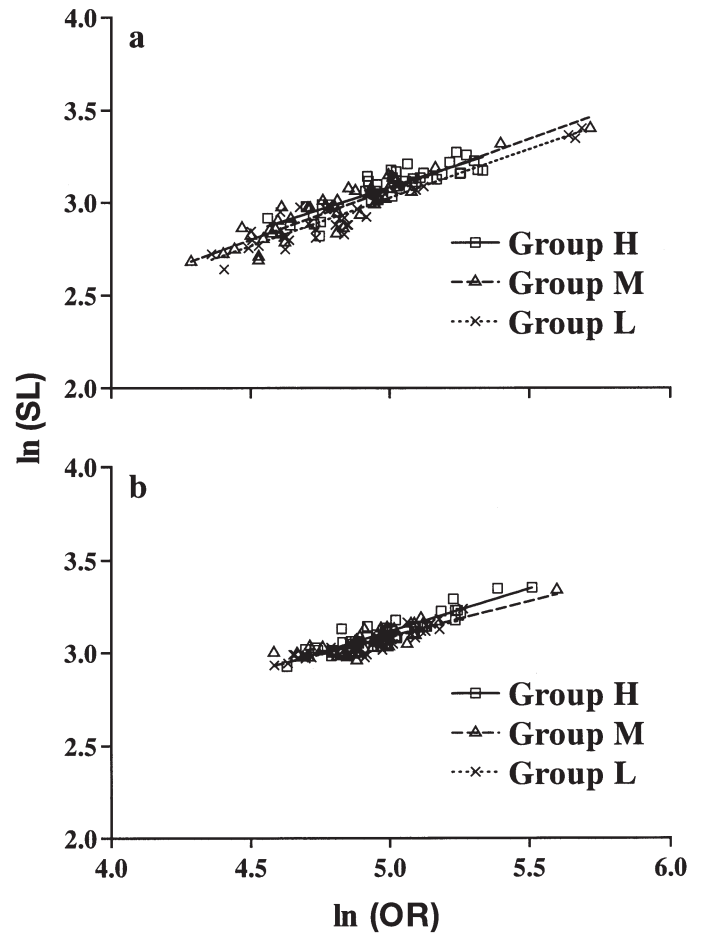


Fig. 3. Effects of growth rates on otolith radius-standard length (OR-SL) relationship of the surviving larvae, (a) S_1 and (b) S_2 . The larvae were classified into 3 groups within each surviving larval sample according to the level of mean growth rates. Group H: high-order, 40 individuals; Group M: middle-order, 40 individuals; Group L: low-order, 40 individuals. Regressions of $\ln SL$ on $\ln OR$ were compared among the groups. (a) Group H: $\ln SL = 0.482 \ln OR + 0.676$ ($r^2 = 0.769$, $n = 40$); Group M: $\ln SL = 0.545 \ln OR + 0.349$ ($r^2 = 0.856$, $n = 40$); Group L: $\ln SL = 0.523 \ln OR + 0.414$ ($r^2 = 0.887$, $n = 40$). (b) Group H: $\ln SL = 0.460 \ln OR + 0.816$ ($r^2 = 0.860$, $n = 40$); Group M: $\ln SL = 0.379 \ln OR + 1.194$ ($r^2 = 0.714$, $n = 40$); Group L: $\ln SL = 0.367 \ln OR + 1.249$ ($r^2 = 0.796$, $n = 40$)

Validation of SL restoration

SL restoration allowed us to examine the growth rates of the prey larvae digested to varying degrees, partly in order to rule out predation in the net; however, the restoration should be validated in a way which avoids the results of growth comparison between the prey larvae and surviving larvae via its monistic estimation process. As previously reported for larval Japanese anchovy (Chiu & Chen 2001, Takahashi et al. 2001), plots of SL against OR for the larvae in this study were also expressed as an allometric rela-

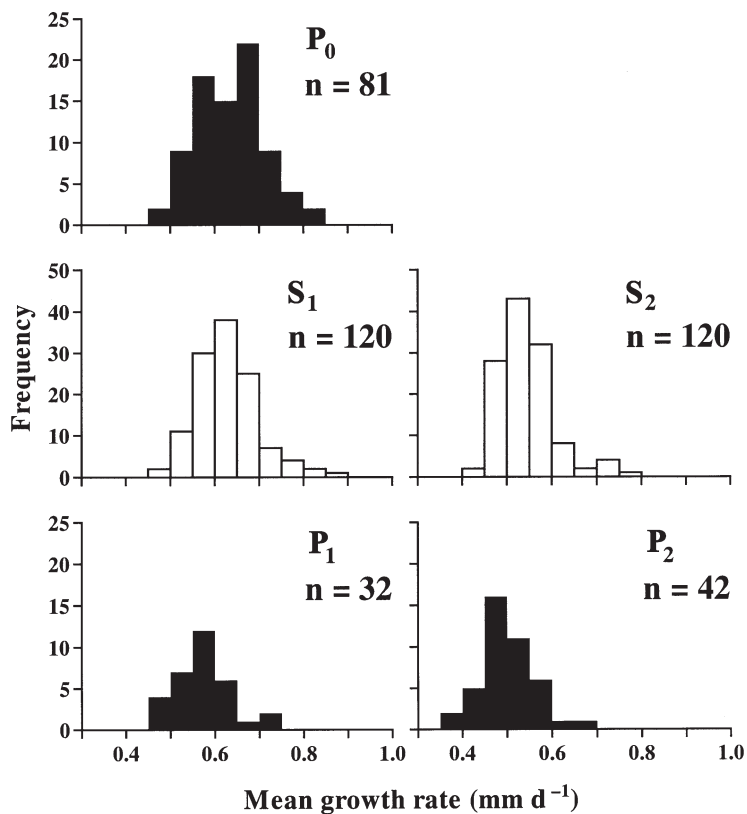


Fig. 4. Comparison of the mean growth rate frequencies between the prey larvae (P_0 , P_1 and P_2) and surviving larvae (S_1 and S_2)

relationship. Somatic growth rates, however, could affect the OR-SL relationship (Templeman & Squires 1956, Reznick et al. 1989, Secor & Dean 1989, García et al. 1998). If so, the monistic restoration process could bias the SL estimates of the prey larvae.

Tests of the effects of growth rates on OR-SL relationships showed that lower growth larvae could have slightly larger otoliths at the same larval sizes (Fig. 3). This phenomenon is consistent with what has already been reported for guppy *Poecilia reticulata* (Reznick et al. 1989), larval and juvenile striped bass *Morone saxatilis* (Secor & Dean 1989, 1992), larval and pelagic juvenile bluefish *Pomatomus saltatrix* (Hare & Cowen 1995), European anchovy *Engraulis encrasicolus* larvae (García et al. 1998), and some other species (e.g. Hovenkamp 1990, Wright et al. 1990, Francis et al. 1993). It happens partly because slower growing larvae accumulate more increments in spite of their narrowness even while scarcely growing (Secor & Dean 1989, Hare & Cowen 1995, García et al. 1998). Uncoupling between otolith and somatic growth existed slightly in the present study. Nonetheless, such directional characteristics of this uncoupling do not affect the results of

growth comparison, as follows: when the SL of a larva with lower growth rates is restored from an OR by the OR-SL relationship representative of the whole corresponding surviving larvae, the estimated SL value could be larger than the real value expected from the OR-SL relationship for the group with lower growth rates, and vice versa. Accordingly, use of SL data restored via such a monistic process tends to underestimate higher growth and overestimate lower growth. In other words, the variations in growth rates of the prey larvae would be reduced and consequently, the restoration process would not exaggerate the differences between the prey larvae and surviving larvae. Moreover, validation for the larvae with measured SLs available confirmed that there were no significant differences between restored estimates and actual measurements. Thus, SL restoration has been validated in the present samples.

Comparison of growth rates between prey larvae and surviving larvae

The mean growth rates of the prey larvae were significantly lower than those of the temporarily surviving larvae from the corresponding population of origin (Fig. 4). This obviously demonstrated that the individuals with higher growth rates were less vulnerable to predation than those with lower growth rates for larval Japanese anchovy in Sagami Bay. Consistent results from 2 cohorts with significantly different growth rates suggested that selective predation on lower growth larvae would depend, at least in part, on the relative values of individual growth rates within a cohort. Elucidation of the role of absolute values, which also might influence the intensity of selection and cohort survival, will need further research with quantitative sampling.

Meekan & Fortier (1996) presented the results supporting the 'growth-mortality' hypothesis for larval Atlantic cod *Gadus morhua* by comparing growth histories of survivors with those of the population during earlier times in the field study. In a similar method, a higher survival probability for faster growing individuals was demonstrated for larval plaice *Pleuronectes platessa* (Hovenkamp 1992). Survivorship of larger members of a cohort of yellow perch *Perca flavescens* during its first growing season was tested by comparing the back-calculated size distribution of survivors

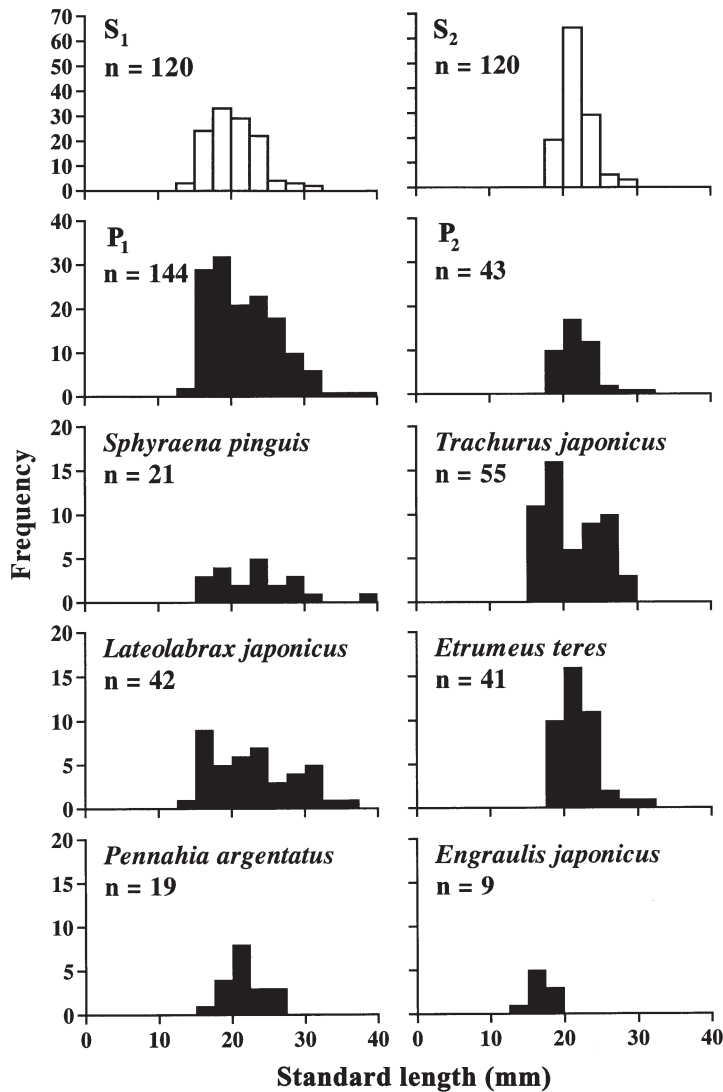


Fig. 5. Standard length (SL) frequencies of the larvae from the stomach contents of each predatory species and surviving larvae (S₁ and S₂). Both measured SLs of the larvae with otoliths unavailable and restored SLs from otolith radius (OR) data were also included. P₀ is not separately shown but included in each predatory species. Three juvenile anchovy of 48.9, 67.4 and 69.5 mm SL from *Sphyraena pinguis* are not shown as prey individuals; a few juvenile anchovy <40 mm SL are included. *Etrumeus teres* to be compared with only S₂; *S. pinguis* compared with both S₁ and S₂; the other species compared with only S₁

with the size distribution observed earlier (Post & Prankevicus 1987). Similarly, the other field tests of the 'growth-mortality' hypothesis and functional mechanisms have also been conducted based entirely on characteristics of survivors versus assumed population of origin including non-survivors (e.g. Healey 1982, West & Larkin 1987, Butler & Nishimoto 1997, Hare & Cowen 1997, Sirois & Dodson 2000, Good et al. 2001, Searcy & Sponaugle 2001). They all provided the

time-integrated picture of mortality over a longer period through larval (and juvenile) stage(s). Our study, on the other hand, presents the instantaneous image (snapshot) of predation mortality at just before the time of capture, independent of stage duration, and was able to directly examine the part of the population dead by predation for the first time, taking advantage of otoliths temporarily preserved in the stomachs. The results are a piece of evidence at a given moment in the field to support the predation part of the 'growth-mortality' hypothesis.

Non-size-related predation mortality

Size-related processes have been central to the role of growth in recruitment dynamics (e.g. Anderson 1988, Sogard 1997 for reviews). Negative size-selective predation mortality might be pervasive in accordance with the 'bigger is better' hypothesis, while survivorship of smaller individuals has been recognized. Fuiman (1989) and Litvak & Leggett (1992) reported higher predation mortality experienced by older or larger larvae in their enclosure studies. In a series of laboratory and mesocosm experiments, positive size-selective predation on young-of-the-year inland silverside *Menidia beryllina* by juvenile bluefish occurred (Gleason & Bengtson 1996a), which was supported by a field study (Gleason & Bengtson 1996b). Bailey & Houde (1989) proposed a conceptual model in which vulnerability of eggs and larvae follows a dome-shaped function, depending on predator type, by using the prey/predator-size ratio, which seems a better perspective than either prey or predator size alone. This relationship was confirmed for various types of predators by Cowan et al. (1996) and Paradis et al. (1996). Such a dome-shaped curve was

based on the component factors, such as encounter, attack and capture rates, as they play significant roles in the prey-predator relationship, while predatory gape limitation would simply contribute to decreases in vulnerability to predation with increasing prey size.

In a field study on the growth-mortality relationship, Hovenkamp (1992) suggested that size-selective mortality was not necessarily required in explaining the observed survival ratios of larval plaice in his demon-

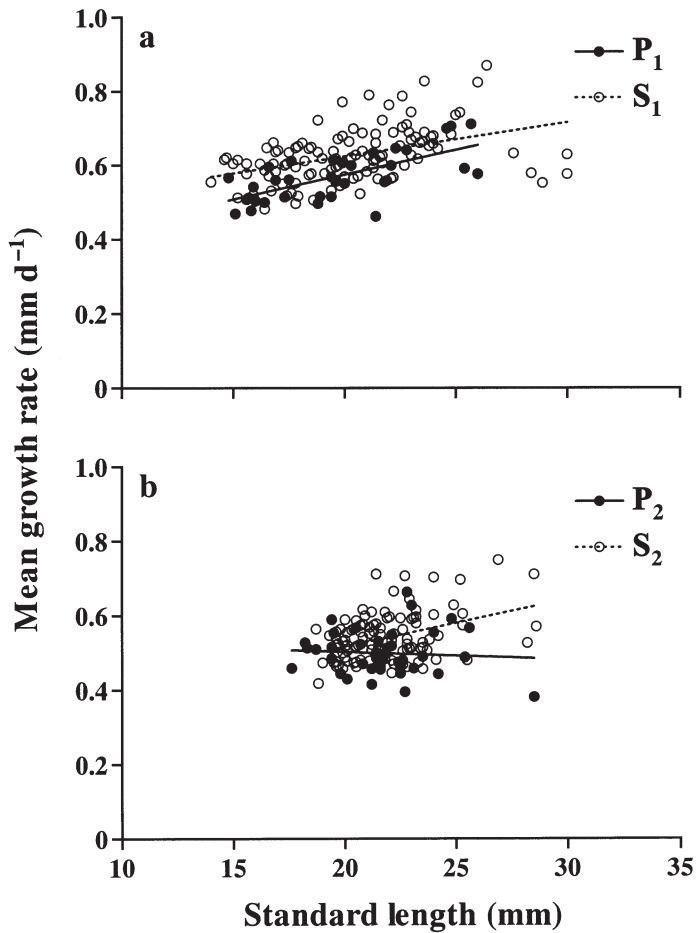


Fig. 6. Regressions of mean growth rate on standard length (SL) for the prey larvae (P₁ and P₂) and surviving larvae (S₁ and S₂). (a) P₁: GR (mean growth rate) = 0.013 SL + 0.307 ($r^2 = 0.443$, $n = 32$); S₁: GR = 0.009 SL + 0.440 ($r^2 = 0.184$, $n = 120$). (b) P₂: GR = -0.002 SL + 0.541 ($r^2 = 0.005$, $n = 42$); S₂: GR = 0.013 SL + 0.263 ($r^2 = 0.154$, $n = 120$)

stration for growth-dependent mortality (the 'stage duration' concept). The direction of size-selective mortality of Atlantic salmon *Salmo salar* fry reversed over 2 consecutive summers, in association with hydroclimatic events (Good et al. 2001). Leggett & DeBlois (1994) concluded that neither the 'bigger is better' nor the 'stage duration' hypothesis was unequivocally supported in their evaluation of these hypotheses.

In our study, both negative and positive size-selective predation mortalities were observed, depending on the predatory species. However, the combined effects of all predators were neutral, showing no size-selective predation in the whole mixed-species predator field (Fig. 5), although the predator compositions in this study may not exactly represent all potential predators in the study area. Purcell (1985) and Sogard (1997) noticed equivocality for extrapolation of single-species prey-size preference to the natural multi-species

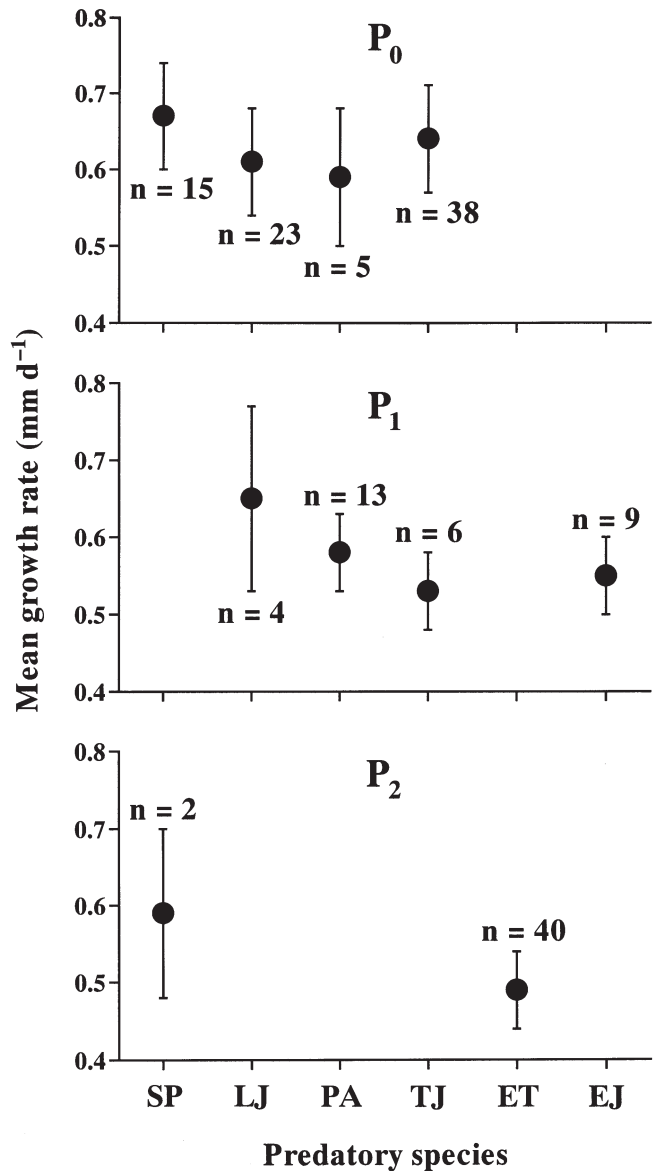


Fig. 7. Comparison of the mean growth rates of the prey larvae (P₀, P₁ and P₂) among their predatory species. SP: *Sphyaena pinguis*; LJ: *Lateolabrax japonicus*; PA: *Pennahia argentatus*; TJ: *Trachurus japonicus*; ET: *Etrumeus teres*; EJ: *Engraulis japonicus*. Mean \pm SD indicated in the diagram

predator field. Substantial size-selective mortality should depend on the natural predator field experienced by a population or cohort. In short, size-selective mortality is neither universal nor unidirectional. The existence of some non-size-related effects of growth on predation mortality, given that individuals with higher growth rates finally gain survivorship, is implied.

Fig. 6 clarifies the above. The significant differences in growth rates between the prey larvae and the corresponding surviving larvae were still visible in comparisons at the same size. Slower growing individuals are

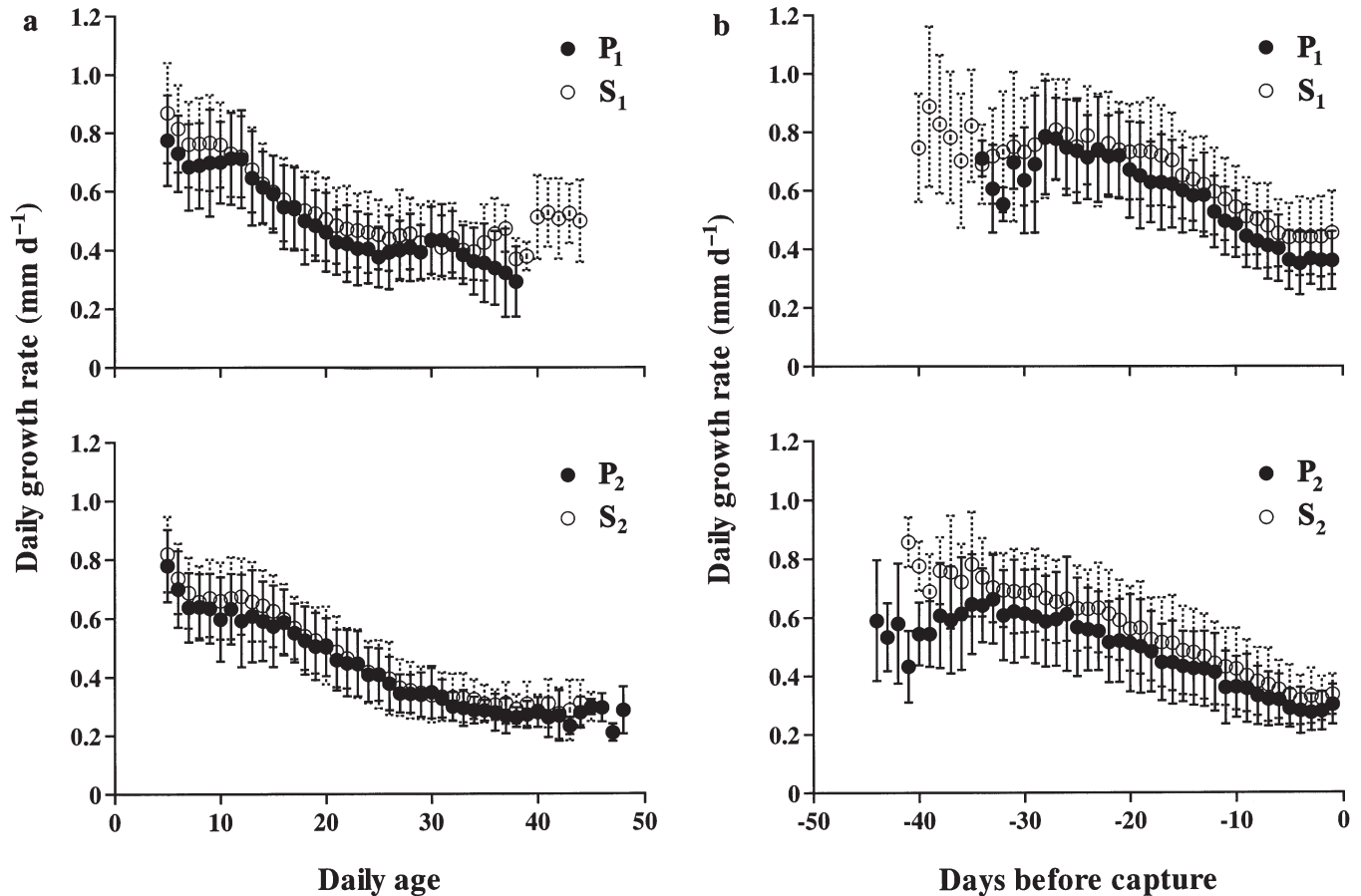


Fig. 8. Back-calculated daily growth rates of the prey larvae (P_1 and P_2) and surviving larvae (S_1 and S_2). Data were pooled by (a) daily age and (b) days before capture. Mean \pm SD shown at each daily age with at least 3 back-calculated growth rate data available

more vulnerable to predation mortality than faster growing conspecifics, even if they are the same size (i.e. non-size-related), at a given moment in the sea. This means that the level of growth rate itself had direct impact on the vulnerability to predation of the larval Japanese anchovy, independently of both size (negative size-selective mortality) and time (stage duration). We propose the 'growth-selective predation' hypothesis (mechanism), which is theoretically independent of and synergistic with the existing hypotheses based on size and time under a general concept of the 'growth-mortality' hypothesis and extend it.

Differences among predatory species

Although the sample sizes in the present study might be considered small, and the effects of size-selective predation cannot be completely discounted for each predatory species considering positive relationships between size and growth rates (Fig. 6), differences in growth rates of the prey larvae among predatory spe-

cies suggest that such impacts could be predator-specific (Fig. 7). Larger and strongly piscivorous predators, such as barracuda, may weakly or not select larvae by growth rates, while smaller predators such as Pacific round herring and juvenile anchovy might prey more selectively on larvae with lower growth rates. In the conceptual model, functions of vulnerability to predation on the prey/predator-size ratio depend on predator types (e.g. filter-feeding or raptorial feeding in Bailey & Houde 1989). In a simulation by Chick & Van Den Avyle (2000), the influences of growth and condition on cohort mortality rate for larval striped bass varied between 2 potential predators, *Alosa aestivalis* and *Pomoxis nigromaculatus*, for which simulation models were constructed. As for size-selective mortality, Post & Prankevicius (1987) mentioned the difference in predator guilds as one of the reasons why the strength of size-selective mortality varied between 2 lakes. In that study, strong removal of smaller yellow perch was found in the lake dominated by gape-limited predators, whereas the other lake was characterized by larger predators, which were expected to

potentially prey on all size classes. Predator-specific impacts, if ever, would be closely related to the feeding habit and ecology of each predatory species.

Ontogenetic and temporal changes in growth rates up to the time of capture or predation

Back-calculated daily growth rates pooled by daily age closely match ontogenetic changes in growth rates, including stage-specific growth. Comparisons of the 5 d mean growth rates pooled by daily age indicated that differences in growth between the prey larvae and surviving larvae had already arisen at least during the prelarval stage, immediately after hatching (Fig. 8a). When data were pooled by daily age, however, temporal changes with real time and trends in older ages were not be considered highly reliable, since there were some time lags among hatching dates in each sample (Fig. 1) and the pooled number decreases with daily age. On the other hand, data pooled by days before capture are well suited to temporal changes with real time before capture, although stage-specific changes and growth history directly after hatching may be masked. The prey larvae were shown to have consistently lower growth rates than the surviving larvae in data pooled by days before capture (Fig. 8b) as well as in data pooled by daily age, suggesting that the instantaneous predation mortality depends on a long-term decline in growth rates from directly after hatching to each encounter with predators. The cumulative decline in growth rates was determinative, rather than a temporary decline at specific stages or just before predation.

Potential for anti-predator behaviors and 'growth-selective predation'

Differences in potential for anti-predator behaviors, such as escape activity and responsiveness in encountering predators, might be the best explanation for the causal background of 'growth-selective predation'. As seen in the studies on selective mortality, most prey-predator interactions have been explained in terms of size-related factors. The case is true for vulnerability to predation composed of a variety of anti-predator behaviors. Webb (1981) recorded responses of larval northern anchovy *Engraulis mordax* to attacks by a biting planktivore, clown fish, on video tape and reported that the proportion of larvae responding to and escaping predator attacks, the escape distances traveled and the mean escape speeds increased linearly with larval size. Similarly, many studies have reported improvement of a variety of anti-predator

performance and decreased susceptibility to predation in relation to size (Webb & Corolla 1981, Bailey 1984, Bailey & Batty 1984, Brownell 1985, Blaxter 1986, Folkvord & Hunter 1986, Purcell et al. 1987, Miller et al. 1988, Williams & Brown 1992, Fuiman 1993, Williams et al. 1996), age (Butler & Pickett 1988, Sugisaki et al. 2001) and developmental stage (Bailey & Batty 1984, Purcell et al. 1987, Fisher et al. 2000, Wennhage 2000).

An exception to the focus on ontogenetic changes was presented by Chick & Van Den Avyle (2000). In their laboratory experiments and subsequent simulations, the effects of feeding ration on swimming speed and responsiveness to simulated predator attacks were examined for larval striped bass. Larvae in the low-feeding treatment had slower swimming speeds and less responsiveness to predator attacks. Although their model simulated cohort mortality and not individual mortality, the emphasis of non-size-related nutritional condition on vulnerability to predation was addressed. A prevailing scenario for the larval survival process is that environmental factors, such as food availability and temperature, determine both larval condition and growth, which can then ultimately determine the predation mortality, as suggested in the 'growth-mortality' hypothesis. Indirect evidence has been obtained for the relationships among condition, growth and susceptibility to predation. Frank & Leggett (1982) showed the correlation between environmentally regulated condition and swimming ability for larval capelin *Mallotus villosus*. Similarly, starvation has been shown to depress responsiveness to predator attacks and escape ability, mediated by deterioration in condition (Yin & Blaxter 1987, Booman et al. 1991, Booth & Hixon 1999). These authors highlighted the potential effects of food ration and condition on survival, as did Chick & Van Den Avyle (2000). An update of the field test of the 'growth-mortality' hypothesis was introduced by Searcy & Sponaugle (2001). They found selective mortality acting on a growth-based characteristic but equivocality for size-selective mortality for 2 coral reef fishes (Labridae), based on comparisons of otolith-derived traits between survivors and initial groups. Detected selective mortality in their study was the time-integrated mortality through metamorphosis and early juvenile period, yet it can be in accordance with the instantaneous predation mortality in our demonstration, in that selection was based not on size but on non-size-related growth variations. Searcy & Sponaugle (2001) attributed such selective mortality to physiological condition. What is given to vulnerability to predation by variations in nutritional (physiological) condition, as well as size, age and stage-related factors, is supposed to run by non-size-related growth rate variations. Synthetically, the deductive inference is that the

non-size-related 'growth-selective predation' would also be a ramification of differences in potential for anti-predator behaviors.

Within-population or cohort survival process depending on such potential of individual larvae could be associated with larval shoaling. One of the evolutionary functions of the shoals is well known as a defense against predation (Magurran 1990, Pitcher & Parrish 1993). The jacks *Caranx ignobilis* broke up the shoals of anchovy *Stolephorus purpureus* and then captured isolated individuals in an enclosure (Major 1978). Individuals separated from the shoals are considered to be more easily captured by the predators through failure to share defensive advantages of shoals (Neill & Cullen 1974, Parrish 1989, Pitcher & Parrish 1993). Mesa et al. (1994) reviewed the experimental studies on prey-predator interactions where prey were put into substandard condition artificially, with toxicants, thermal shocks, physical stresses, disease or starvation. They mentioned, although speculatively, disruption of the shoaling behavior of prey as one possible mechanism underlying increased vulnerability of substandard prey to predation. Postlarval anchovy generally form shoals with high density (Mitani 1988), as is often the case with the adult anchovy and many other pelagic species. When a larval shoal is attacked by predators, lower growth larvae, if the same in size, may tend to become isolated from their companions, probably because of their lower responsiveness to predators and swimming activity, and end up becoming more vulnerable to predation. If differences in potential for anti-predator behaviors and related shoaling behaviors are responsible for the 'growth-selective predation', the characteristics of each predator should be significant. This would also explain the differences among predatory species discussed above.

Significance of 'growth-selective predation' and further study

Prey-size selection is often explained by optimal foraging theory (see Hart 1993, Gerking 1994 for reviews). In this theory, the forager attempts to maximize the rate of food consumption per unit time (Wootton 1998). This will be determined under a trade-off between net gain as energy and cost as handling time. Hence, a little decline in prey size could mean much energy loss, since the energy content provided by the consumed prey would be proportional to its weight, which increases exponentially with length. Selectivity on lower growth prey, however, would lead to little if any energy loss in spite of ease of capture, as far as among individual prey of the same length. The 'growth-selective predation' would also be theoretically rational on the

side of predators in terms of benefit versus cost, since it would almost unidirectionally lead to improved prey capture facilities for predators.

Further studies on the 'growth-selective predation' should be conducted from 3 viewpoints. First, we may reveal predator-specific impacts by collecting a larger number of various predators and examining their feeding ecology in detail. Secondly, differences among seasons should be examined since the growth rates of the larvae in this study were relatively low, probably owing to lower sea temperature in autumn. Selection for fast growth might be stronger in a slower growing group (Post & Prankevicius 1987, Meekan & Fortier 1996). Also, the predator field would temporally vary. Finally, ontogenetic changes would be of concern. Sissenwine (1984) emphasized the significance of predation on juvenile stages, and Watanabe et al. (1995) pointed out the importance of cumulative mortality after the first feeding stage rather than episodic mortality during larval stage as determinants of recruitment success. Growth and survival would be specific to each life history stage (Anderson 1988). It is necessary to determine the threshold and terminal limit of the impacts through larval and juvenile stages in order to identify the 'window' of vulnerability to predation.

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