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Interannual growth differences and growth-selective survival in larvae and juveniles of marbled sole (*Pseudopleuronectes yokohamae*)

Running head: Growth-selective survival in marbled sole larvae and juveniles

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ABSTRACT: Flatfishes drastically change their habitat, body form, and feeding during metamorphosis, thus the early juvenile stage is viewed as being critical for early survival (as is the larval stage). However, to the best of our knowledge, no studies have tested the growth-mortality hypothesis for both larval and juvenile stages of flatfishes. Thus, we

20 investigated the relationship between growth rate and environmental factors and test the
21 hypothesis for both larval and juvenile stages of marbled sole (*Pseudopleuronectes*
22 *yokohamae*) in Hakodate Bay, Japan in 2001–2003. For both larval and juvenile stages, otolith
23 growth correlated with water temperature. Eye-migrating larvae were defined as survivors of
24 planktonic life (SV_{pelagic}). Large juveniles captured in late June and July were defined as
25 survivors of shrimp predation (SV_{juvenile}). To test the growth–mortality hypothesis, otolith
26 growth was compared between the SV and the original population (OP). During the pelagic
27 larval stage, growth-selective survival was not detected in any of the three years. During the
28 early juvenile stage, fast growing individuals survived selectively in 2002 but not in 2003. In
29 2002, population growth of juveniles was slow because the temperature experienced by
30 juveniles was low. Thus, juveniles in 2002 required time to exceed the size spectrum that is
31 vulnerable to shrimp predation, and consequently, the individuals that grew more rapidly were
32 able to survive selectively. The present study showed the importance of the early juvenile
33 stage for the survival of flatfishes.

34

35 **INTRODUCTION**

36 Fluctuations in the recruitment level of marine fishes are mainly determined by variations
37 in survival during the early life stages (Houde 1987). Anderson (1988) summarized the theory
38 of recruitment in fishes and hypotheses pertaining to causes of recruitment fluctuation and

39 suggested that the growth-mortality hypothesis was a rational concept for recruitment
40 research and a solid basis for future study. This hypothesis states that fast growing individuals
41 can pass the spectrum of somatic size that is vulnerable to predation and thus increase their
42 chance of survival. Therefore, understanding the growth pattern during early life and the
43 relationship between growth and environmental factors is fundamental to understanding
44 recruitment and survival. Moreover, we can assess the growth-mortality hypothesis by
45 comparing growth between survivors and their OP.

46 The relationships between growth and survival of larvae have been investigated for
47 numerous species (Campana 1996, Meekan & Fortier 1996, Bergenius et al. 2002, Takahashi
48 & Watanabe 2004, Takasuka et al. 2004a, b), and the mortality of that stage is many times
49 greater than that of later stages. Larvae of flatfish species are planktonic, thus their habitat is
50 the three-dimensional water column. After metamorphosis, flatfish larvae become juveniles
51 and their habitat shifts to the two-dimensional sea floor. When this shift occurs, the
52 morphology and feeding habits of flatfishes change dramatically. In addition, there are many
53 benthic organisms on the sea floor, and predation of flatfish juveniles by small decapods such
54 as crangonid shrimp has been reported for many flatfish species (van der Veer et al. 1991,
55 Witting & Able 1995, Oh et al. 2001, Taylor & Collie 2003). Thus, mortality during the early
56 juvenile stage likely is high, just as it is during the planktonic larval stage for flatfishes (van
57 der Veer et al. 2000). Hovenkamp (1992) investigated the relationship between growth and

58 mortality during the planktonic larval stage of plaice (*Pleuronectes platessa*), and Fox et al.
59 (2007) studied birth-date selectivity in the survival of the species. However, to the best of our
60 knowledge no studies have tested the growth-mortality hypothesis for both larval and juvenile
61 stages of flatfishes.

62 Marbled sole (*Pseudopleuronectes yokohamae*) is a temperate flatfish species distributed in
63 coastal areas ranging from Japan to the Yellow and Bohai Seas, with latitudinal expansion
64 from the southern part of Hokkaido Island to Kyushu Island. Marbled sole is an important
65 species in bottom-trawl and gill net fisheries. Hakodate Bay, which lies at the southern end of
66 Hokkaido Island, is the northernmost habitat of marbled sole. The spawning season of
67 marbled sole is early spring (February–April) in this area. Environmental factors in this area
68 are variable in spring, and this may affect survival of marbled sole larvae and juveniles.

69 The ecology of the early life stages of marbled sole have been studied previously in
70 Hakodate Bay. For example, Nakaya et al. (2004a, b, 2007) studied predation on marbled sole
71 larvae and juveniles by the sand shrimp *Crangon uritai*, and Joh et al. (2005) described daily
72 periodicity of otolith ring formation. In late March 2003, the Oyashio Coastal Water, which is
73 characterized by low temperature ($< 3^{\circ}\text{C}$) and low salinity (≤ 33.0), flowed into Hakodate Bay,
74 and water temperature in late March became extremely low. Joh et al. (2009) suggested that
75 almost all larvae hatched earlier in the season may have died due to the extremely low water
76 temperature. To date, however, the growth patterns of wild *P. yokohamae* larvae and juveniles

77 have not been studied, nor has the importance of growth for survival been investigated.

78 In the present study, we investigated the growth patterns of marbled sole larvae and
79 juveniles, the relationship between environmental factors and their growth, and the
80 relationship between pelagic larval growth and planktonic larval duration (PLD). Additionally,
81 we investigated the growth selectivity in survival during both the pelagic larval and early
82 juvenile stages.

83

84 **MATERIALS AND METHODS**

85 **Study area, sampling, and treatment of specimens**

86 Hakodate Bay is a small bay (ca. 66.9 km²) located at the southern end of Hokkaido Island
87 (Fig. 1). Adult marbled sole females spawn demersal adhesive eggs on the bottom along the
88 30 m isobath in the eastern part of the bay mouth near Mt. Hakodate (Fig. 1). Pelagic larvae
89 are abundant in the eastern part of Hakodate Bay but are scarce in the western part and outside
90 of the bay (Nakagami et al. 2001). Settled juveniles are abundant off Nanaehama in the inner
91 part of Hakodate Bay. Therefore, larvae and juveniles were collected along a transect
92 consisting of five stations beginning at Nanaehama and heading in the direction of the
93 spawning ground (Joh et al. 2009). These sampling stations were at depths of 3, 5, 10, 15, and
94 20 m, respectively.

95 In 2001, 2002, and 2003, sampling for marbled sole larvae and small juveniles was

96 conducted from March to May (Table 1). Pelagic larvae were collected in triplicate oblique
97 tows of a plankton net (net opening diameter: 80 cm; mesh aperture: 0.33 mm; a flow meter
98 was installed at the mouth) at each station. Larvae and juveniles distributed near and on the
99 sea floor were collected by simultaneous tows with two Hirota's sledge nets (mouth opening:
100 60×40 cm; mesh aperture: 0.50 mm; Hirota et al. 1989). Sampling for larger juveniles was
101 carried out in June and July. Simultaneous tows with two sledge nets were conducted two or
102 three times at each station. Larvae and juveniles were preserved in a 90% ethanol solution.
103 The densities of larvae collected by plankton net were converted to number per square meter
104 based on the rotations of the flow meter, the mouth opening of the net (0.50 m^2), and the
105 length of warp. The density of juveniles collected by sledge net was converted to the number
106 per 100 m^2 . The catch efficiency of the sledge net was assumed to be 1 (Joh et al. 2009).

107 Notochord length was measured for larvae and standard length (SL) was measured for
108 juveniles using digital calipers. We used the lapilli for otolith microstructure analysis.
109 Throughout the larval and juvenile stages, the lapilli of marbled sole can be observed without
110 being sectioned (Joh et al. 2005). The shapes of lapillar otoliths from both sides are similar
111 during the larval stage, but the lapilli of large juveniles are bilaterally asymmetrical (Joh et al.
112 2005). Therefore, we used ocular side lapilli for otolith measurements for the juveniles. The
113 number of otolith increments was counted and the increment widths were measured using an
114 otolith measurement system (ARP Ver. 5.00, Ratoc System Engineering Co., Tokyo, Japan).

115 See Joh et al. (2005, 2009) for details about otolith preparation and analysis for marbled sole.

116

117 **Water temperature and prey density**

118 On each sampling day, water temperature was measured using a Seabird CTD system
119 (SBE-19, Sea Bird Electronics Inc., Bellevue, Washington, USA) in every 3 or 5 m depth
120 layer from the sea surface to the sea floor (i.e., 0 and 3 m at Stn 3; 0 and 5 m at Stn 5; 0, 5,
121 and 10 m at Stn 10; 0, 5, 10, and 15 m at Stn 15; 0, 5, 10, 15, and 20 m at Stn 20). In
122 Hakodate Bay, pelagic larvae of marbled sole are scarce in the 0 m depth layer (Nakagami et
123 al. 2001). Thus, for each sampling date, the mean water temperature for pelagic larvae was
124 calculated for all layers except for the 0 m depth layer. Because juvenile marbled sole inhabit
125 the sea floor, the mean water temperature for juveniles was calculated from temperatures
126 measured on the sea floor at the five stations on each sampling date. Unfortunately, we could
127 not measure water temperature daily; therefore, the estimation of water temperature between
128 two sampling dates was required. We assumed that the change in temperature between two
129 sampling days was linear, and we interpolated the water temperature on each day between two
130 sampling dates based on each line. In this way we obtained the daily sequence of water
131 temperature for each year and generated a "temperature calendar."

132 Using these data, we estimated the temperature that individual larvae and juveniles
133 experienced. For each larva, the date on which otolith ring formation began was estimated

134 based on otolith microstructure analysis, and the trajectory of temperatures that each larva
135 experienced from that date to the sampling date was extracted from the temperature calendar.
136 For juveniles, the date on which each individual reached the juvenile stage was estimated
137 from otolith microstructure analysis (see below: "Definition of larval and juvenile ages"), and
138 the trajectory of temperatures that each juvenile experienced from that date to the sampling
139 date was extracted from the temperature calendar. Individual data then were pooled by year
140 and mean experienced water temperature was calculated for each age (see Fig. 2).

141 For pelagic larvae, the densities of copepod nauplii (the principle prey item for pelagic
142 larvae) were estimated for each sampling day (Joh et al. 2009). Using the same method as that
143 used to generate the temperature calendar, we assumed that the change in prey densities
144 between two sampling days was linear, and we obtained the daily sequence of prey density for
145 each year. Based on this daily sequence of prey density, the trajectory of prey density that
146 each pelagic larva experienced was estimated individually.

147

148 **Definition of larval and juvenile ages**

149 For marbled sole, the onset of daily otolith increment formation occurs at the time of
150 transition from endogenous to exogenous nutritional sources (Joh et al. 2005). In the present
151 study, the age of larva was defined as the number of days after the onset of otolith ring
152 formation (larval age: LA), not as the days after hatching.

153 Settlement of marbled sole larvae occurs before the completion of eye migration (Fukuhara
154 1988). On the lapillus, the outer check is formed at the onset of eye migration, thus the rings
155 formed inside and outside of the outer check are thought to be formed during the pelagic and
156 demersal phases, respectively (Joh et al. 2005). For eye-migrating larvae, we measured the
157 distance from the outer check to the otolith edge of the ocular side lapillus, and we pooled
158 those measurements for the 2001–2003 year classes. Mean distance for the largest 10% of
159 individuals was 17.1 μm . Therefore, we assumed that the first otolith ring in the juvenile stage
160 formed 17.1 μm outside of the outer check. We defined the number of otolith rings formed
161 outside that first ring as juvenile age (JA), not as the age after hatching.

162

163 **Interannual growth differences and planktonic larval duration (PLD)**

164 The otolith radii and body lengths were positively correlated for pelagic larvae,
165 eye-migrating larvae, and juveniles of marbled sole. However, we did not express that
166 relationship as a single formula throughout the larval and juvenile stages (Fig. 3). Therefore,
167 we did not estimate somatic growth trajectories using back-calculation techniques. Instead,
168 we treated the width of the otolith increment for each age (WA: width at age) as an alternative
169 measure of somatic growth, as in Searcy and Sponaugle (2000) and Robert et al. (2007, 2010).
170 In late March 2003, low temperature and low salinity Oyashio Coastal Water flowed into the
171 study area, thus water temperature in this area declined considerably. Joh et al. (2009)

172 reported that pelagic larvae that hatched before 17 March 2003 (i.e., the early hatched cohort)
173 did not appear in the nutritional transition date distribution (NTDD) after April. They
174 suggested that almost all of the early hatched cohort may have died because of the critical
175 decline in temperature. Therefore, we did not include the early hatched cohort collected in
176 March 2003 in the analysis of present study.

177 The growth patterns of pelagic larvae in the three year classes were compared using
178 repeated measures MANOVA, which is suitable for analysis of longitudinal data such as
179 successive increment width data from fish otoliths (Chambers & Miller 1995). Repeated
180 measures MANOVA allows for differences in the number of fish individuals among year
181 classes, but it requires that the length of repeated measurements in each individual be equal.
182 In the present study, we used ≥ 10 days LA larvae and compared WAs during 0–10 days LA.
183 Similarly, we used ≥ 30 days JA juveniles and compared otolith growth during 0–30 days JA
184 (Table 2).

185 To investigate the effect of water temperature and prey density on the growth of pelagic
186 larvae, we used the generalized linear model (GLM). Individual mean WA, mean experienced
187 temperature, and mean prey density during 0–10 days LA in 2001–2003 were pooled. Mean
188 WA was used as the response variable, and mean experienced temperature, prey density, and
189 the interaction term were used as explanatory variables. The response variable was assumed
190 to follow the normal distribution. To minimize the number of parameters, model selection was

191 conducted by maximizing the goodness of fit given by Akaike's information criterion (AIC;
192 Akaike 1974). Analyses were carried out using the statistical software R, version 2.15.1
193 (<http://cran.r-project.org/>). To investigate the relationship between the experienced water
194 temperature and juvenile growth, individual mean WA and mean experienced temperature
195 during 0–30 days JA in 2001–2003 were pooled, and the correlation between temperature and
196 growth was analyzed.

197 On the otoliths of eye-migrating larvae and juveniles, the number of rings formed from the
198 start of ring formation to the end of pelagic life was defined as the PLD, and the relationship
199 between growth during the pelagic larval phase and PLD was investigated.

200

201 **Growth-selective survival**

202 Marbled sole larvae settle on the sea floor during the eye-migrating stage (Fukuhara 1988),
203 thus those eye-migrating larvae are assumed to have survived pelagic larval life. We defined
204 the eye-migrating larvae captured in late April–May as survivors (SV_{pelagic}), and their growth
205 trajectories during the early pelagic larval stage (0–10 days LA) were compared with those of
206 their original population (OP_{pelagic}). OP_{pelagic} refers to the planktonic larval population that
207 satisfied the following conditions: 1) larvae were collected from March to early April; 2) the
208 nutritional transition date (NTD) of larvae was included in the range of the NTDD of
209 SV_{pelagic} ; and 3) larvae were older than 10 days LA.

210 The sand shrimp *C. writai* preys on metamorphosing larvae and juveniles (Nakaya et al.
211 2004a, b, 2007); to date other demersal predators of marbled sole larvae and juveniles have
212 not been found in Hakodate Bay (Nakaya 2004). Marbled sole juveniles larger than
213 15.4 mm SL were not vulnerable to predation by *C. writai* (Joh et al. 2009). Thus, we defined
214 large juveniles (20.2–59.7 mm SL) collected in late June and July as survivors of predation
215 (SV_{juvenile}), and we compared their otolith growth during 0–20 days JA with that of their
216 original population (OP_{juvenile}). OP_{juvenile} refers to small juveniles that satisfied the following
217 conditions: 1) juveniles were collected from April to early June; 2) the date on which each
218 juvenile started its juvenile life was included in the range of distribution of dates on which
219 SV_{juvenile} started their juvenile life; and 3) juveniles were older than 20 days JA and smaller
220 than 15.4 mm SL. We did not compare growth trajectories between $SV_{\text{juveniles}}$ and $OP_{\text{juveniles}}$ in
221 2001 because we did not collect sufficient numbers of small juveniles that satisfied the
222 conditions for the original population.

223 If the ranges of the NTDD for SV_{pelagic} and the date when they became juveniles for
224 $SV_{\text{juveniles}}$ are very wide, the environmental factors experienced by the early and the late
225 cohorts of SV might differ. In this case, dividing the SVs into seasonal sub-groups may be a
226 more appropriate way of conducting the analysis. However, we did not conduct the
227 sub-grouping. One of the reasons that we did not conduct sub-grouping was small numbers of
228 specimens (see Discussion).

229

230 **Comparison of early pelagic larvae and large juvenile densities**

231 To evaluate interannual differences in survivorship from the nutritional transition (NT)
232 stage to the end of shrimp predation, we compared the density of larvae that were at the NT
233 stage and large juveniles collected in July. In each year, the density of large juveniles
234 collected in July was plotted vs. the density of larvae at the NT stage, and the slope was
235 calculated. If the density of large juveniles is low and the density of larvae is high (low
236 survivorship), the slope is low. Then, the slope was defined as the survival index, and the
237 index values were compared among years.

238

239 **RESULTS**

240 **Water temperatures and prey densities experienced by larvae and juveniles**

241 The water temperatures experienced by pelagic larvae from 0 to 10 days LA differed
242 among the three years (repeated measures MANOVA: F value: 225.7, $p < 0.001$). Mean
243 temperature at 0 day LA was 7.1 °C in 2001, 8.0 °C in 2002, and 5.6 °C in 2003, and the
244 temperatures increased with time. The mean temperatures for the 0 to 10 day LA interval were
245 high in 2002 (8.4 °C; Fig. 2), medium in 2001 (7.5 °C), and low in 2003 (6.1 °C).

246 The prey densities experienced by pelagic larvae from 0 to 10 days LA also differed among
247 the three years (Fig. 2; repeated measures MANOVA: F value: 574.6, $p < 0.001$). The mean

248 prey densities experienced by pelagic larvae were high in 2001 (61.6 inds/L), medium in 2003
249 (50.8 inds/L), and low in 2002 (19.7 inds/L).

250 The water temperatures experienced by juveniles from 0 to 30 days JA differed among the
251 three years (repeated measures MANOVA: F value: 16.37, $p < 0.001$). The mean temperatures
252 that juveniles experienced from 0 to 12 days JA were 9.7 °C in 2002 and 2003 and 9.3 °C in
253 2001 (Fig. 2). After 13 days JA, the increase in temperature in 2002 was slower than in the
254 other years, and the mean temperatures experienced by juveniles from 13 to 30 days JA were
255 low in 2002 (10.4 °C), medium in 2001 (11.1 °C), and high in 2003 (11.6 °C).

256

257 **Comparison of otolith growth among year classes**

258 In all year classes, the WAs were roughly constant during 0–10 days LA. The mean WAs
259 (\pm SD) during 0–10 days LA (2001: $0.56 \pm 0.12 \mu\text{m}$; 2002: $0.60 \pm 0.12 \mu\text{m}$; 2003:
260 $0.56 \pm 0.12 \mu\text{m}$) differed among year classes (repeated measures MANOVA: F value: 6.88,
261 $p = 0.001$). The mean WA in 2002 was significantly higher than those in 2001 and 2003
262 (Fig. 4), but the WAs in 2001 and 2003 did not differ significantly during 0–10 days LA
263 (Scheffe post hoc comparison: range of p values: 0.36–0.99).

264 The effect of water temperature and prey density on the growth of pelagic larvae was
265 analyzed using the GLM (Table 3), and the AIC of the model in which only water temperature
266 was included as the explanatory variable was smallest among the models tested.

267 The mean WAs (\pm SD) during 0–30 days JA (2001: $1.56 \pm 0.35 \mu\text{m}$; 2002: $1.58 \pm 0.41 \mu\text{m}$;
268 2003: $1.77 \pm 0.40 \mu\text{m}$) differed among year classes (Fig. 4; repeated measures MANOVA: F
269 value: 19.47, $p < 0.001$). For most ages, the WAs in 2003 were higher than those in other
270 years. From 2 to 13 days JA, the WAs in 2002 were medium and those in 2001 were low.
271 However, from 14 to 18 days JA, the WAs in 2001 were similar to those in 2002, and the
272 former then became higher than the latter after 19 days JA. In the 2002 and 2003 year classes,
273 the WAs of older juveniles decreased gradually. The WAs in 2001, however, decreased during
274 0–10 days JA, increased during 11–25 JA, and then decreased slightly after 26 days JA. The
275 mean WA during 0–30 days JA and experienced water temperature were significantly
276 positively correlated ($r = 0.39$, $p < 0.001$; Fig. 5).

277 The mean (\pm SE) PLDs of eye-migrating larvae and juveniles were 23 (± 0.56) in 2001,
278 20 (± 0.21), and 22 (± 0.30) in 2003. The PLD and the mean WA during pelagic life were
279 significantly negatively correlated ($r = -0.46$, $p < 0.001$).

280

281 **Growth-selective survival**

282 In 2001–2003, the WAs in 0–10 days LA did not differ between SV_{pelagic} and OP_{pelagic}
283 (repeated measures MANOVA: 2001, 2002, and 2003: $p = 0.91$, 0.34 , and 0.08 , respectively;
284 Fig. 6).

285 For the 2002 year class, the WAs of SV_{juvenile} were significantly higher than those of

286 OP_{juvenile} (repeated measures MANOVA: F value: 6.58, p = 0.01, Fig. 6). For the 2003 year
287 class, the WAs of SV_{juvenile} were similar to those of OP_{juvenile} (repeated measures MANOVA: F
288 value: 0.52, p = 0.47). In 2002 and 2003, the WAs of both groups decreased with age.

289

290 **Comparison of early pelagic larvae and large juvenile densities**

291 The densities of larvae in the NT stage in March and April 2001, 2002, and 2003 were 2.1,
292 12.5, and 3.6 inds/m², respectively. The densities of large juveniles collected in July 2001,
293 2002, and 2003 were 0.77, 2.25, and 1.57 inds/100 m² respectively (Fig. 7). Thus, the survival
294 indices in 2001, 2002, and 2003 were 0.36, 0.18, and 0.46, respectively. In 2002, larvae and
295 large juveniles were abundant, but the survival index was the lowest among the three years
296 studied.

297

298 **DISCUSSION**

299 **The effects of environmental factors on growth**

300 Among the three years studied, the growth of pelagic larvae was highest in 2002 when
301 water temperature was highest. For other flatfish species, positive relationships between water
302 temperature and larval growth rate have been reported from rearing experiments (Japanese
303 flounder *Paralichthys olivaceus*: Seikai et al. 1986; summer flounder *Paralichthys dentatus*:
304 Burke et al. 1999; sole *Solea solea*: Lagardere 1989) and in the field (plaice larvae:

305 Hovenkamp 1989, 1990). Generally, prey abundance is an important factor affecting larval
306 growth. Copepod nauplii are major prey items for marbled sole larvae (Nakagami 2001).
307 However, in the present study the density of copepod nauplii was not an explanatory variable
308 for the growth of pelagic larvae. Thus, our results suggest that water temperature may be a
309 key factor affecting the growth of marbled sole pelagic larvae and that larvae may grow fast
310 in the high water temperature range observed in 2001–2003. In contrast, the prey densities
311 observed in 2001–2003 may not affect the growth of marbled sole larvae.

312 Pelagic larvae experienced distinctly different water temperatures in 2001 and 2003 (the
313 mean values were 7.5 and 6.0 °C, respectively). However, the mean WAs of pelagic larvae did
314 not differ significantly between these two years (the mean value was 0.56 µm in both years).
315 Nakagami (2001) investigated the effect of water temperature and prey density on feeding by
316 marbled sole pelagic larvae in Hakodate Bay in 1997–2000. He found that marbled sole
317 larvae could not feed on prey organisms satisfactorily in < 7.5 °C water even if prey density
318 was abundant. Moreover, he proposed that almost all larvae in 1999 might have starved and
319 died due to feeding failure caused by the low water temperature. Feeding condition data for
320 pelagic larvae in 2001–2003 were not available; however, water temperatures were 7.5 °C in
321 2001 and < 7.5 °C in 2003. Therefore, the growth rate of pelagic larvae in 2001 and 2003 may
322 have been low due to feeding failure caused by low water temperatures.

323 The PLD of eye-migrating larvae and juveniles negatively correlated with growth during

324 pelagic life. The present study showed that high water temperature may have enhanced the
325 growth of pelagic larvae and that fast growth quickened larval development and shortened the
326 PLD. In a rearing experiment, Mutsutani (1988) found that a positive relationship between
327 high water temperature and larval growth, and that a negative relationship between larval
328 growth and the length of PLD for marbled sole (range: 10–18 °C). In the field, larval growth
329 of North Sea plaice was high and the number of days until the completion of metamorphosis
330 was small in a warm year (Hovenkamp and Witte, 1991).

331 The investigation of the effects of larval growth and the length of PLD on the body size of
332 newly-settled juveniles allowed us to examine whether such larval features affect
333 size-selective mortality during the early juvenile phase. However, the relationship between
334 otolith radii and body length was non-linear during the pelagic and eye-migrating stages (Joh
335 et al. 2005). Similar non-linearity has been reported for many flatfish species. This non-linear
336 relationship precludes the back calculation of body length by the biological intercept method
337 (Campana 1990). Thus, we could not examine the effects of larval growth and the length of
338 PLD on the body size of newly-settled juveniles.

339 Juvenile growth and water temperature correlated positively. Moreover, the patterns of
340 seasonal and interannual change in otolith growth in the 2001 and 2002 year classes were
341 similar to seasonal and interannual changes in water temperature. These results suggest that
342 water temperature strongly affected the growth of juveniles, as it did for larvae. The positive

343 relationships between water temperature and the growth of juveniles have been reported for
344 other flatfish species (sole and plaice: Amara 2003). Conversely, May and Jenkins (1992)
345 reported that the relationships between water temperature and the growth of juvenile flounder
346 *Rhombosolea tapirina* were positive for the early cohort that hatched in winter but negative
347 for the late cohort that hatched in spring. The relationship between water temperature and the
348 growth of larvae and juveniles is usually dome shaped (Boehlert 1981), and growth rate
349 increases with the rise of temperature below the most appropriate temperature but decreases
350 beyond the optimum. In the present study, the growth rate of juvenile marbled sole was high
351 during the warmer year. Thus, in Hakodate Bay, the highest water temperature observed might
352 be below the optimum, and growth stagnation caused by unsuitable high water temperature
353 might not have occurred for marbled sole juveniles in 2001–2003.

354 Generally, prey abundance is one of the important factors affecting the growth of fish
355 juveniles (Malloy et al. 1996, Karakiri et al. 1989, 1991). However, van der Veer (1986)
356 reported that prey abundance did not affect the growth of juvenile plaice. The principal prey
357 item for small marbled sole juveniles in May–August in Hakodate Bay is demersal
358 harpacticoid copepods (Nakagami et al. 2000). We did not investigate the effect of prey
359 abundance on marbled sole juveniles in the present study because of the difficulty in sampling
360 demersal harpacticoid copepods. The effects of prey abundance on the growth of marbled sole
361 juveniles need to be evaluated with rearing experiments in the future.

362

363 **Growth-selective survival**

364 In the growth comparison between SV and OP, the larvae and juveniles included in OP
365 were limited by their NTD or by the date when they became juveniles. If the ranges of the
366 NTDD for SV_{pelagic} and the date when they became juveniles for $SV_{\text{juveniles}}$ are very wide, the
367 environmental factors experienced by the early and the late cohorts of SV might differ. In this
368 case, dividing the SVs into seasonal sub-groups may be a more appropriate way of conducting
369 the analysis. However, the numbers of days between the 25 and 75 percentiles of the NTD of
370 SV_{pelagic} were relatively narrow (9 days in 2001, 8 days in 2002 and 2003; Fig. 8). The
371 numbers of days between the 25 and 75 percentiles of the day when they became juveniles of
372 $SV_{\text{juveniles}}$ were also narrow (9 days in 2002, 7 days in 2003), and the changes in water
373 temperature were relatively stationary. Thus, we did not conduct sub-grouping in the present
374 study. Water temperature during the larval phase in 2003 was lower in the early phase than in
375 the late phase (upper panel in Fig. 8), so the survival pattern might differ between the early
376 and the late cohorts of SV_{pelagic} . However, sub-grouping also could not be conducted for
377 SV_{pelagic} in 2003 because of small numbers of specimens.

378 During the early pelagic stage, growth-selective larval survival was not detected for any of
379 the year classes. Although water temperature was low in 2003, growth-selective survival was
380 not detected. The growth-mortality hypothesis is based on the concept that fast growing larvae

381 and juveniles have the advantage of high survival by growing large enough to avoid predation
382 (Anderson 1988). However, predators of marbled sole pelagic larvae have not been identified
383 to date, and predation risk has not been estimated in Hakodate Bay and its vicinity.

384 Starvation might be another source of larval and juvenile mortality. Almost all larvae that
385 underwent NT before 17 March 2003 were thought to have died due to feeding failure caused
386 by extremely low water temperature (Joh et al. 2009). However, larvae that underwent NT
387 after 17 March 2003 could have survived to the juvenile stage, and growth-selective mortality
388 was not detected for larvae in 2003.

389 Among flatfish species, the PLD of marbled sole is relatively short, and this may be
390 another reason for the absence of growth-selective survival of pelagic larvae. Of the 120
391 flatfish species that inhabit the northern Pacific, only five (including marbled sole) spawn
392 adhesive and demersal eggs. This characteristic probably avoids the risk of advection of eggs
393 (i.e., passive transport) to inappropriate locations (Rijnsdorp & Witthames 2005). Moreover,
394 eye-migrating larvae of marbled sole start their demersal life before the completion of
395 metamorphosis (Fukuhara 1988). Therefore, the PLD of marbled sole larvae may be shorter
396 than that of other flatfishes that spawn floating eggs and start their demersal life after the
397 completion of eye migration.

398 In the early juvenile stage, growth-selective survival was detected in 2002 but not in 2003.
399 Sand shrimps are known to be predators of demersal larvae and juveniles for some flatfish

400 species (van der Veer et al. 1991, Witting & Able 1995, Oh et al. 2001, Taylor & Collie 2003).
401 In Hakodate Bay, predation on demersal larvae and juveniles of marbled sole by *C. uritai* has
402 been reported (Nakaya et al. 2004a, b, 2007), but no other predator has been observed
403 (Nakaya 2004). Therefore, we propose that growth-selective survival of the juvenile stage
404 may occur in relation to predation by *C. uritai*. Population growth of juveniles was slow in
405 2002 because of low water temperature. Thus, juveniles required time to exceed the size
406 spectrum that is vulnerable to shrimp predation; the individuals that grew more rapidly were
407 able to survive, thereby exhibiting growth-selective survival. In contrast, survival in the
408 juvenile stage was not growth related in 2003. In 2003, water temperature experienced by
409 pelagic larvae was low, but it quickly increased during the early juvenile stage, thus allowing
410 juveniles to grow quickly in the warmer environment. In 2003, juveniles likely passed more
411 rapidly through the risky size spectrum preferred by shrimp, and consequently
412 growth-selective survival was not detected in 2003.

413

414 **Comparison of early pelagic larvae and large juvenile densities**

415 The survival index in 2002 was 0.18 and was the lowest among the three year classes (2001
416 and 2003: 0.36 and 0.46, respectively). This means that survivorship between the completion
417 of the NT and the end of the phase vulnerable to predation by sand shrimps likely was low in
418 2002. The growth rate of pelagic larvae and water temperature were high in 2002 but low in

419 2001 and 2003. Additionally, survival of the pelagic larval stage was not growth selective in
420 any of the years studied. These results suggest that the difference in survivorship between
421 2002 and 2003 was not related to the pelagic larval stage.

422 Population growth rate of juveniles and water temperature were lowest in 2002, and
423 survival of the early juvenile stage was growth selective in 2002 (but not in 2003). These
424 findings suggest that for marbled sole in Hakodate Bay, interannual fluctuations in cumulative
425 survivorship throughout the pelagic larval and early juvenile stages were more affected by
426 growth and survival of the juvenile stage than those of the pelagic larval stage. Although we
427 did not evaluate the occurrence of density-dependent mortality of early juveniles in 2002,
428 predation on larval and juvenile marbled sole by *C. uritai* reportedly is density independent,
429 size specific, and spatial-distribution-overlap dependent (Nakaya et al. 2004a, 2007).

430 Joh et al. (2009) suggested that almost all of the pelagic larvae hatched before 17 March
431 2003 may have died due to the critical decline of temperature caused by intrusion of cold
432 Oyashio Coastal Water. Therefore, we propose that the pelagic larval stage also is an
433 important period for survival of the population under extremely severe conditions. The
434 Tsugaru Warm Current flows into the bay throughout the year. Hakodate Bay is the
435 northernmost habitat of marbled sole. The spawning season of marbled sole in Hakodate Bay
436 starts in late winter and ends in early spring (February–April) and water temperatures in this
437 season were lowest of the years. We suggest that the large volume of thermal transport by the

438 Tsugaru Warm Current to the bay probably sustains the reproduction of marbled sole in
439 Hakodate Bay.

440

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451

452 **LITERATURE CITED**

453 Akaike H (1974) A new look at the statistical model identification. *IEEE Trans Autom Contr*
454 19: 716–723

455 Amara R (2003) Seasonal ichthyodiversity and growth patterns of juvenile flatfish on a
456 nursery ground in the Southern Bight of the North Sea (France). *Env Biol Fish* 67:

- 457 191–201
- 458 Anderson JT (1988) A review of size dependent survival during pre-recruit stages of fishes in
459 relation to recruitment. *J Northw Atl Fish Sci* 8: 55–66
- 460 Bergenius MA, Meekan MG, Robertson RD, McCormick MI (2002) Larval growth predicts
461 the recruitment success of a coral reef fish. *Oecologia* 131: 521–525
- 462 Boehlert G (1981) The effects of photoperiod and temperature on laboratory growth of
463 juvenile *Sebastes diploproa* and a comparison with growth in the field. *Fish Bull* 79:
464 789–794
- 465 Burke JS, Seikai T, Tanaka Y, Tanaka M (1999) Experimental intensive culture of summer
466 flounder, *Paralichthys dentatus*. *Aquaculture* 176: 135–144
- 467 Campana SE (1990) How reliable are growth back-calculations based on otoliths? *Can J Fish*
468 *Aquat Sci* 47: 2219–2227
- 469 Campana SE (1996) Year-class strength and growth rate in young Atlantic cod *Gadus morhua*.
470 *Mar Ecol Prog Ser* 135: 21–26
- 471 Chambers RC, Miller TJ (1995) Evaluating fish growth by means of otolith increment
472 analysis: special properties of individual-level longitudinal data. In: Secor DH,
473 Campana SE (eds) *Recent Developments in Fish Otolith Research*. University of
474 South Carolina Press, Columbia, USA, p 155–175
- 475 Fox CJ, Geffen AJ, Taylor N, Davison P, Rossetti H, Nash RDM (2007) Birth-date selection

476 in early life stages of plaice *Pleuronectes platessa* in the eastern Irish Sea (British
477 Isles). Mar Ecol Prog Ser 345: 255–269

478 Fukuhara O (1988) Morphological and functional development of larval and juvenile
479 *Limanda yokohamae* (Pisces: Pleuronectidae) reared in the laboratory. Mar Biol 99:
480 271–281

481 Hirota Y, Tominaga S, Ueharako T, Kodama K, Sadayuki T, Tanaka M, Yoshida S, Kojima H,
482 Okiishi Y (1989) Spatial distribution of mysids in coastal areas in the Japan Sea.
483 Cont Fish Res Jpn Sea Block 15: 43–57 (in Japanese)

484 Houde ED (1987) Fish early dynamics and recruitment variability. Ame Fish Soc Sym
485 2:17–29

486 Hovenkamp F (1989) Within-season variation in growth of larval plaice (*Pleuronectes*
487 *platessa* L.). Rapp P -v Reun Cons Int Explor Mer 191: 248–257

488 Hovenkamp F (1990) Growth differences in larval plaice *Pleuronectes platessa* in the
489 Southern Bight of the North Sea as indicated by otolith increments and RNA/DNA
490 ratios. Mar Ecol Prog Ser 58: 205–215

491 Hovenkamp F (1992) Growth-dependent mortality of larval plaice *Pleuronectes platessa* in
492 the North Sea. Mar Ecol Prog Ser 82: 95–101

493 Hovenkamp F, Witte JIJ (1991) Growth, otolith growth and RNA/DNA ratios of larval plaice
494 *Pleuronectes platessa* in the North Sea 1987 to 1989. Mar Ecol Prog Ser 70:

495 105–116

496 Joh M, Takatsu T, Nakaya M, Higashitani T, Takahashi T (2005) Otolith microstructure and
497 daily validation of marbled sole *Pseudopleuronectes yokohamae*. Mar Biol 147:
498 59–69

499 Joh M, Takatsu T, Nakaya M, Yoshida N, Nakagami M (2009) Comparison of the nutritional
500 transition date distributions of marbled sole larvae and juveniles in Hakodate Bay,
501 Hokkaido. Fish Sci 75: 619–628

502 Karakiri M, Berghahn R, von Westernhagen H (1989) Growth differences in 0-group plaice
503 *Pleuronectes platessa* as revealed by otolith microstructure analysis. Mar Ecol Prog
504 Ser 55: 15–22

505 Karakiri M, Berghahn R, van der Veer HW (1991) Variations in settlement and growth of
506 0-group plaice (*Pleuronectes platessa* L.) in the Dutch Wadden Sea as determined by
507 otolith microstructure analysis. Neth J Sea Res 27: 345–351

508 Lagardere F (1989) Influence of feeding conditions and temperature on the growth rate and
509 otolith-increment deposition of larval Dover sole (*Solea solea* (L.)). Rapp P –v Reun
510 Cons Int Explor Mer 191: 390–399

511 Malloy KD, Yamashita Y, Yamada H, Targett TE (1996) Spatial and temporal patterns of
512 juvenile stone flounder *Kareius bicoloratus* growth rates during and after settlement.
513 Mar Ecol Prog Ser 131: 49–59

- 514 May HMA, Jenkins GP (1992) Patterns of settlement and growth of juvenile flounder
515 *Rhombosolea tapirina* determined from otolith microstructure. Mar Ecol Prog Ser
516 79: 203–214
- 517 Meekan MG, Fortier L (1996) Selection for fast growth during the larval life of Atlantic cod
518 *Gadus morhua* on the Scotian Shelf. Mar Ecol Prog Ser 137: 25–37
- 519 Mutsutani K (1988) Growth and metamorphosis of the marbled sole larvae *Limanda*
520 *yokohamae* (Günter) in Culture. Aquaculture Sci 36: 27–32
- 521 Nakagami M (2001) The spatial and temporal distributions and feeding habits of marbled sole
522 *Pleuronectes yokohamae* larvae and juveniles in the coastal areas of Tsugaru Strait,
523 Hokkaido. PhD Dissertation, Graduate School of Fisheries Sciences, Hokkaido
524 University, Hakodate
- 525 Nakagami M, Takatsu T, Matsuda T, Takahashi T (2000) Feeding on harpacticoid copepods by
526 marbled sole *Pleuronectes yokohamae* juveniles in the coastal area of Tsugaru Strait,
527 Hokkaido. Nippon Suisan Gakkaishi 66: 818–824 (in Japanese with English abstract)
- 528 Nakagami M, Takatsu T, Nakaya M, Takahashi T (2001) Spatial and temporal distribution of
529 larval and juvenile marbled sole *Pleuronectes yokohamae* in Hakodate Bay. Bull Jpn
530 Soc Fish Oceanogr. 65: 85–93 (in Japanese with English abstract)
- 531 Nakaya M (2004) Spatial and temporal distribution, and feeding habits of a sand shrimp
532 *Crangon uritai* as a predator for larval and juvenile marbled sole in Hakodate Bay.

533 PhD dissertation, Graduate School of Fisheries Sciences, Hokkaido University,
534 Hakodate

535 Nakaya M, Takatsu T, Nakagami M, Joh M, Takahashi T (2004a) Spatial distribution and
536 feeding habits of the shrimp *Crangon uritai* as a predator on larval and juvenile
537 marbled sole *Pleuronectes yokohamae*. Fish Sci 70: 445–455

538 Nakaya M, Takatsu T, Nakagami M, Joh M, Takahashi T (2004b) Prey choice order of
539 *Crangon uritai* as a predator for juvenile *Pleuronectes yokohamae*. Aquaculture Sci.
540 52: 121–128

541 Nakaya M, Takatsu T, Joh M, Nakagami M, Takahashi T (2007) Annual variation of potential
542 predation impacts on larval and juvenile marbled sole *Pseudopleuronectes*
543 *yokohamae* by sand shrimp *Crangon uritai* in Hakodate Bay, Hokkaido. Fish Sci 73:
544 112–122

545 Oh CW, Hartnoll RG, Nash RDM (2001) Feeding ecology of the common shrimp *Crangon*
546 *crangon* in Port Erin Bay, Isle of Man, Irish Sea. Mar Ecol Prog Ser 214: 211–223

547 Rijnsdorp AD, Witthames PR (2005) Ecology of reproduction. In: Gibson RN (ed) Flatfishes.
548 Blackwell Publishing Professional, Iowa, USA. p. 68–93

549 Robert D, Castonguay M, Fortier L (2007) Early growth and recruitment in Atlantic mackerel
550 *Scomber scombrus*: discriminating the effects of fast growth and selection for fast
551 growth. Mar Ecol Prog Ser 337: 209–219

- 552 Robert D, Takasuka A, Nakatsuka S, Kubota H, Oozeki Y, Nishida H, Fortier L (2010)
553 Predation dynamics of mackerel on larval and juvenile anchovy: is capture success
554 linked to prey condition? Fish Sci 76: 183–188
- 555 Searcy SP, Sponaugle S (2000) Variable larval growth in a coral reef fish. Mar Ecol Prog Ser
556 206: 213–226
- 557 Seikai T, Tanangonan JB, Tanaka M (1986) Temperature influence on larval growth and
558 metamorphosis of the Japanese flounder *Paralichthys olivaceus* in the laboratory.
559 Bull Jpn Soc Sci Fish 52: 977–982
- 560 Takahashi M, Watanabe Y (2004) Growth rate-dependent recruitment of Japanese anchovy
561 *Engraulis japonicus* in the Kuroshio-Oyashio transitional waters. Mar Ecol Prog Ser
562 266: 227–238
- 563 Takasuka A, Aoki I, Mitani I (2004a) Three synergistic growth-related mechanisms in the
564 short-term survival of larval Japanese anchovy *Engraulis japonicus* in Sagami Bay.
565 Mar Ecol Prog Ser 270: 217–228
- 566 Takasuka A, Oozeki Y, Kimura R, Kubota H, Aoki I (2004b) Growth-selective predation
567 hypothesis revisited for larval anchovy in offshore waters: cannibalism by juveniles
568 versus predation by skipjack tunas. Mar Ecol Prog Ser 278: 297–302
- 569 Taylor DL, Collie JS (2003) Effect of temperature on the functional response and foraging
570 behavior of the sand shrimp *Crangon septemspinosa* preying on juvenile winter

571 flounder *Pseudopleuronectes americanus*. Mar Ecol Prog Ser 263: 217–234

572 van der Veer HW (1986) Immigration, settlement, and density-dependent mortality of a larval
573 and early postlarval 0-group plaice (*Pleuronectes platessa*) population in the western
574 Wadden Sea. Mar Ecol Prog Ser 29: 223–236

575 van der Veer HW, Bergman MJN, Dapper R, Witte JIJ (1991) Population dynamics of an
576 intertidal 0-group flounder *Platichthys flesus* population in the western Dutch
577 Wadden Sea. Mar Ecol Prog Ser 73: 141–148

578 van der Veer HW, Berghahn R, Miller JM, Rijnsdorp AD (2000) Recruitment in flatfish, with
579 special emphasis on North Atlantic species: Progress made by the Flatfish Symposia.
580 ICES J Mar Sci 57: 202–215

581 Witting DA, Able KW (1995) Predation by sevenspine bay shrimp *Crangon septemspinosa* on
582 winter flounder *Pleuronectes americanus* during settlement: laboratory observations. Mar
583 Ecol Prog Ser 123: 23–31

584

585 Fig. 1. The location of sampling stations and isobaths in Hakodate Bay. Solid circles indicate
586 sampling stations used in present study (each numeral shows the depth at each station).

587 Fig. 2. *Pseudopleuronectes yokohamae*. Mean water temperature that pelagic larvae (upper
588 panel) and juveniles (lower panel) experienced. Vertical bars indicate standard errors. The
589 ages of larvae and juveniles were defined as the number of the days after the onset of
590 otolith ring formation (larval age: LA) and the number of otolith rings formed outside the
591 first increment in juvenile stage as juvenile age (JA).

592 Fig. 3. *Pseudopleuronectes yokohamae*. Relationship between otolith radii and body lengths.

593 Fig. 4. *Pseudopleuronectes yokohamae*. Width of otolith rings at each age (WA: width at age)
594 in pelagic larval stages (upper panel) and juvenile stage (lower panel). Vertical bars
595 indicate standard errors.

596 Fig. 5. *Pseudopleuronectes yokohamae*. Relationship between mean water temperatures
597 experienced and mean width of otolith rings (WAs) of juveniles in 0–30 days JA.

598 Fig. 6. *Pseudopleuronectes yokohamae*. Width of otolith rings (WA) of survivor (SV) and its
599 original population (OP) in pelagic larval stages (left panels) and juvenile stage (right
600 panels). Vertical bars indicate standard errors.

601 Fig. 7. *Pseudopleuronectes yokohamae*. Relationship between the densities of larvae at the
602 nutritional transition stages (NT) and large juveniles collected in July.

603 Fig. 8. Seasonal changes in water temperature in water column exclusive of surface layer
604 (upper panel) and on the sea floor (lower panel). Horizontal box plots in upper panel
605 shows the ranges of NTD of SV_{pelagic} and those in lower panel shows the range of the day
606 that $SV_{\text{juveniles}}$ started its demersal life. Left and right ends of bars indicate the minimum
607 and maximum values. Left and right ends of boxes indicate the 25 and 75 percentiles and
608 the vertical bars in the boxes indicate the mean.

Table 1 The numbers of sampling casts and the density of larvae collected with a plankton net and that of larvae and juveniles collected with a sledge net

Year	Number of casts		Density of larvae and juveniles		
	Plankton net	Sledge net	Plankton net (inds./m ²)	Sledge net (inds./100m ²)	
2001					
	9 March	15	10	0.1	0 (0)
	26 March	15	10	8.9	0.5 (0)
	6 April	15	14	0.7	0 (0)
	16 April	15	14	0.0	0 (0)
	25 April	15	14	1.1	0.8 (0.0)
	8 May	10	16	0.0	0.9 (1.1)
	23 May	4	19	0	0.0 (0.1)
	10 July	0	18	-	0 (0.8)
2002					
	13 March	15	5	18.5	3.7 (0)
	25 March	15	10	16.9	10.1 (0)
	5 April	15	14	61.3	73.7 (0)
	15 April	13	8	2.2	10.3 (2.6)
	24 April	15	18	0.1	4.1 (2.2)
	6 May	12	16	0	0.3 (2.4)
	20 May	0	18	-	0 (0.9)
	17 June	0	12	-	0 (1.4)
	28 June	0	12	-	0 (1.8)
	26 July	0	12	-	0 (2.3)
2003					
	6 March	15	10	13.6	0.3 (0)
	14 March	15	12	59.8	9.9 (0)
	25 March	15	10	6.4	3.8 (0)
	1 April	15	12	5.7	0.0 (0)
	15 April	15	12	4.5	1.8 (0)
	25 April	15	12	0.2	3.2 (0)
	6 May	15	16	0.1	1.3 (0.4)
	23 May	0	14	-	0.1 (0.6)
	9 June	0	8	-	0 (2.8)
	30 June	0	10	-	0 (2.0)
	30 July	0	13	-	0 (1.6)

Numbers in parentheses represent the density of juveniles

Table 2 The numbers of larvae and juveniles collected, used for growth comparison among years, and used for the comparison between survivor (SV) and original population (OP)

Date	Number of larvae				Number of juveniles			
	collected	inter annual growth comparison	comparison between OP and (SV)		collected	inter annual growth comparison	comparison between OP and (SV)	
2001								
9 March	6	0	0	(0)	-	-	-	
26 March	403	78	0	(0)	0	-	-	
6 April	21	8	1	(0)	0	-	-	
16 April	2	1	1	(0)	0	-	-	
25 April	54	27	12	(5)	1	0	-	
8 May	26	6	0	(5)	30	10	-	
23 May	0	-	-		4	3	-	
10 July	0	-	-		23	21	-	
2002								
13 March	407	98	0	(0)	0	-	-	
25 March	511	87	9	(0)	0	-	-	
5 April	2,922	88	18	(1)	0	-	-	
15 April	207	32	8	(18)	44	10	0	(0)
24 April	127	53	0	(32)	66	44	0	(0)
6 May	8	6	0	(1)	65	39	3	(0)
20 May	0	-	-		26	15	6	(0)
17 June	0	-	-		28	23	0	(0)
28 June	0	-	-		37	23	0	(11)
26 July	0	-	-		45	40	0	(18)
2003								
6 March	350	112	0	(0)	0	-	-	
14 March	1,604	115	0	(0)	0	-	-	
25 March	231	64	0	(0)	0	-	-	
1 April	179	58	3	(0)	0	-	-	
15 April	125	44	12	(0)	0	-	-	
25 April	68	44	12	(8)	0	-	-	
6 May	48	17	0	(14)	17	4	0	(0)
23 May	2	1	0	(1)	15	9	1	(0)
9 June	0	-	-		37	29	7	(0)
30 June	0	-	-		33	31	0	(31)
30 July	0	-	-		34	33	0	(31)

Table 3 Results of the generalized linear model (GLM) analysis
for the effect of water temperature and prey density
experienced by pelagic larvae on the growth

Variables	Coefficient	Standard error	P
Temp	6.610×10^{-2}	2.435×10^{-2}	0.007
Prey	7.311×10^{-3}	4.287×10^{-3}	0.09
Temp : prey	9.126×10^{-4}	5.362×10^{-4}	0.09

Models	AIC
Full	-361.5
Temp + Prey	-360.6
Temp	-362.6
Prey	-344.1

“Temp” and “Prey” are mean water temperature and prey density that pelagic larvae experienced during 0–10 days LA. “temp : prey” means interaction term.















