Predator-specific growth-selective predation and dynamics of the growth-based survival mechanisms in anchovy larvae

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Extended abstract:
Slower growing individuals are more vulnerable to predation mortality than faster growing conspecifics even if they are the same size at a given moment. This “growth-selective predation” mechanism was proposed as one of three functional mechanisms of the general “growth–mortality” hypothesis in our previous study, which focused on the characteristics of the actually ingested larvae versus the original populations. This talk summarizes our subsequent studies on predator-specific “growth-selective predation” and dynamics of the growth-based survival mechanisms in Japanese anchovy Engraulis japonicus larvae in Sagami Bay, Japan. The mechanism was tested based on comparisons of growth rates between the ingested larvae from the stomachs of predatory fish and the surviving larvae from the original populations (Fig. 1). Through this approach, predator-specific “growth-selective predation” was demonstrated by comparisons among different predatory species. Small pelagic fish were identified as growth-selective predators, whereas piscivorous fish were identified as non-growth-selective predators (Fig. 2). On the other hand, the three growth-based survival mechanisms (“bigger is better”, “stage duration”, and “growth-selective predation”) were tested for multiple cohorts of anchovy larvae based on the characteristics of the survivors versus the original populations (Fig. 3). As a result, each mechanism was detected to be effective at least in some cohorts, but none of the mechanisms was universally appropriate for all of the cohorts. The three different mechanisms actually regulated the short-term survival processes independently and
synergistically. The relative contributions of the mechanisms were dynamic although the “growth-selective predation” was identified to be the major one regulating survival in anchovy larvae in the study site.

**Keywords**: growth-selective predation, bigger is better, stage duration, anchovy larvae

**Notes:**

The present paper at ICES 2011 Session H (H:30) mainly summarizes the following published or submitted papers.


These studies were based on the following background papers.


The abstracts of the papers are listed below. For details of the contents, please refer to the links to the journal websites.
Fig. 1. Japanese anchovy *Engraulis japonicus* larvae, predators, and otolith. (a) Ingested larvae in the stomach of Japanese jack mackerel *Trachurus japonicus*; (b) ingested larvae dissected from the stomach of *Scomber* sp. juvenile; (c) larvae captured simultaneously with predators; (d) otolith of anchovy larva. Otoliths were extracted from the larvae dissected from the stomach contents of the predators (ingested larvae) and the larvae captured simultaneously with the predators (original larvae). Growth rates as well as somatic sizes were compared between the ingested larvae and original larvae to test size- and growth-selective predation mortality.
<table>
<thead>
<tr>
<th>Growth-selective predator</th>
<th>Non-growth-selective predator</th>
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<tr>
<td>Japanese anchovy</td>
<td>Japanese sea bass</td>
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<td><em>Engraulis japonicus</em></td>
<td><em>Lateolabrax japonicus</em></td>
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<td>Pacific round herring</td>
<td>Greater amberjack</td>
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<td><em>Etrumeus teres</em></td>
<td><em>Seriola dumerili</em></td>
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<td>Japanese jack mackerel</td>
<td>Skipjack tuna</td>
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<td><em>Trachurus japonicus</em></td>
<td><em>Katsuwonus pelamis</em></td>
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<td>White croaker</td>
<td>Chub mackerel &amp; spotted</td>
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<tr>
<td><em>Pennahia argentatus</em></td>
<td>mackerel <em>Scomber japonicus</em> &amp; S. australasicus*</td>
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Fig. 2. Categorizing predators based on the tests of growth-selective predation on Japanese anchovy *Engraulis japonicus* larvae: growth-selective predators and non-growth-selective predators. Small pelagic fish selectively preyed upon slower growing larvae and thus were identified as growth-selective predators, whereas piscivorous fish randomly preyed upon larvae and thus were identified as non-growth-selective predators.
Fig. 3. Examples of comparison of the growth histories of the survivors with those of the original populations. The 3 day mean growth rate immediately before the start of the survival period was compared between the survivors (SV) and the original populations (OP). There was no significant difference in growth rates between SV and OP for the samples collected in Sagami Bay in summer 2004, indicating that the ‘growth-selective predation’ was not effective. On the contrary, growth rate was significantly higher for SV than for OP for the sample collected in Sagami Bay in spring 2005, indicating that the ‘growth-selective predation’ was effective.
Abstracts of the relevant/background papers in chronological order
Please refer to the links to the journal websites for the full texts.


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 ± 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 *Pennahiaargentatus*, 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.


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


Abstract (http://www.int-res.com/abstracts/meps/v278/p297-302/)
The ‘growth-selective predation’ hypothesis was revisited for larval Japanese anchovy Engraulis japonicus, focusing on larval cannibalism by juveniles and larval predation by skipjack tunas Katsuwonus pelamis, in offshore waters. Larval anchovy and predators were captured simultaneously in June 1997 and in May 2000 in the western North Pacific. Growth rates estimated through otolith microstructure analysis, as well as somatic sizes, were compared between the ingested larvae from the stomach contents of the predators and the surviving larvae from the original population. Size-selective mortality was directed negatively for cannibalism by juveniles and positively for predation by skipjack tunas. The cannibalised larvae had lower growth rates than the
larvae from the original population in the same larval size range. On the other hand, a similar comparison showed no differences in larval growth rates for predation by skipjack tunas. Larval cannibalism by juveniles would potentially regulate growth-selective survival as well as survival rate itself during early life history stages of Japanese anchovy, while predation by skipjack tunas would influence survival rate itself but not growth-selective survival.

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Abstract (http://www.int-res.com/abstracts/meps/v350/p99-107/)
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.

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Abstract (http://dx.doi.org/10.1007/s12562-009-0205-y)
We tested whether the predation dynamics of chub mackerel Scomber japonicus and spotted mackerel S. australasicus on young anchovy Engraulis japonicus relates to individual growth characteristics of the prey and could account for the growth-selective survival predicted by recruitment hypotheses. Juvenile and adult mackerel were sampled along with their young anchovy prey field in 2004 (juvenile mackerel and larval anchovy) and 2005 (adult mackerel and juvenile anchovy) off the Pacific coast of
Honshu, Japan. The recent 5-day mean growth rate of larval and juvenile survivors and prey found in the stomach of mackerel was estimated from the otolith microstructure. No significant difference was found between the recent growth of larval or juvenile survivors and that of preyed individuals. We conclude that despite a relatively small body size, the high activity level and predation skills displayed by mackerel prevent fast-growing larvae and early juveniles from benefitting in terms of the expected survival advantage over slow-growers. Hence, growth-selective predation mortality of larval fish would depend on the feeding ecology of the predator rather than predator size. Selection for fast growth is more likely to occur under predation pressure from invertebrate organisms and small pelagic fish specialized on zooplankton, such as herring and anchovy.


**Abstract**

Three growth-based survival mechanisms (‘bigger is better’, ‘stage duration’ and ‘growth-selective predation’) were tested for multiple cohorts of Japanese anchovy *Engraulis japonicus* larvae collected repeatedly in Sagami Bay during autumn 2003 to winter 2005. 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 also 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 (3 and 9 of 17 pairs of the survivors and the original populations), respectively, although different pairs showed different results in some cohorts. The results contrary to the ‘bigger is better’ mechanism were obtained from 3 cohorts (6 pairs), while the ‘growth-selective predation’ mechanism was rejected in 2 cohorts (2 pairs). The ‘stage duration’ mechanism was evaluated to be effective for both of 2 cohorts which were testable. Each mechanism was detected to be effective at least in some cohorts, but none of these 3 mechanisms was universally appropriate for all of the cohorts. Comparison of multiple cohorts showed that the 3 different growth-based mechanisms actually regulated the short-term survival processes independently and synergistically, and that the relative contributions of the 3 mechanisms were dynamic although the ‘growth-selective predation’ mechanism was identified to be the major one regulating survival in anchovy larvae in the study site.