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Do early growth dynamics explain recruitment success in Japanese flounder *Paralichthys olivaceus* off the Pacific coast of northern Japan?

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Abstract

We examined the relative importance of growth-related processes operating during the larval and early juvenile stage in explaining variability in year-class success of Japanese flounder off the Pacific coast of northern Japan. Early growth trajectory of larvae and juveniles sampled in 2005 (strong year class) and in 2006 (weak year class) was estimated from the analysis of the lapillar otolith. The larval pelagic stage was characterized by lower growth and developmental rates, as well as high selection for fast growth in the metamorphosis/settlement period, during the strong recruitment event of 2005 relative to 2006. Growth appeared higher in 2005 only after settlement despite high density in the nursery, which likely reflected superior productivity during that year combined with an increased probability of cannibalism from early settlers on late settlers. This implies that larval growth dynamics did not play an important role in determining recruitment strength in the two years considered. The decreasing distance from the nursery areas of pelagic larvae through ontogeny in 2005, combined with low age at settlement, suggest that larvae benefited from positive transport conditions during the dominant year class. To the contrary, unfavorable hydrographic conditions likely prevailed in 2006 as distance from the nurseries increased with ontogeny and settlement occurred later than in 2005 despite faster growth potential and developmental rate. We conclude that transport conditions to the nursery grounds, rather than larval growth potential, represented the most important determinant of year-class success in the two years considered.

Keywords: Japanese flounder; Pelagic larvae; Settled juveniles; Otolith microstructure; Growth selective mortality; Year-class strength

1. Introduction

It is generally accepted that fast growth during the larval stage of marine fish is a prerequisite for the production of a strong year class (Anderson, 1988; Cushing, 1990; Houde, 2008). Fast larval growth would largely reduce the probability of being preyed upon by planktivorous predators (Chambers and Leggett, 1987; Miller et al., 1988; Takasuka et al., 2003). This premise is supported by several studies which confirmed, through the assessment of larval growth and selection for fast growth (a symptom of planktivorous predation pressure), that juvenile survivors usually represent the fastest-growing larvae among a given cohort (Meekan and Fortier, 1996; Hare and Cowen, 1997; Robert et al., 2007) and that survival rate is in general positively linked to mean larval growth rate at the cohort level (Campana, 1996; Ottersen and Loeng, 2000; Jenkins and King, 2006). Following the larval-stage survival bottleneck, predation pressure and mortality generally decrease sharply due to larger body size and well-developed anti-predator behaviour in the juvenile stage (Anderson, 1988). However, while this conceptual framework generally applies to pelagic fish, it may not extend to species in which metamorphosis is characterized by drastic habitat and physiological changes (Bradford and Cabana, 1997).

Flatfish undergo a rapid and demanding habitat shift during metamorphosis when they settle on the seafloor after a pelagic larval stage (Geffen et al., 2007). Contrary to most pelagic fish which encounter a continuum of environmental conditions in the water column through the first year of life, the physical and biotic environment experienced by young flatfish is drastically altered when metamorphosing larvae settle in the nursery areas (Van der Veer et al., 2000a; Bailey et al., 2005). This unique early life history trait in flatfish implies that in addition to larval growth dynamics, recruitment variability could be regulated by settlement success (Van der Veer et al., 2000a) as well as post-settlement predation (Bailey, 1994), even if field evidence remains limited (Van der Veer et al., 2000a, b). The assessment of selection for fast growth generally provides the means of evaluating two of the main potential biotic mortality sources in young flatfish: predation from planktivorous organisms during the larval stage (Takasuka et al., 2003; Takasuka et al., 2007a) and predation from benthic organisms after settlement (Van der Veer and Bergman, 1987; Van der Veer et al., 1997). While these mortality sources may both account for recruitment variability (Van der Veer et al., 1997), their relative contribution to total early mortality have not been assessed along with the development of individual cohorts.

Japanese flounder *Paralichthys olivaceus*, a commercially important fish species, is widely distributed from subtropical to subarctic areas of Japan. Its spawning season varies from winter to summer depending on location (Minami and Tanaka, 1992). After hatching at a size of 2-3 mm, young flounder experience a larval pelagic stage of 20-50 d duration, and settle on sandy bottoms at a size from 9 to 14 mm in total length (TL), around the time of metamorphosis, like a typical coastal flatfish (Tanda, 1990; Noichi, 1997; Tanaka et al., 1998). In populations distributed along the coasts of northern Japan, strong year classes are usually produced only once or twice per decade (Yamashita et al., 2004). In addition to high variability in year-class strength, recruitment is positively correlated to juvenile fish density (Kato, 1996; Maeda, 2002), which suggests that mechanisms driving recruitment operate before or soon after settlement. This species is thus an ideal candidate for investigating links between early life growth dynamics and year-class strength. During the period 2001-2006, Kurita et al. (2009) estimated recruitment strength for this stock in the waters off Fukushima Prefecture (northern Pacific coast) from the abundance of one-year-old flounder captured in the commercial fishery. Variability in relative year-class strength was enormous, and the number of recruits was 4 to 19 times larger in 2005 relative to the 5 other years. In this study, using otolith daily increments as a proxy for larval and juvenile growth, we compared growth potential and growth-selective mortality experienced by young stages during the exceptionally strong year class (2005) and a weak year class (2006). We examined the relative importance of growth-related processes operating during the larval and early juvenile stage in explaining recruitment strength. The effect of environmental factors on larval growth-related processes will be the focus of another study.

2. Materials and methods

2.1. Study area

This study was conducted off the Pacific coast of northern Japan, in an area ranging between Hitachi City to the south and Sendai Bay to the north (Fig. 1). A population of Japanese flounder spawns offshore relative to their coastal nurseries and the pelagic larvae are transported inshore to nurseries where they settle after metamorphosis (Minami and Tanaka, 1992).

2.2. Field sampling

Larval and juvenile Japanese flounder were sampled from early July to late August onboard RV Wakataka-maru (Tohoku National Fisheries Research Institute, Fisheries Research Agency) in the years 2005 and 2006 (Fig. 1). Pelagic larvae were captured using a 6-feet Isaacs-Kidd midwater trawl (IKMT) and a 1-m^2 multiple opening-closing net system (MOCNESS) equipped with 920 μm and 333 μm mesh nets, respectively. The samplers were deployed from the surface to a depth of 50 m, or down to 5 m over the bottom in shallow stations. Settled juveniles were sampled in coastal areas shallower than 15 m using a 2-meter beam trawl with a tickler chain equipped with a 4 or 6 mm mesh net (Fig. 1). Pelagic larvae and settled juveniles were sorted, and then preserved onboard in 90% ethanol. Pelagic larval density (PLD, based on IKMT data) and settled juvenile density (SJD) were calculated based on the towed distance estimated from GPS data. Subsamples of 138 (2005) and 239 (2006) larvae were assembled, and 30 juveniles in each year were provided us for growth-related analysis. Spawning stock biomass (SSB) data taken from Kurita et al. (2009) were used as a proxy for abundance of spawned eggs.

2.3. Otolith microstructure analysis

In the laboratory, the body length of pre-metamorphosis larvae, metamorphosing larvae and settled juveniles was measured to the nearest 0.01 mm using the ocular micrometer of a stereoscope (larvae) or a digital caliper (juveniles). Larval flounder were staged following Tanaka et al. (1989a, b), according to the criteria described by Minami (1982) and Hossain et al. (2003). The eyed-side lapillus of each individual was dissected under a stereomicroscope, mounted on a glass slide with clear nail polish, and examined using an image analysing system (RATOC System Engineering, Tokyo, Japan) consisting of a light microscope connected to a computer with a video camera. The number of daily growth increments and the distance between adjacent increments (measured to the nearest 0.1 µm) were taken along the longest axis at 1000× for larvae, and at 1000× (< 25 days of age) and 200-500× (>25 days of age) in juveniles. The focus was repeatedly adjusted to optimize measurement precision (Fig. 2).

Clarity of daily growth increments in the innermost area (close to the core) of Japanese flounder otoliths being extremely low, daily ageing by the means of simple increment counting proves to be difficult (Fig. 2). However, Uehara and Fujinami (unpubl. data) have confirmed that in laboratory-reared (thus age-known) larvae, the relationship between daily age and lapillus radius closely follows an exponential function (R^2 = 0,985) during the early larval stage (up to 20 µm radius, corresponding to a mean age of 18 d):

(1) $$OR_n = OR_0 \times e^{an}$$

where OR_n is the otolith radius at age n d and OR_0 is the otolith radius at hatch (hatch check, identifiable for all samples). Because age of field-sampled individuals is unknown, we firstly assigned to the equation a standard provisional n of 10 d. Then, slope a was individually resolved with the minimum square method using five sequential increments observed on each otolith. In this study, the first visible daily growth increment occurred at a distance of about 15 μm from the nucleus. In order to estimate age *n*’ at which this first visible increment was formed, the above exponential equation was transformed as follows:

$$(2) \qquad n' = \frac{1}{a} \ln\left(\frac{OR_{n'}}{OR_0}\right)$$

from which we individually calculated *n*’. Individual age was then determined by summing up the *n*’ and the number of visible increments starting from the distance of 15 μm from the core. Uehara and Fujinami (unpubl. data) also reported that settlement induced a drastic alteration of otolith growth. We thus considered this apparent growth shift as individual age at settlement in juveniles (Fig. 2b).

2.4. Statistical analyses

Following Meekan and Fortier (1996) and Chambers and Miller (1995), between-year differences in growth trajectory were assessed using repeated-measures ANOVA analyses. The same statistical procedure was used to determine the occurrence and timing of growth-selective mortality by comparing growth trajectory among consecutive developmental stages (early larvae ≤20 d, metamorphosing larvae >20 d, recently-settled juveniles ≤40 d, and settled juveniles >40 d) within a given year. In the eventuality that significant differences were found, post-hoc univariate *F*-tests were examined to determine the age interval when both trajectories differed. Interannual differences in pelagic larval duration, or age at settlement were assessed with t-tests and ontogenetic changes in larval spatial distribution were examined using *G*-tests.

3. Results

3.1. SSB, PLD, and SJD

SSB appeared twice larger in 2005 than 2006 (Fig. 3a). However, variability in SSB did not lead to a between-year difference in PLD (Fig. 3b; t-test, $p = 0.95$). On the other hand, SJD was much higher in 2005 than 2006 (Fig. 3c; t-test, $p<0.05$).

3.2. Relationship between somatic and otolith growth

Otolith radius was related to body length both during the pelagic larval and settled juvenile stages (Fig. 4). The strong correlation between otolith and somatic growth indicated that daily increment width provides a reliable estimate of individual somatic growth trajectory. The relation between otolith radius and body length appeared trimodal with its slope changing at a body length of about 4 mm and at settlement. No interannual difference was detected in the three distinct growth phases (ANCOVA, $p>0.05$). Because such variations in the otolith-somatic growth relationship are likely to bias the back-calculation of somatic growth trajectory in juveniles, otolith growth (increment width) was used directly as a proxy for daily somatic growth in further analyses.

3.3. Hatch date frequency distribution of pelagic larvae and settled juveniles

The first visible daily growth increment, which occurred at a distance of about 15 μm from the otolith nucleus, corresponded to 12.2 ± 2.0 and 12.1 ± 1.8 d (mean ± SD) in 2005 and 2006, respectively. Uehara and Fujinami (unpubl. data) showed that this age relates to vertebral calcification. In 2005, back-calculated hatch date of settled juveniles ranged from mid July to early September, overlapping relatively well with the hatching period of the sampled larval population (Fig. 5). On the other hand, the hatch date frequency distribution of juveniles in 2006 ranged from early May to late July, meaning that our sampling did not cover the whole larval season (Fig. 5). Hence, we only considered those juveniles hatched within the common time period as the captured pelagic larvae (late June to mid August in 2005, and mid June to late July in 2006) in further growth-selective mortality assessment to insure all individuals originated from the same cohort.

3.4. Interannual variability in growth and developmental rate

The growth trajectory of larvae (which survived to be sampled) differed among individuals captured during the two years (Fig. 6; two-way repeated-measures ANOVA, $F_{\mathrm{year}} = 62.57$, $p<0.001$). Mean growth rate was higher in 2006 than in the 2005 strong year class during the 12-16 d age interval (F-tests, $p<0.05$). Fast growth achieved in 2006 was paralleled by observed younger age at all developmental stages relative to 2005 (Fig. 7; two-way repeated-measures ANOVA, $F_{\mathrm{year}} = 24.99$, $p<0.001$).

The growth trajectory of settled juveniles also differed among years, but showed a reverse pattern as growth was higher during the dominant year class of 2005 compared to 2006 (Fig. 8; two-way repeated-measures ANOVA, $F_{\mathrm{year}} = 307.01$, $p<0.001$). Pelagic larval stage duration, inferred from the apparent growth shift on juvenile otoliths, was significantly shorter in 2005 (23.3 ± 2.5 d) relative to 2006 (24.9 ± 1.4 d) (t-test, $p<0.05$). Larval developmental rate in this study compared well to that found at the warm condition (19°C) in the laboratory (Seikai et al., 1986).

3.5. Growth-selective mortality

When comparing the growth trajectory of metamorphosing larvae >20 d (early larval stage survivors) to that of early larvae ≤20 d (reference population), there was no evidence of growth selection in both years (Fig. 9a, d; two-way repeated-measures ANOVA, $p > 0.07$). However, when comparing the growth trajectory of juveniles (larval stage survivors) to that of all pelagic larvae (reference population), the dominant year class of 2005 was characterized by strong selection for fast growth (two-way repeated-measures ANOVA, $F_{\text{stage}} = 217.51$, $p<0.001$) as daily increments were significantly wider in juveniles during the 12-23 d age interval (Fig. 9b; F-tests, $p<0.05$). Significant growth selection was also detected in 2006 (two-way repeated-measures ANOVA, $F_{\text{stage}} = 15.18$, $p<0.001$), but was milder and only significant at the age of 13 d (Fig. 9e; F-test, $p<0.05$). Finally, growth selection during the juvenile stage could only be assessed in 2005 due to the low number of early juveniles captured in 2006. During that year, no selection for fast growth was found when comparing growth of juveniles >40 d (early juvenile stage survivors) to that of recently settled juveniles ≤40 d (Fig. 9c; two-way repeated-measures ANOVA, $F_{\text{stage}} = 0.59$, $p = 0.44$).

3.6. Spatial distribution of Japanese flounder larvae

This analysis was also conducted using the larvae collected by IKMT. Ontogenetic changes in larval spatial distribution were found in both cohorts (Fig. 10). In 2005, an increasing proportion of larvae were captured in the In- and Near-shore areas from the pelagic larval stage to metamorphosis (G-test, $G = 45.39$, $p<0.001$). The opposite pattern was observed in 2006 as the average distance from the shore increased with development (G-test, $G = 23.35$, $p<0.001$). During the dominant recruitment event of 2005, more than 80% of metamorphosing larvae were distributed In- and Near-shore, while this proportion fell below 40 % in 2006.

4. Discussion

Fast growth during the pelagic larval stage is often considered the most important prerequisite for the production of a strong year class in marine fish (Anderson, 1988; Cushing, 1990; Houde, 2008). This assumption is supported by a growing body of evidence indicating that, in a large number of species, larval survival is related to individual growth performance (Campana, 1996; Takasuka et al., 2003; Jenkins and King, 2006; Robert et al., 2007) and that year-class strength depends on factors promoting larval growth such as optimal temperature (Ottersen and Loeng, 2000; Takasuka et al., 2007b) or food availability (Beaugrand et al., 2003; Platt et al., 2003; Castonguay et al., 2008). However, because of their atypical early life history, it is still debated whether recruitment hypotheses based on larval growth systematically apply to flatfish (Van der Veer et al., 1994; Van der Veer et al., 2000a).

The results presented here are contradictive to the larval growth paradigm as low recruitment in 2006 was associated to faster larval growth and developmental rate relative to the dominant year class of 2005. Furthermore, the weak growth-selective mortality observed in 2006 eliminates the risk admonished by Robert el al. (2007) that this reverse pattern is an artifact of strong selection for fast growth. In addition to higher growth in 2006, the ratio of pelagic larvae density over SSB appeared higher in 2006 relative to 2005, suggesting lower early mortality rate due to favorable growth conditions during the weak year class. Our results thus suggest that interannual variability in larval growth potential was not an important determinant of recruitment within these two years. Only one episode of high growth-selective mortality was observed during or soon after settlement in the strong year class of 2005, when large juvenile numbers settled in the nursery areas.

While mean growth level observed during the juvenile stage in 2005 certainly reflects to some extent the removal of slow-growing individuals from the population, average fast growth rate could nevertheless be maintained in survivors despite a tenfold superior density relative to 2006. This suggests that juveniles did not suffer from food shortage in 2005. Such a result may reflect the combined effects of two different factors. First, nursery productivity was likely higher in 2005, allowing the maintenance of optimal foraging and growth under increasing settler density. Settled juveniles usually prey mainly on mysid crustaceans (Tanaka et al., 1996; Yamamoto et al., 2004; Tanaka et al., 2005). Stomach content analysis however revealed that young anchovy contributed to a large proportion of the diet of juveniles in 2005 (Kurita et al., submitted). The availability of this highly calorific prey could have fueled the fast growth achieved by juveniles during that year. The second factor that may explain the observed fast growth at high density in 2005 is cannibalism from early settlers on late ones (Minami and Tanaka, 1992). Episodes of growth-selective predation are common during the juvenile stage of flatfish (Van der Veer and Leggett, 2005) and while usually attributed to invertebrate organisms (Van der Veer and Bergman, 1987; Witting and Able, 1995; Ansell et al., 1999), the main predators of newly-settled Japanese flounder juveniles may consist in their larger siblings (Minami and Tanaka, 1992) that settled earlier. In the present study, the conjunction of selection for fast growth and fast growth despite high settler density suggests the occurrence of size-selective cannibalism in addition to high productivity in the nurseries.

A key finding in this study is the failure of early life growth processes to explain the exceptionally strong recruitment event of 2005 relative to the weak year class of 2006. Larval growth appeared slower in 2005, and no growth-selective pressure was observed during larval life in both years. Then juveniles grew faster in 2005, leading to a 10 times higher juvenile density despite occurrence of selection for fast growth in that year only. These combined results suggest that recruitment strength was already determined at the end of the pelagic larval stage. This is consistent with the conclusions of several studies that assessed the links between early life dynamics and recruitment in flatfish and proposed that larval supply to the nurseries drives recruitment magnitude while post-settlement processes would only relate to fine-tuning (Van der Veer et al., 2000a, Van der Veer and Leggett, 2005). As opposed to the offspring of most pelagic fish, larval flatfish hatch at a very small size and exhibit poor swimming ability (Bailey et al., 2005). Because metamorphosing larvae can only settle successfully on highly specific grounds (the so-called nurseries), physical processes influencing retention on / transport to the nursery areas may constitute a major source of survival variability (Neilson et al., 1988; Nielsen et al., 1998; Van der Veer et al., 1998; Nakata et al., 2000; Bailey et al., 2005). Japanese flounder from the Pacific coast of northern Japan spawns in the Kuroshio-Oyashio transition region, which is characterized by particularly high spatial and temporal hydrographic variability (e.g. Takahashi et al., 2001). In turn, this feature likely generates high variability in transport conditions that could impact year-class strength for this stock.

The hypothesis of an “aberrant drift” (sensu Hjort, 1914) and “member vagrant” (Sinclair, 1988) explaining low settlement success in 2006 could unfortunately not be assessed directly in this study in the absence of detailed hydrographic monitoring. However, indirect evidence strongly suggests pelagic larvae hatched during the dominant year class of 2005 benefited from favorable transport conditions while a large proportion of those hatched in 2006 were advected away from the nurseries. We base this assumption on two results: (1) the stage-specific spatial distribution of captured larvae denotes the expected inshore migration in 2005 while it suggests an offshore advection in 2006 (Fig. 9), and (2) juveniles in 2005 were characterized by younger age at settlement despite slower developmental rate. In light of these results, we argue that while larvae reached their nursery ground relatively early in 2005, the 2006 cohort needed to delay settlement, despite faster development, due to adverse transport conditions. Mean pelagic larval stage duration in 2006 lasted only 1.6 days over that in 2005. However, considering that larvae grew and developed faster in 2006 (hence reaching settlement capability at a younger age), this apparently small difference in pelagic life duration could reflect the failure of a large portion of pelagic larvae to reach the nursery area in a proper time window. This supports the idea that transport processes affecting the larval stage may account for a large fraction of recruitment variability in Japanese flounder.

Our results suggest that high larval growth potential does not necessarily trigger dominant recruitment events in Japanese flounder. The “Stage-duration” hypothesis (e.g. Chambers and Leggett, 1987), proposing that fast growth enhances survival through the decrease of larval stage duration, is a central idea of the growth-predation paradigm (Anderson, 1988). In populations undergoing larval migration to distant nursery areas, a short larval stage may however bear bilateral implications. While short larval life likely reduces overall predation mortality, it would also increase risks of settlement failure when transport conditions are adverse. We hypothesize that in flatfish populations, the relative importance of growth-related (e.g. Anderson, 1988; Cushing, 1990) and transport-related (e.g. Sinclair, 1988; Townsend, 1992) recruitment mechanisms respectively follow negative and positive gradients along with the migration distance to the nursery ground. Hence, growth-related survival mechanisms would apply well for recruitment prediction in populations characterized by overlapping spawning and nursery areas like yellowtail flounder *Limanda ferruginea* and American plaice *Hippoglossoides platessoides* in the Northwest Atlantic (Neilson et al., 1988; Walsh, 1992), while transport or retention conditions would become more important determinants of recruitment in populations characterized by moderate (e.g. Japanese flounder) to long larval migration to the nursery grounds like European plaice *Pleuronectes platessa* in the North Sea (Van der Veer et al., 1998) or northern rock sole *Lepidpsetta polyxystra* and arrowtooth flounder *Atheresthes stomias* in the eastern Bering Sea (Wilderbuer et al., 2002). Our hypothesis is supported by the fact that most reports of transport effects on flatfish recruitment concerned populations characterized by moderate to long larval migration distance (reviewed by Bailey et al., 2005). One should thus consider cautiously the applicability of the growth-predation conceptual framework (Anderson, 1988) in flatfish recruitment studies.

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Figure captions

Fig. 1. Map of the study area, off the Pacific coast of northern Japan, with stations where Japanese flounder larvae (○) and settled juveniles (☆) were sampled in 2005 and 2006.

Fig. 2. Japanese flounder lapillar otoliths: (a) 5.62 mm pelagic larva at 1000× and (b) 40.45 mm settled juvenile at 200×. The distance between daily increments was measured along the maximum radius. In lapillus of settled juveniles, daily increments from the nucleus to the growth inflexion point represent growth during the pelagic larval stage while following increments represent post-settlement growth.

Fig. 3. Annual variation in (a) spawning stock biomass (SSB: Kurita et al., 2009), (b) pelagic larval density (PLD), and (c) settled juvenile density (SJD). Error bars (b, c) represent the standard error.

Fig. 4. Relationship between body length (BL) and otolith radius (OR) for (a) pelagic larvae and (b) settled juveniles captured in 2005 and 2006. Equations with both BL and OR log-transformed are, for larvae <4 mm (broken line) and ≥4 mm (full line), $\mathrm{LOG}(OR) = 0.49\times\mathrm{LOG}(BL)+0.97$ ($n = 101$, $r^2 = 0.35$, $p<0.001$) and $\mathrm{LOG}(OR) = 1.23\times\mathrm{LOG}(BL)+0.51$ ($n = 527$, $r^2 = 0.69$, $p<0.001$), respectively. The equation for settled juveniles was $\mathrm{LOG}(OR) = 0.61\times\mathrm{LOG}(BL)+1.27$ ($n = 60$, $r^2 = 0.94$, $p<0.001$).

Fig. 5. Hatch date frequency distribution of sampled Japanese flounder pelagic larvae (upper panels) and settled juveniles (bottom panels) in 2005 and 2006. E, M and L

respectively indicate the early, mid and late period of each month. Only those juveniles hatched during the common period with sampled larvae, delineated with the black arrows, were used in further growth comparisons with larvae.

Fig. 6. Comparison of mean increment width at age between pelagic larvae hatched in 2005 and 2006. The shaded area indicates the age interval when larval growth was significantly higher in 2006 relative to 2005. Error bars represent standard deviation.

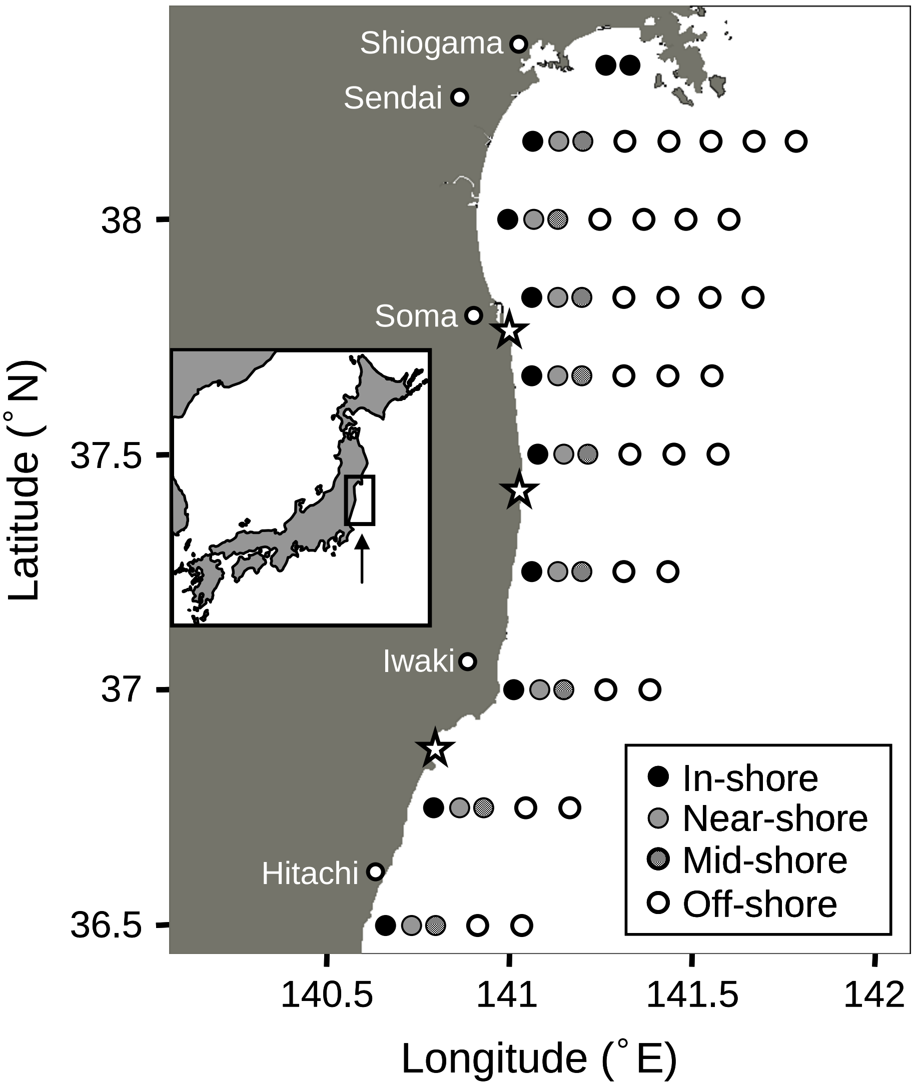
Fig. 7. Mean age at each developmental stage (Minami, 1982) of pelagic larvae in 2005 and 2006. Error bars represent standard deviation.

Fig. 8. Comparison of post-settlement growth trajectory in juveniles sampled in 2005 and 2006. Error bars represent standard deviation and the shaded area indicates the post-settlement period when growth was significantly higher in 2005 relative to 2006.

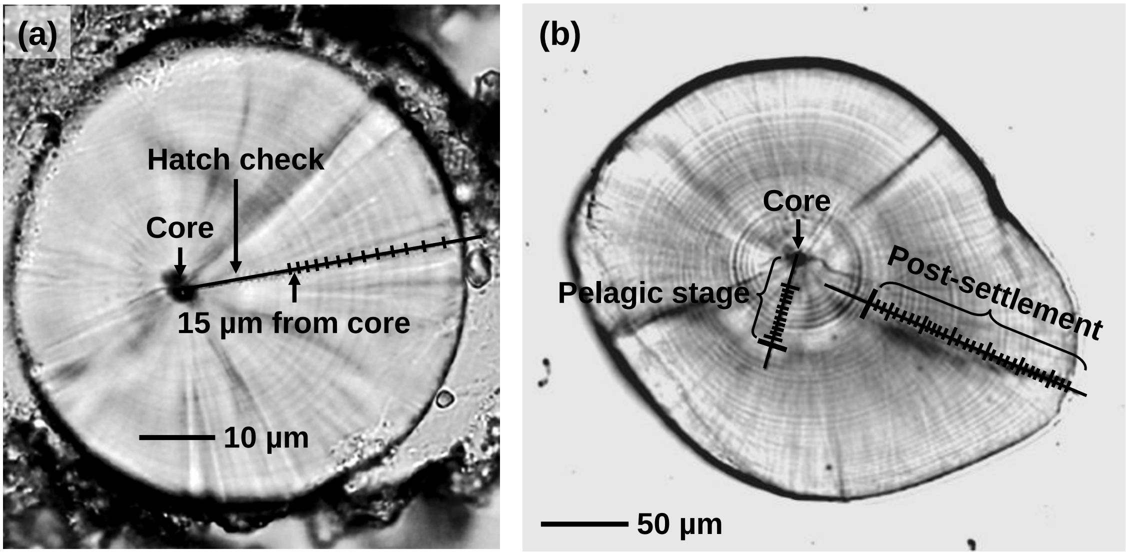
Fig. 9. Comparison of mean increment width at age (a,b,d,e) or at days after settlement (c) between a reference population (○) and survivors (△) during the larval (a,d), metamorphosis (b,e) and juvenile (c) stages in 2005 (left panels) and 2006 (right panels). Shaded areas indicate age intervals during which mean increment width of the survivor group differed significantly from that of the original population. Error bars represent standard deviation.

Fig. 10. Proportion (CPUE) of pre-, early- and mid-metamorphosis larvae sampled in In-,

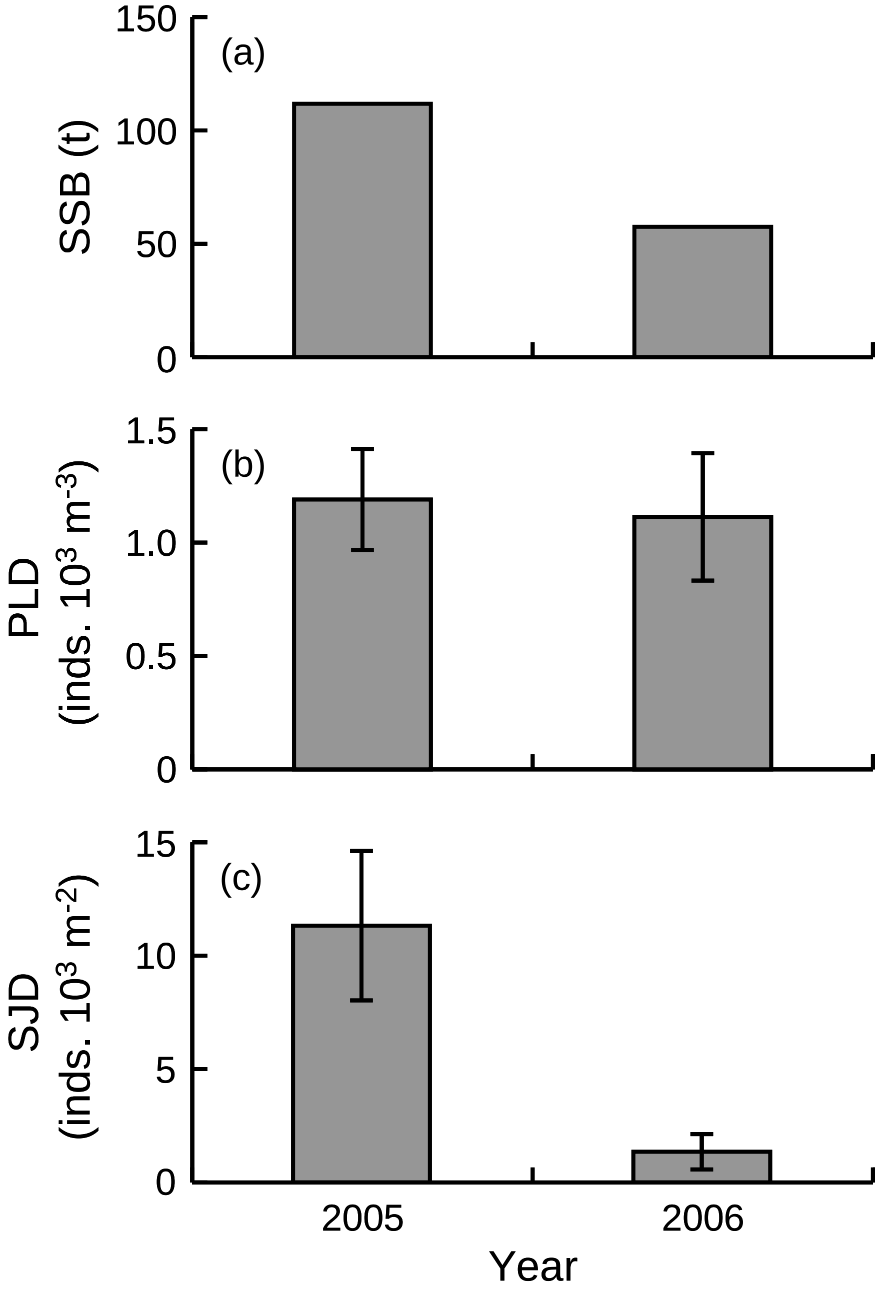
Near-, Mid- and Off-shore stations (see Fig. 1). Larvae were staged according to criteria provided by Minami (1982) and Hossain et al. (2003).



Oshima et al., Figure 1



Oshima et al., Figure 2



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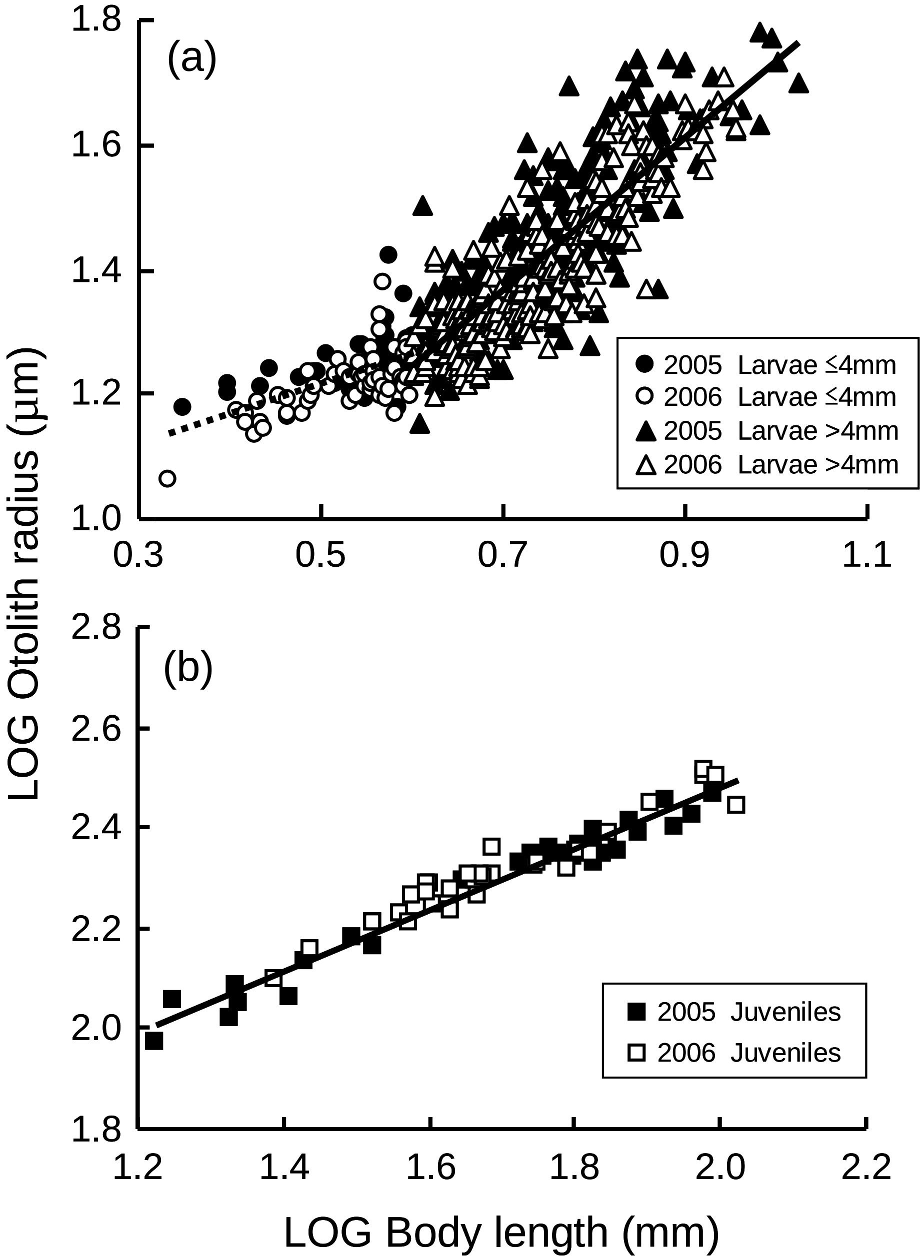

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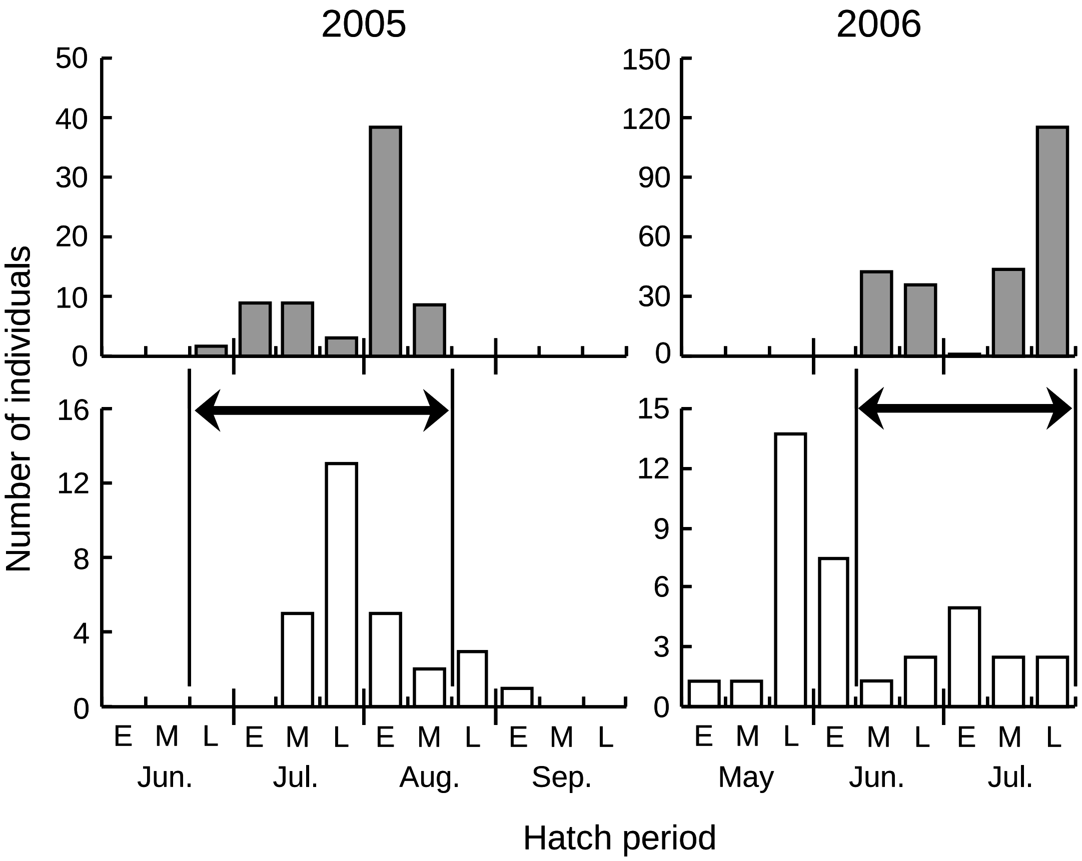

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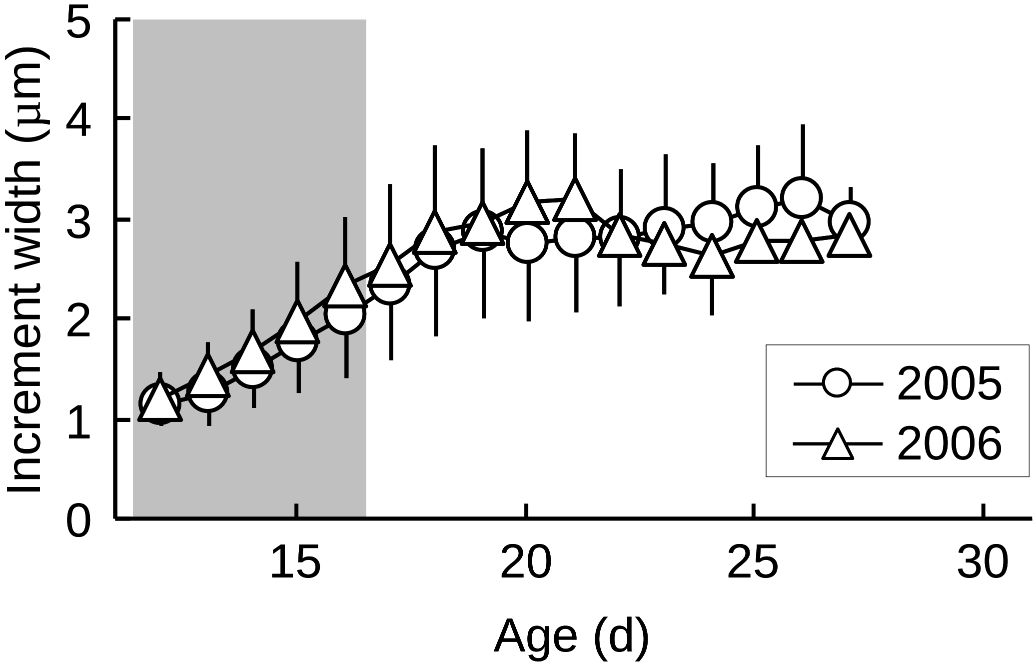
Oshima et al., Figure 5



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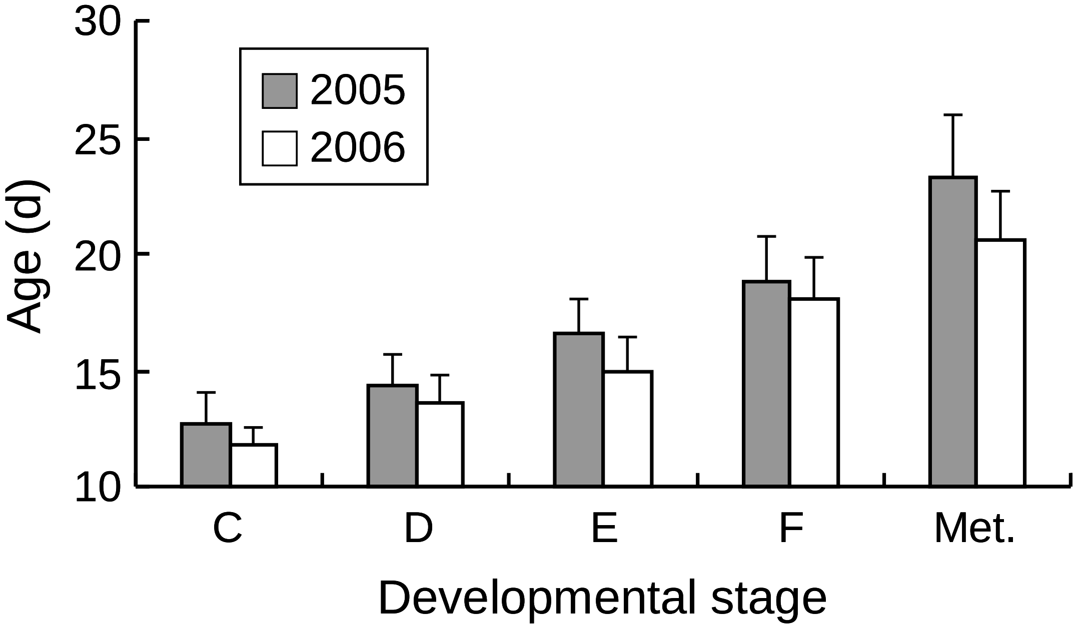

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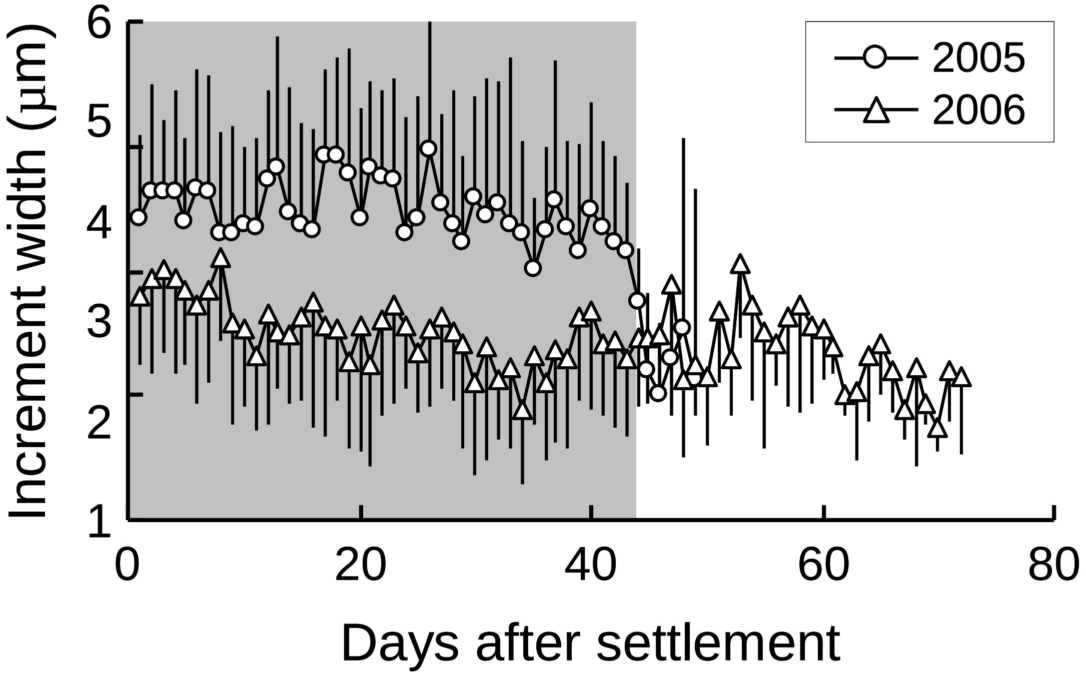

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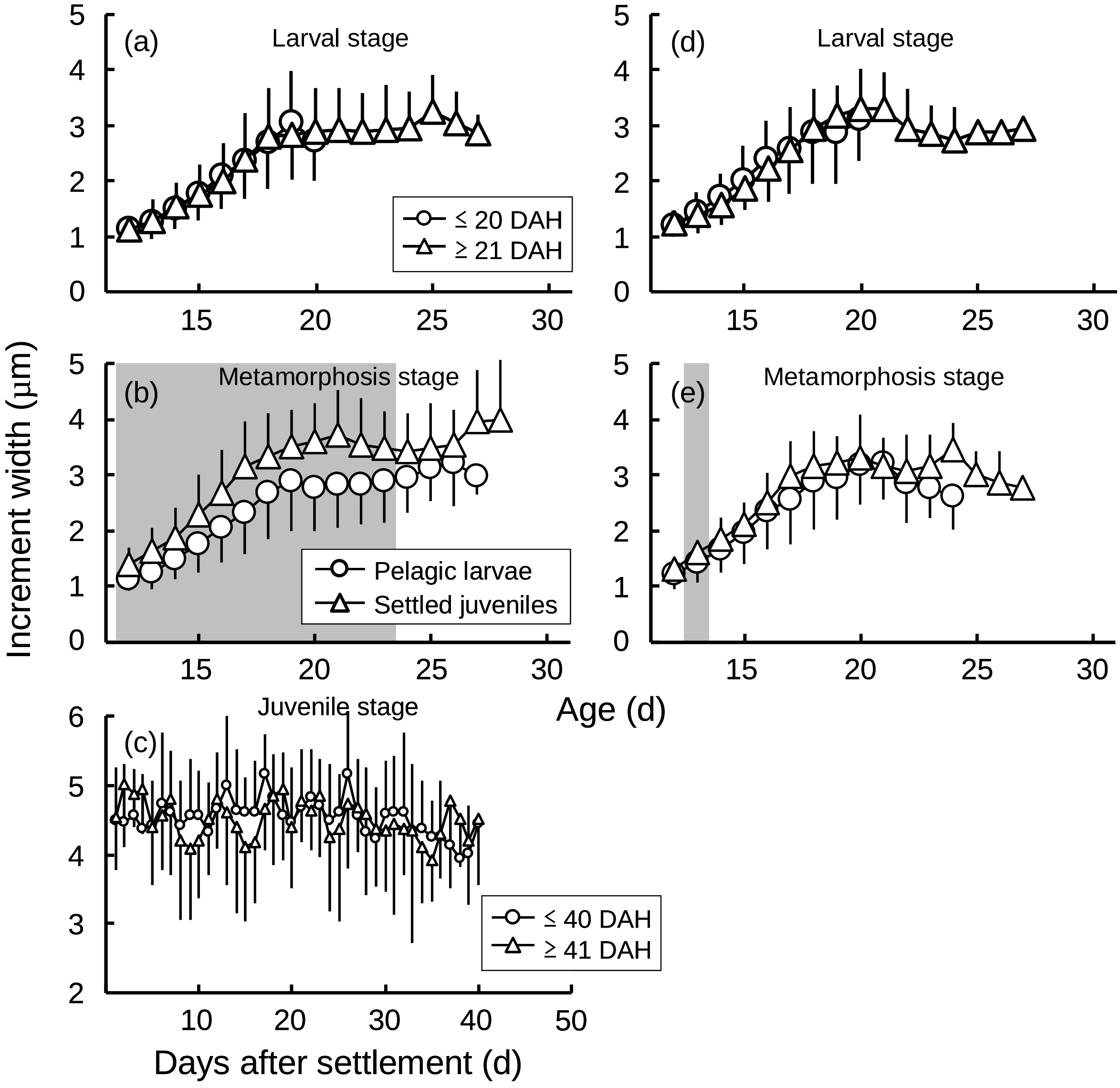

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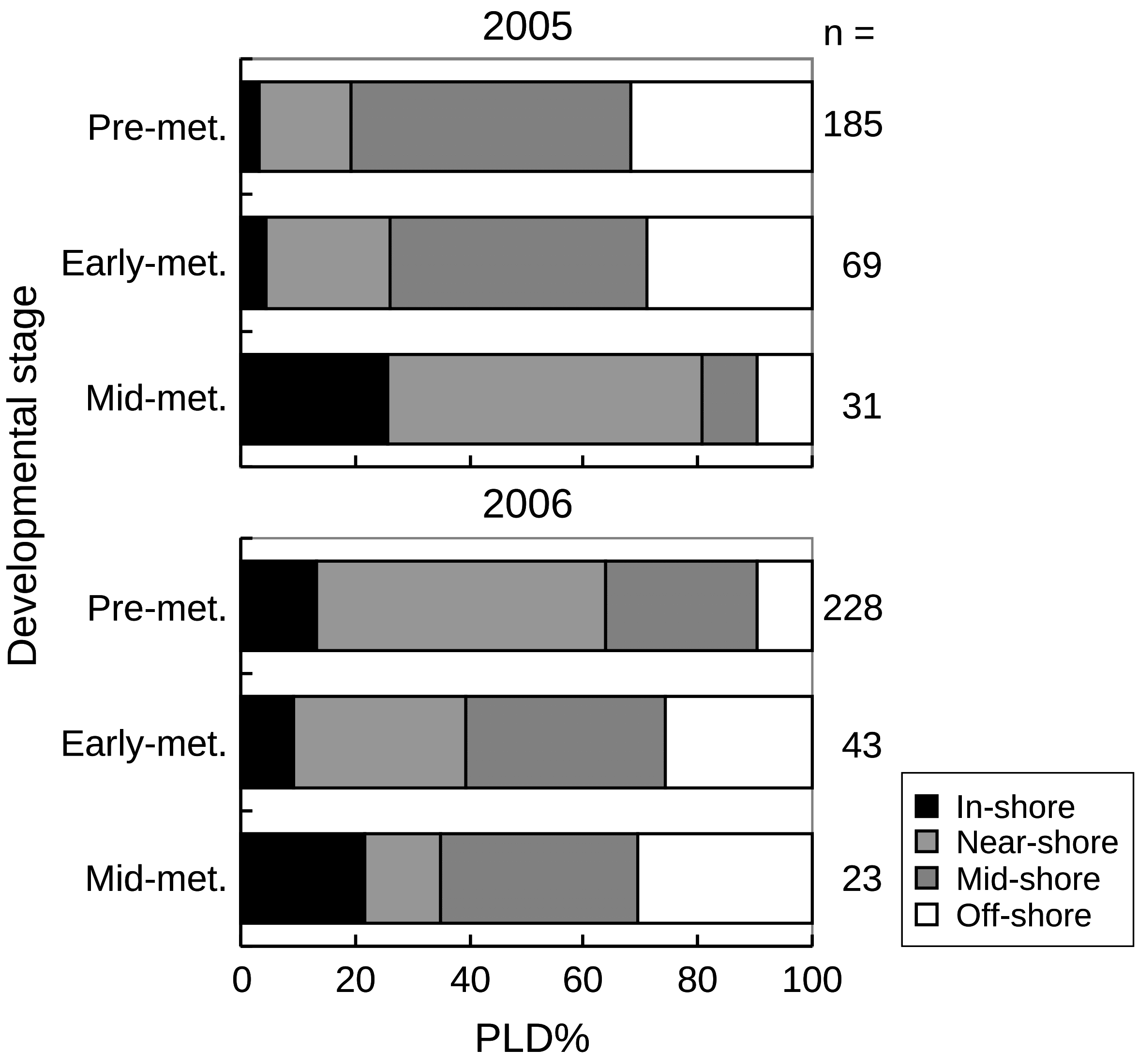

Oshima et al., Figure 10