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Annual variation in otolith increment widths of walleye pollock (*Gadus chalcogrammus*) larvae in Funka Bay, Hokkaido, Japan

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Running title (7 words): Annual variation in growth of pollock larvae

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ABSTRACT

To clarify relationships between year-class strength and larval growth of walleye pollock (*Gadus chalcogrammus*), and oceanographic conditions in the Pacific stock off Hokkaido and Tohoku, Japan, we undertook CTD observations and investigated larval densities, larval otolith increment widths, and larval prey densities (of copepod nauplii) of the 2008, 2009, 2010, and 2011 year classes in Funka Bay. Oyashio Coastal Water (OCW) flowed into the bay in late February in 2008, 2010, and 2011, and mean water temperatures decreased to 1.9–3.1 °C in March. OCW was not observed in 2009, and it was warm in late February (≥ 3.4 °C). Increment widths of lapillar otoliths during the yolk-sac stage were wide in 2009 and 2011, medium in 2010, and narrow in 2008. Increment widths during the first-feeding stage tended to become wider as the hatch month progressed, and the annual variation during the first-feeding stage was larger than that of the yolk-sac stage. The densities of the primary food for the larvae were high in 2008 when larval increment widths were narrowest, so the effect of prey abundance on larval growth appeared to be small. The ranking of the larval abundance in March was nearly coincident with that of the increment width during the larval stage. We therefore suggest that larval growth rate is associated with mortality rate, and that the growth–mortality hypothesis may be applicable to walleye pollock in Funka Bay. Feeding success under warm water conditions may be an important factor that contributes towards high growth rates.

Key words: copepod nauplius, growth-mortality hypothesis, increment width, otolith, Oyashio Coastal Water, recruitment, walleye pollock

INTRODUCTION

As is characteristic of marine fishes, annual fluctuations in survival rates are substantial during the early life stage from egg to young during the first year of life. Various studies have been carried out to clarify the mechanisms that result in this fluctuation (Leggett and DeBlois, 1994). The growth-mortality hypothesis (Campana, 1996; Meekan and Fortier, 1996) is one of the rational hypotheses proposed to explain patterns of early survival. As an example, growth rates of Atlantic cod (*Gadus morhua*; Campana, 1996) and Atlantic mackerel (*Scomber scombrus*; Robert *et al.*, 2007) showed annual fluctuations, and year classes that showed high growth rates and experienced favorable oceanographic conditions became strong year classes. Three growth-dependent survival frameworks have been proposed. First, bigger size at hatch during the early life stage tends to lead to faster growth (bigger-is-better hypothesis; Bailey and Houde, 1989). Second, faster growing larvae can shorten the duration of the vulnerable stage (stage-duration hypothesis; Houde, 1987), and third, they have a survival advantage in escaping from predators (growth selective mortality hypothesis; Litvak and Leggett, 1992; Pepin *et al.*, 1992; Takasuka *et al.*, 2003).

Walleye pollock (*Gadus chalcogrammus*; formerly *Theragra chalcogramma*; Page *et al.*, 2013) is an important commercial fish in the subarctic Pacific Ocean. The walleye pollock Pacific stock that inhabits waters along the Pacific coast of Hokkaido to the Tohoku area is targeted by fishermen using bottom gill nets and set nets operated from the mouth of Funka Bay to the continental shelf outside the bay (Nakatani and Maeda, 1981). Validation of daily otolith increment formation on sagittal otoliths (Nishimura and Yamada, 1984), feeding habits of the first-feeding larvae (Nakatani, 1995), and environmental conditions during the larval stage (Nakatani, 2007) of this

stock have been studied previously. High water temperature in February (Funamoto, 2007; Funamoto *et al.*, 2013), early spawning and hatching (Nishimura *et al.*, 2007; Shida, 2011), and favorable food availability and water temperature during the larval stage due to delay of the Oyashio Coastal Water advection (Nakatani, 2007) are thought to be essential for the occurrence of the strong year classes. The growth of larval walleye pollock as well as the prevailing oceanographic conditions and primary food availability in the western Gulf of Alaska, have been extensively studied and recruitment fluctuations have been discussed in terms of the growth-mortality hypothesis (Bailey *et al.*, 1995; Bailey *et al.*, 1996b). Bailey *et al.* (1995), who compared larval growth to oceanographic conditions between 1990 and 1991, found that larval length-at-age was low and mortality rate was high in 1991, when sea surface temperatures were anomalously cold. Bailey *et al.* (1996b) concluded that the effect of larval growth on late larval abundance and recruitment was not clear, and documented that a large year class (in 1988) had been preceded by a period of warm sea surface temperature, a low larval mortality rate, and a high juvenile growth rate. Detailed information on larval growth fluctuations from the yolk-sac stage to the first-feeding stage of the Pacific stock off Hokkaido and Tohoku, and the relationships between the growth of these larvae and changing oceanographic conditions are unknown.

In this study, otolith increment width was used as an indicator of larval growth, and we evaluated the relationships between oceanographic conditions, larval density and growth of the 2008, 2009, 2010, and 2011 year classes of walleye pollock larvae caught in Funka Bay. The results are discussed from viewpoint to test the growth-mortality hypothesis may applicable for walleye pollock in Funka Bay.

MATERIALS AND METHODS

95 *Field sampling*

Sampling was conducted from the T/S *Ushio-maru* of Hokkaido University Faculty of Fisheries to obtain walleye pollock larvae, measure water temperature and salinity, and collect copepod nauplii. Sampling conducted at 15 stations in Funka Bay, which is the major nursery area for the larval stage of the Pacific stock off Hokkaido and Tohoku
100 (Nakatani and Maeda, 1981; Fig. 1). Each of four year classes of walleye pollock larvae was sampled from December through April (e.g. The 2008 year class was sampled from December 2007 through April 2008). Sampling was conducted once a month in December and April, and twice a month from January to March. Sampling was not always conducted at all 15 stations because of rough seas. Walleye pollock larvae
105 mostly inhabit the 10–30 m depth layers in Funka Bay (Kamba, 1977; Nakatani, 1988). Thus, larvae were collected by vertical hauls from the 3 m above the sea floor to the sea surface and by horizontal hauls in the 15 m depth layer using a ring net (net diameter: 80 cm; length: 270 cm; mesh aperture: 0.33 mm; a flow-meter was mounted at the mouth). Larvae were immediately preserved in 90% ethanol solution.

110 Water temperature and salinity were measured at all stations from 2 m above the sea floor to the sea surface using a CTD (SBE-19 plus, Sea-Bird Electronics, Inc., USA). In accordance with Ohtani (1971), we defined water masses as Tsugaru Warm Water (TWW; ≥ 33.6 salinity and ≥ 6 °C), which flows into Funka Bay in summer and autumn; Winter Funka Bay Water (WFBW; ≥ 33.8 salinity and ≤ 6 °C) after the TWW
115 was cooled by wintertime vertical mixing; and Oyashio Coastal Water (OCW; ≤ 33.3 salinity and ≤ 3 °C), which flows into Funka Bay in winter and spring. Water masses that were not coincident with these three water masses were defined as transition water.

We integrated water temperature and salinity at 10–30 m depth. Water temperature and salinity means were weighted by larval walleye pollock density at each station.

120 Small zooplankton were collected with a van-Dorn bottle sampler (6.8 L) at
15 m depth. The sampled water was filtered through a hand net (mesh aperture: 40 μm)
and the retained plankton was fixed in a 5% buffered formalin sea water solution. In the
laboratory, zooplankton samples were divided appropriately using a Motoda plankton
splitter, and copepod nauplii were counted using a microscope. Counts were
125 standardized to volume filtered and expressed as density (inds. l^{-1}). Each naupliar
density was weighted by larval walleye pollock density and averaged by year to give
weighted means, which we use to indicate prey availability because first-feeding
walleye pollock larvae mainly feed on copepod nauplii (Kamba, 1977; Nakatani, 1995).

130 *Otolith analysis*

Larval walleye pollock were sorted from the ring-net samples and counted under a
microscope. Most larvae were collected in vertical tows, but some were from horizontal
tows to increase sample size. No more than 20 larvae were analyzed from each sample;
for large samples (> 20 larvae), individuals were randomly subsampled. Larvae were
135 too scarce in December 2007–2010 and April 2008 to include in this study. The total
number of larvae examined was 466: 106 larvae in 2008, 120 larvae in 2009, 100 larvae
in 2010, and 140 larvae in 2011. The notochord length (NL) of each larva was measured
to the nearest 0.1 mm under a microscope, using an ocular micrometer. Prior to making
these measurements, we calibrated the ocular micrometer with an objective micrometer,
140 at a fixed magnification.

Lapillar otoliths were removed from each larva and daily increments were

counted and measured following Bailey and Stehr (1988). Otoliths removed from each larva were cleaned and mounted with epoxy resin on glass slide. Otolith surfaces were polished with water-proof sandpaper (#1500) and lapping film (9 μm particles) so that the nucleus could be observed clearly. The left otolith was preferred for subsequent examination of daily increments. Only the increments that formed after the larva hatched were considered. All counts and measurements were made using a light microscope connected to a video monitor and an otolith reading system (ARP ver. 5.27, Ratoc System Engineering Co. Ltd, Japan). Increment widths were measured to the nearest 0.1 μm .

Data analysis

Increment width was compared among hatch-date groups and year classes for yolk-sac stage and then for first-feeding stage. We defined yolk-sac stage as newly hatched to 6 days after hatching (DAH) in accordance with Nishimura and Yamada (1984), and first-feeding stage as 7 DAH to 23 DAH when the larvae finish gut coiling and lipid vacuoles are observed in the midgut of the larvae (Oozeki and Bailey, 1995; Porter and Theilacker, 1999) in order to detect stage specific variation in increment width. The hatch date was calculated by subtracting the number of increments from the collection date. Larvae were grouped by hatch date: early-hatch, December 21 to January 31; middle-hatch, February; and late-hatch, March 1 to April 13 (Table 1). Generalized linear models (GLMs) were applied to mean increment width of each individual for the yolk-sac stage (1 DAH to 6 DAH) and the first-feeding stage (7 DAH to 23 DAH) to examine the significance of the effects of the two explanatory variables (sampling year and hatch-date group) as well as an interaction term among these two explanatory

variables. A normal distribution was assumed as the error distribution. The null hypothesis is that there is no significant difference in mean increment width between the sampling years and the hatch-date groups. The GLM calculations were made with R2.15.1 (R Development Core Team, <http://cran.r-project.org/bin/windows/base/>).

170 Because the successive increment width data from fish otoliths are longitudinal, we did not use the increment width, by each DAH of each individual, as the age effect of the explanatory variable (to exclude pseudo-replication). Repeated measures MANOVA is an adequate statistical test for fish aging data (Chambers and Miller, 1995), which requires equal repeated numbers of individuals. In other words, in this particular study
175 the individual increment width data of larvae with ≥ 6 DAH or ≥ 23 DAH can be used for this test. It should however be noted that data from younger individuals (< 6 DAH or < 23 DAH olds) are exclusive (there is a bias obtained from older larvae). Therefore, we did not use this statistic test for avoiding the exclusion of data on younger individuals.

Multiple comparison tests were applied to identify where differences in
180 increment width occurred among year classes (Scheffe's test) and among hatch-date groups (William's test, which compare the data in order of month). There were insufficient numbers (only 2) of individual late-hatch larvae of the first-feeding stage in 2008, so data on these larvae were not inclusive of William's test. Notochord length (NL) was back-calculated from the otolith radius (OR) using the biological intercept
185 method (Campana, 1990) to express increment width as growth rate in NL (as mm d^{-1}). NL-at-hatch (i.e. hatch check deposition) was fixed at 4.68 mm (as the biological intercept of this species; Nishimura and Yamada, 1984). In this study, we used the increment width as a proxy for the specific growth rate, in order to exclude bias, described by Robert *et al.* (2007, 2010) and Joh *et al.* (2013), associated with the

190 back-calculation of length-at-age from OR.

RESULTS

Oceanographic condition

Weighted mean water temperatures of the 10–30 m depth layer decreased from
195 December, reached a minimum from late February to late March, and increased in April
for all years (Fig. 2). Salinities gradually decreased from January to April, but the
pattern of the decrease varied among years. For the 2008 year class, the bay was
covered with TWW in December and WFBW in January and early February. Water
temperatures and salinities decreased and OCW intruded into Stns 25, 19, and 18 near
200 Cape Chikyu on March 5–6. On March 19, OCW covered the bay and weighted mean
water temperature and salinity reached 3.1 °C and 33.20, respectively. For the 2009 year
class, weighted mean water temperatures were warmer than 3 °C throughout the
sampling period, and transition water covered the bay from January to April. For the
2010 year class, weighted mean salinity (33.20) in December was the lowest among the
205 four years. The weighted mean water temperature was 2.5 °C on February 27–28, and
OCW covered all of the stations. For the 2011 year class, weighted mean salinities
(33.58 on December 14) were lower than those measured in 2008 and 2009 and
transition water covered the bay, except in March when the weighted mean water
temperature was 2.6 °C because OCW covered all stations. Thus for the period between
210 January and April, the 2010 year class experienced the lowest water temperatures due to
early intrusion of OCW. In contrast, the 2009 year class experienced the highest water
temperatures due to the absence of any OCW intrusion.

Density of copepod nauplii

215 Densities of copepod nauplii at 15 m depth decreased from January to early and
mid-February and increased after mid-February in all four years (Fig. 3). Comparing all
4 years, weighted mean densities of copepod nauplii from January to March were the
highest in 2008 (11.0 – 18.9 – 32.4 inds. l^{-1} ; minimum – weighted mean – maximum),
second highest in 2009 (6.0 – 13.7 – 30.9 inds. l^{-1}), third highest in 2011
220 (4.7 – 12.3 – 26.2 inds. l^{-1}) and lowest in 2010 (5.1 – 11.9 – 22.9 inds. l^{-1}).

Density of walleye pollock larvae

The density of larvae from each year class peaked during late winter or early spring
(Fig. 4). Maximum mean density occurred in early February 2008 (72.7 inds. m^{-2}), in
225 late February 2009 (717.5 inds. m^{-2}), in early January 2010 (253.7 inds. m^{-2}), and in
early March 2011 (549.4 inds. m^{-2}). Densities in March were higher in 2009
(553.0 inds. m^{-2}) and 2011 (549.4 and 382.2 inds. m^{-2}) than in 2010 (95.8 inds. m^{-2}) and
2008 (20.8 and 13.4 inds. m^{-2}).

230 *Monthly and annual variation in otolith increment width*

Larval increment widths averaged $0.8 \mu m d^{-1}$ from 1 DAH to 23 DAH, which
encompassed yolk-sac and first-feeding stages, and then increased after 23 DAH
(Fig. 6). Back-calculations based on an allometric relationship between OR (μm) and
NL (mm) (Fig. 5; $\text{Log}(NL) = 0.585 * \text{Log}(OR) + 0.0639$, $N = 466$, $r^2 = 0.91$, $P < 0.05$)
235 indicate that an increment width of $0.8 \mu m d^{-1}$ corresponded to $0.22 mm d^{-1}$,
 $0.17 mm d^{-1}$, $0.14 mm d^{-1}$ and $0.12 mm d^{-1}$ growth in NL at 4, 6, 8 and 10 mm NL,
respectively.

Mean increment width varied among yolk-sac stage (1–6 DAH) by year and hatch-date group. GLM results indicated that the year ($F = 28.55$; $df = 3$; $P < 0.001$) and hatch-date group ($F = 3.23$; $df = 2$; $P = 0.040$) effects were significant and did not interact ($F = 0.92$; $df = 6$; $P = 0.48$). The year effect was attributable to wide increments for the 2009 ($0.90 \pm 0.20 \mu\text{m d}^{-1}$; mean $\pm$ standard deviation) and the 2011 ($0.88 \pm 0.17 \mu\text{m d}^{-1}$) year classes (Scheffe's multiple comparison test; $P > 0.05$) as compared to the 2010 year class ($0.81 \pm 0.16 \mu\text{m d}^{-1}$) and the 2008 year class ($0.77 \pm 0.17 \mu\text{m d}^{-1}$) ($P < 0.05$). The mean increment width of the 2010 year class was significantly wider than that of the 2008 year class ($P < 0.05$), which had the narrowest increments width of all four year classes (Fig. 6). The hatch-date group effect was generally attributable to greater widths of late-hatch larvae, although this was not detected for the 2008 year class (Fig. 7A). For the 2009 year class, mean increment width of late-hatch larvae was significantly wider than that of early- and middle-hatch larvae (William's multiple comparison test; $P < 0.05$). For the 2010 year class, increment width of late-hatch larvae was significantly wider than that of early-hatch larvae ($P < 0.05$). For the 2011 year class, increment widths of late- and middle-hatch larvae were significantly greater than those of early-hatch larvae ($P < 0.05$). Increment width differences between middle-hatch larvae and late-hatch larvae were large in 2009 (mean of $0.05 \mu\text{m}$) but small in 2010 ($0.03 \mu\text{m}$) and 2011 ($0.03 \mu\text{m}$).

For the first-feeding stage (7–23 DAH), mean increment width differed by year and hatch-date group. GLM results indicated that the year ($F = 42.72$; $df = 3$; $P < 0.001$) and hatch-date group ($F = 10.09$; $df = 2$; $P < 0.001$) effects were significant and did not interact ($F = 0.85$; $df = 6$; $P = 0.53$). Increment widths of the 2009 year class ($0.94 \pm 0.27 \mu\text{m d}^{-1}$) were the widest, followed by that of the 2011 year class

($0.88 \pm 0.19 \mu\text{m d}^{-1}$) and the 2010 year class ($0.83 \pm 0.20 \mu\text{m d}^{-1}$); the increment width of the 2008 year class was the narrowest ($0.71 \pm 0.18 \mu\text{m d}^{-1}$) (Scheffe's multiple comparison test; all $P_s < 0.05$; Fig. 6). The hatch-date group effect was mostly attributable to increasing width for later hatch groups, although this was not detected for the 2008 year class (Fig. 7B). For the 2009 and 2010 year classes, the mean increment width became significantly wider as the hatch month progressed (William's multiple comparison test; $P < 0.05$). For the 2011 year class, increment widths of late- and middle-hatch larvae were significantly greater than those of early-hatch larvae ($P < 0.05$). Increment width differences between middle-hatch larvae and late-hatch larvae were large in 2009 (mean of $0.07 \mu\text{m}$) relative to 2010 ($0.03 \mu\text{m}$) and 2011 ($0.01 \mu\text{m}$).

Summary of the four year classes of walleye pollock larvae in Funka Bay

Characteristics associated with abundance, growth, environmental conditions, and recruitment during four year classes of walleye pollock larvae in Funka Bay are shown in Table 2. Larval abundance was the highest in 2009, second in 2011, third in 2010, and lowest in 2008. Increment width during the first-feeding stage was the widest in 2009, second in 2011, third in 2010, and narrowest in 2008. Increment width became wider with passing hatch months. Water temperature was the highest in 2009, second in 2008, third in 2011, and lowest in 2010. Copepod nauplii density was the highest in 2008, second in 2009, third in 2011, and lowest in 2010.

DISCUSSION

Our results indicate a correspondence between fast growth and population density for

larval walleye pollock suggesting that the growth-mortality hypothesis may be applicable to the survival framework of walleye pollock larvae in Funka Bay. The ranking of mean increment width corresponded with that of the density of walleye pollock larvae collected in March (Fig. 4). The ranking of the recruitment (2009 > 2008 > 2010) (Funamoto *et al.*, 2015) was roughly coincident with that of the increment width (2009 > 2011 > 2010 > 2008: Table 2) exclusive of recruitment abundance in 2011 that was not available in 2015.

The increment width of the 2010 year class was narrow due to the earliest OCW intrusion in February, and the increment width of late-hatch larvae of the 2011 year class was suppressed by the low water temperature due to the OCW intrusion in March (Table 2). Intrusion of OCW with water temperature $\leq 3^{\circ}\text{C}$ might result in decreased feeding and growth rates of walleye pollock larvae. Contrarily the water temperature in 2009 was relatively high because OCW did not flow into the bay, and the increment width of late-hatch larvae in 2009 was wide (Table 2). High water temperature during the larval stage, especially in March of 2009 without OCW intrusion, might be necessary for a high growth rate of walleye pollock larvae in Funka Bay. Sagittal otolith increment widths of Chinese sucker (*Myxocyprinus asiaticus*) larvae from the yolk-sac stage to the first-feeding stage increased as water temperature increased (Song *et al.*, 2008). Paul (1983) reported that water temperature appeared to be relatively important in determining the percent of larvae that initiate feeding. Feeding success, under warm water-temperature conditions, during the first-feeding stage may be one of the factors responsible for the high growth rate, which in turn affects the mortality rate of walleye pollock in Funka Bay. Funamoto (2007) reported that high water temperature in February led to high recruitment of the walleye pollock Pacific

stock, and suggested that the strong year classes exhibited high growth rate during larval stage. Nakatani (2007) showed that water temperatures were relatively high during the years when strong year classes occurred and he suggested that the delay of OCW advection resulted in high water temperature regimes. With the exception of results obtained in 2008 when the increment width was narrow and environmental conditions were favorable, our interpretation of results relating to the importance of water temperature is generally in agreement with the conclusions reached by Funamoto (2007) and Nakatani (2007). Therefore we hypothesize that the absence of OCW intrusion into Funka Bay allows walleye pollock larvae to grow faster and maintain higher population densities.

The minimum weighted mean density of copepod nauplii in all four years was 8.1 inds. l⁻¹ (Fig. 3). Paul (1983) reported that the feeding ratio of walleye pollock larvae did not change at the densities of copepod nauplii above 8.0 inds. l⁻¹. Thus we assumed that the primary food source did not constrain larval growth rate.

In this study we were not able to clarify relationships between the recruitment, larval abundance and growth rate inferred from increment width. Bailey *et al.* (1996b) documented that the effect of larval growth on late larval abundance and recruitment was not clear in the western Gulf of Alaska, and concluded that larval mortality rates are highly variable and tend to mask effects of moderate variability in growth on later abundance. It therefore became clear that, in Funka Bay, predications based solely on larval growth rates, of the survival rate during the recruitment process, were not reliable, as was the case in the western Gulf of Alaska. In the previous study of growth rate and hatch date distribution of juvenile walleye pollock in Funka Bay (Nishimura *et al.*, 2007), a strong year class in 2000 hatched early and exhibited a low growth rate,

whereas weak year classes in 2001 and 2002 hatched late and exhibited high growth
335 rates. Our result that late hatched larvae showed a wide increment width is consistent
with the result of Nishimura *et al.* (2007). Hattori *et al.* (2006) studied the hatch date
distribution of walleye pollock juveniles from Funka Bay to the Tohoku area and found
that the strong year class of 2000 hatched from January to March. They suggested that
the larvae, which hatched over a wide time range from January to March, would be able
340 to survive and consequently the year class strength was high. Bailey *et al.* (1996a)
examined the timing of critical periods in the recruitment process, and hypothesized that
pollock recruitment levels can be established at any life stage depending on sufficient
supply from prior stages. The determination of juvenile hatch-date distribution, juvenile
growth rates, and population densities during periods of recruitment, will enable us to
345 identify critical periods in the recruitment process of the walleye pollock Pacific stock.

The relationship between larval growth rate and recruitment was not clear in this
study. The ranking of the larval abundance in March was nearly coincident with that of
the larval growth rate. Therefore, we suggest that the growth rate of pelagic larval stage
would be a good indicator of larval abundance but not of the recruitment level of the
350 walleye pollock Pacific stock off Hokkaido and Tohoku, Japan. Kamchatka flounder
(*Atheresthes evermanni*), Pacific cod (*Gadus macrocephalus*) (Yamamura *et al.*, 1993;
Yamamura, 2004), and walleye pollock larger than 300 mm in standard length
(Yamamura *et al.*, 2001, 2002) are reported to be the major predators of walleye pollock
settled juveniles in the Doto area off the Pacific coast of Hokkaido (Fig. 1), and
355 Funamoto *et al.* (2013) found that the predation pressure of these demersal fishes plays
a dominant role in the recruitment fluctuation of walleye pollock. Yolk-sac volume and
the large body size of larvae may be important factors affecting growth rate, and the

nutritional condition of yolk-sac larvae could be affected by the maternal attributes of
spawners (i.e. body size, age, and nutritional condition: Kjesbu *et al.*, 1996; Solemdal,
360 1997; Higashitani *et al.*, 2007). We recommend that future studies on this topic should
focus on certain aspects that will facilitate a more comprehensive understanding of the
survival frameworks of walleye pollock in Funka Bay: maternal effects; the feeding
environment during the prey transition from copepod nauplii to copepodites and other
pelagic crustaceans; and growth rates, from the pelagic stage to settlement.

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Figure 1. Locations of sampling stations (labeled with numbers) in Funka Bay and its vicinity. Walleye pollock larvae were collected by vertical hauls with a ring net, and prey plankton were collected using a van-Dorn bottle followed by sieving through a 40 μm mesh aperture. Locations of CTD measurements are marked with solid circles. Open circles show locations where larvae were sampled from the 15 m depth layer by horizontal hauls with a ring net.

Figure 2. Temperature-salinity diagram showing weighted mean values with range for the 10–30 m depth layer by larval walleye pollock density at each station in Funka Bay from December to April in 2007–2011 with range (maximum and minimum). Oyashio Coastal Water (OCW; ≤ 33.0 salinity and ≤ 3.0 $^{\circ}\text{C}$), Tsugaru Warm Water (TWC; ≥ 33.6 salinity and ≥ 6.0 $^{\circ}\text{C}$), and Winter Funka Bay Water (WFBW; ≥ 33.8 salinity and ≤ 6.0 $^{\circ}\text{C}$) were defined by Ohtani (1971). From December 2008 to April 2009, weighted mean water temperature was not ≤ 3.0 $^{\circ}\text{C}$ throughout the sampling period.

Figure 3. Seasonal change in mean density of copepod nauplii for the 15 m depth layer weighted by larval walleye pollock density at each station with range (maximum and minimum) in Funka Bay from January to March in 2008–2011.

Figure 4. Seasonal change in mean density of walleye pollock larvae collected by vertical hauls with a ring net with range (maximum and minimum) in Funka Bay from January to March in 2008–2011. All values were common log-transformed.

Figure 5. Relationship between notochord length (NL; mm) and lapillar otolith radius (OR; μm) in larval walleye pollock. Allometric regression was $\text{Log}(\text{NL}) = 0.585 * \text{Log}(\text{OR}) + 0.0639$ ($N = 466$, $r^2 = 0.91$, $P < 0.05$).

Figure 6. Mean daily increment width (μm) with error bar (standard deviation) of

walleye pollock larvae in Funka Bay for the 0–80 day after hatching range (DAH; upper) and the 0–25 DAH range (lower) from January to April in 2008–2011. Error bars are not all shown for the sake of clarity.

Figure 7. Temporal change in mean increment width (μm) with error bar (standard deviation) of walleye pollock larvae in Funka Bay. Larvae were classified into three groups (early-hatch, December-January; middle-hatch, February; and late-hatch, March-April) based on hatch month. A: yolk-sac stage (1–6 day after hatching (DAH)), B: first-feeding stage (7–23 DAH). Hatch months with the same letters are not significantly different as determined by William’s multiple comparison test.

Table 1. Numbers of walleye pollock *Gadus chalcogrammus* larvae collected by vertical hauls and analyzed for each hatch date group in four years.

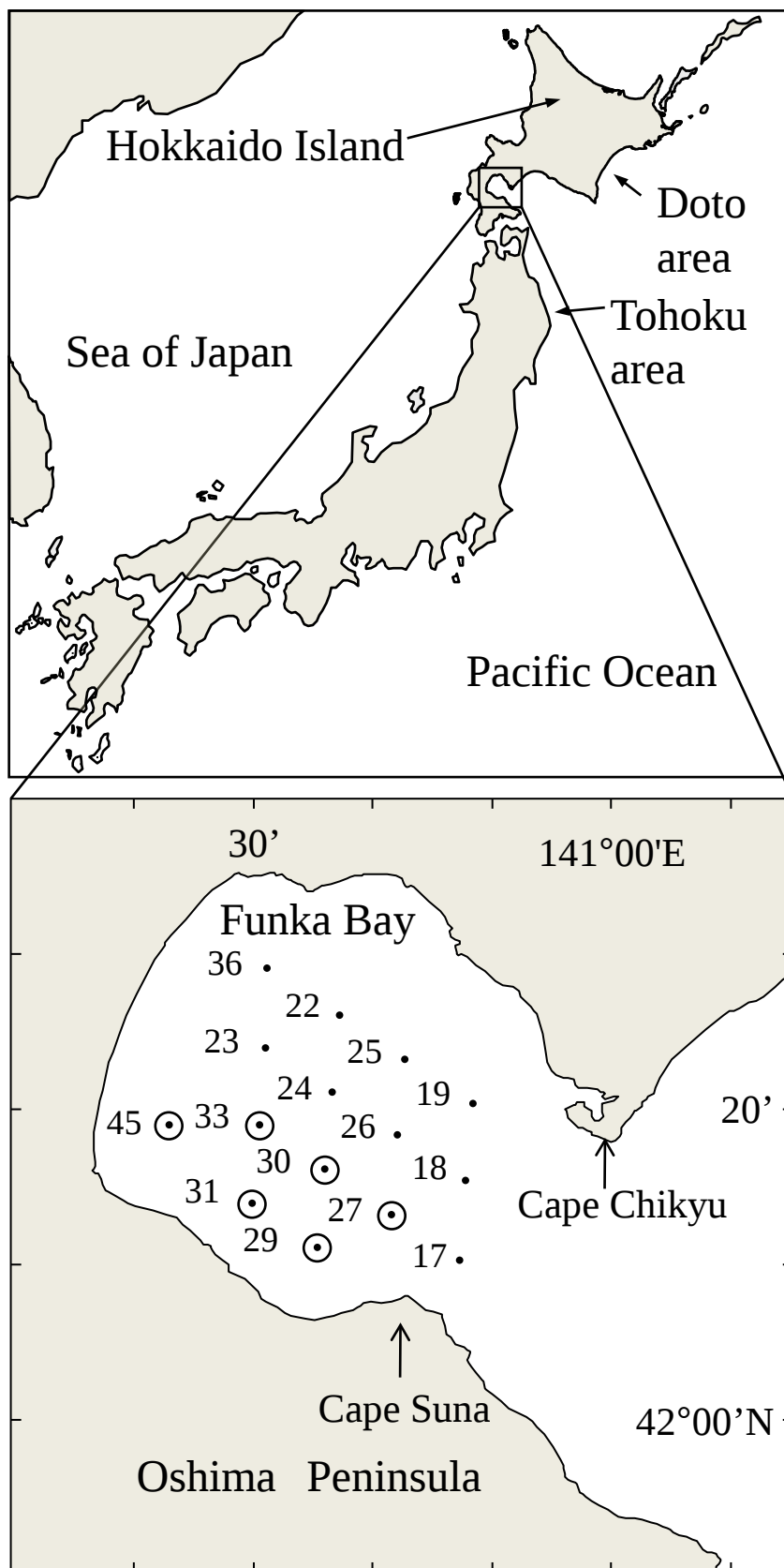
Year	Total collected	Early-hatched	Mid-hatched	Late-hatched
class	larvae	larvae	larvae	larvae
2008	1749	65	35	6
2009	60688	59	39	22
2010	7017	41	30	29
2011	25680	71	43	26

Table 2. The characteristic of abundance, growth, environmental conditions, and recruitment during four year classes of walleye pollock larvae in Funka Bay.

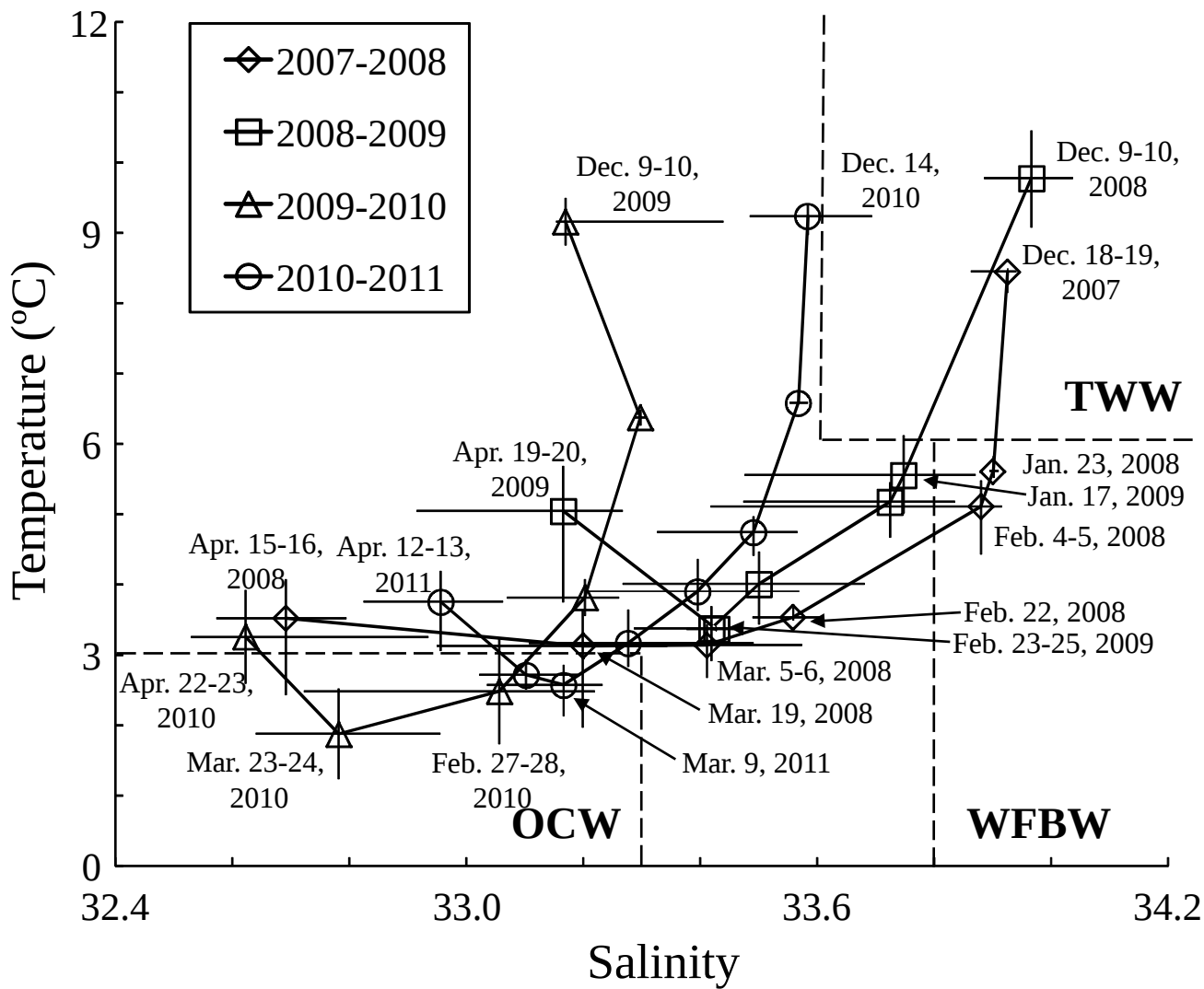
Factor	Characteristic
Larval abundance in March	2009 = 2011 > 2010 > 2008
Increment width during yolk-sac stage (1–6 DAH)	2009 = 2011 > 2010 > 2008
Increment width during first-feeding stage (7–23 DAH)	2009 > 2011 > 2010 > 2008
Monthly variation in increment width during first-feeding stage	2008: January = February 2009, 2010: January < February < March 2011: January < February = March
Temperature (timing of the Oyashio Coastal Water intrusion)	2009* > 2008 (early Mar.) > 2011 (late Feb.) > 2010 (early Feb.)
Density of copepod nauplii as primary food source for larvae	2008 > 2009 > 2011 > 2010
Recruitment (Funamoto <i>et al.</i> , 2015)	2009 > 2008 > 2010**

*: Oyashio Coastal Water was not observed in Funka Bay in 2009.

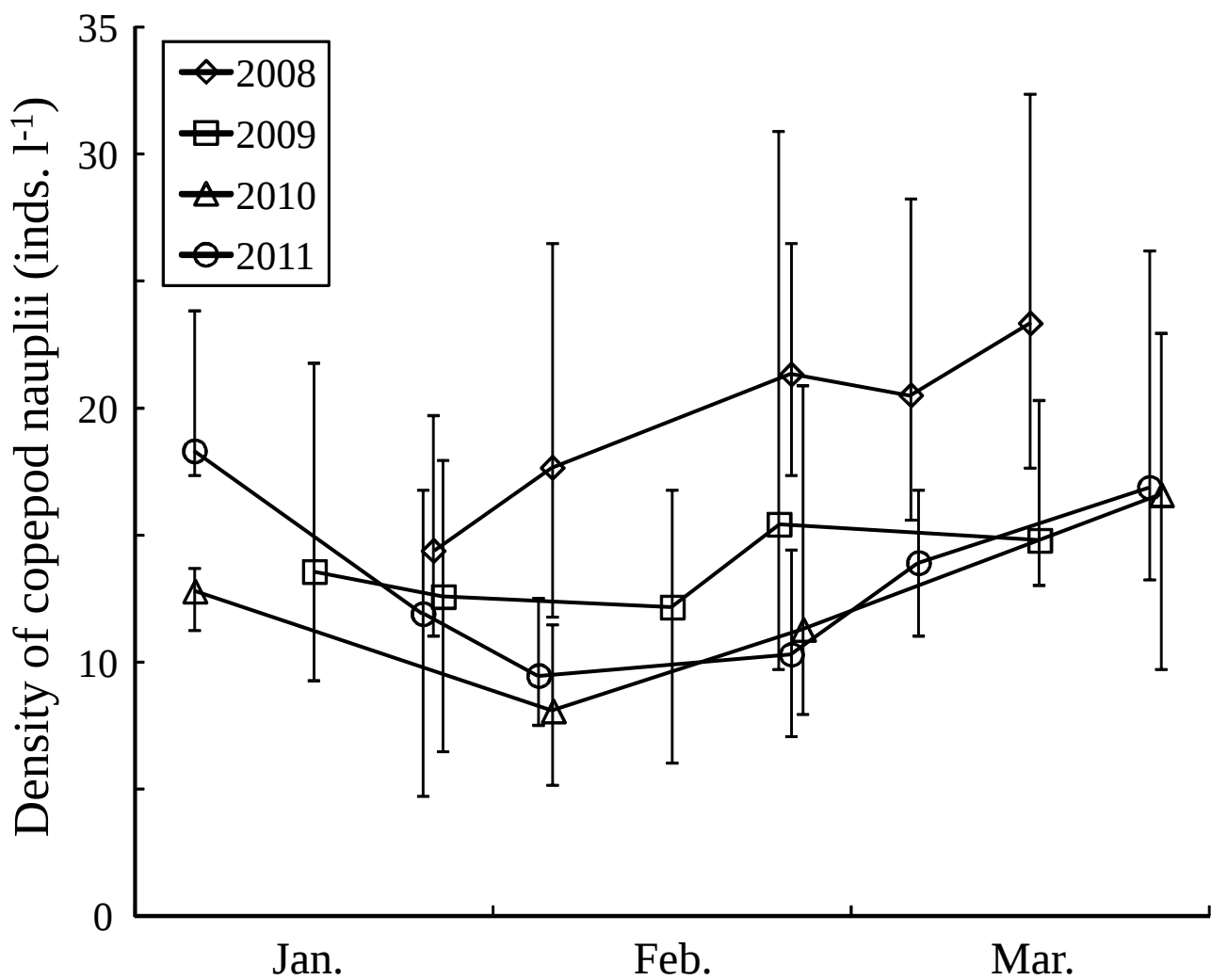
** : Abundance in 2011 is not available in 2015.



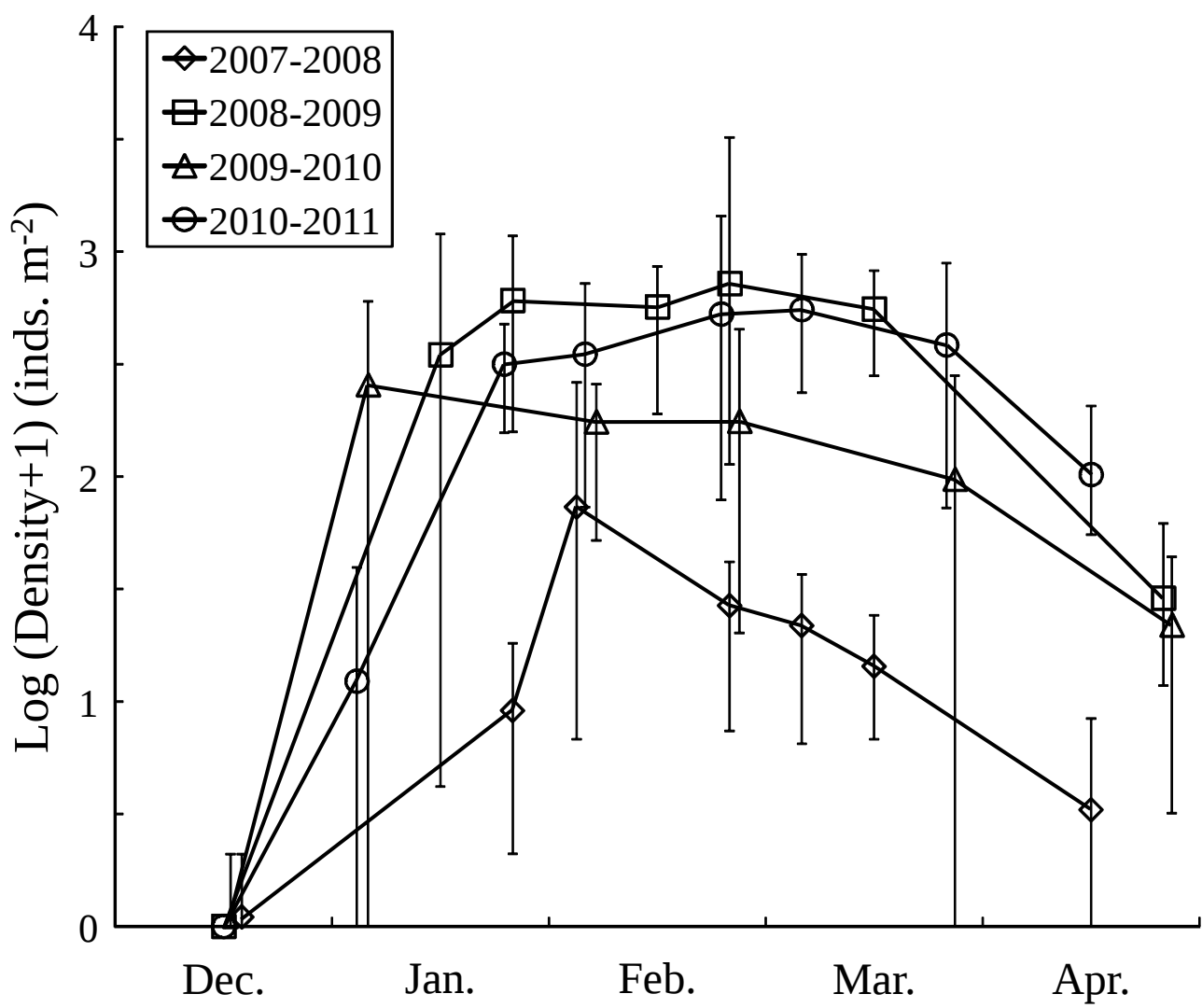
Kano et al. Figure 1



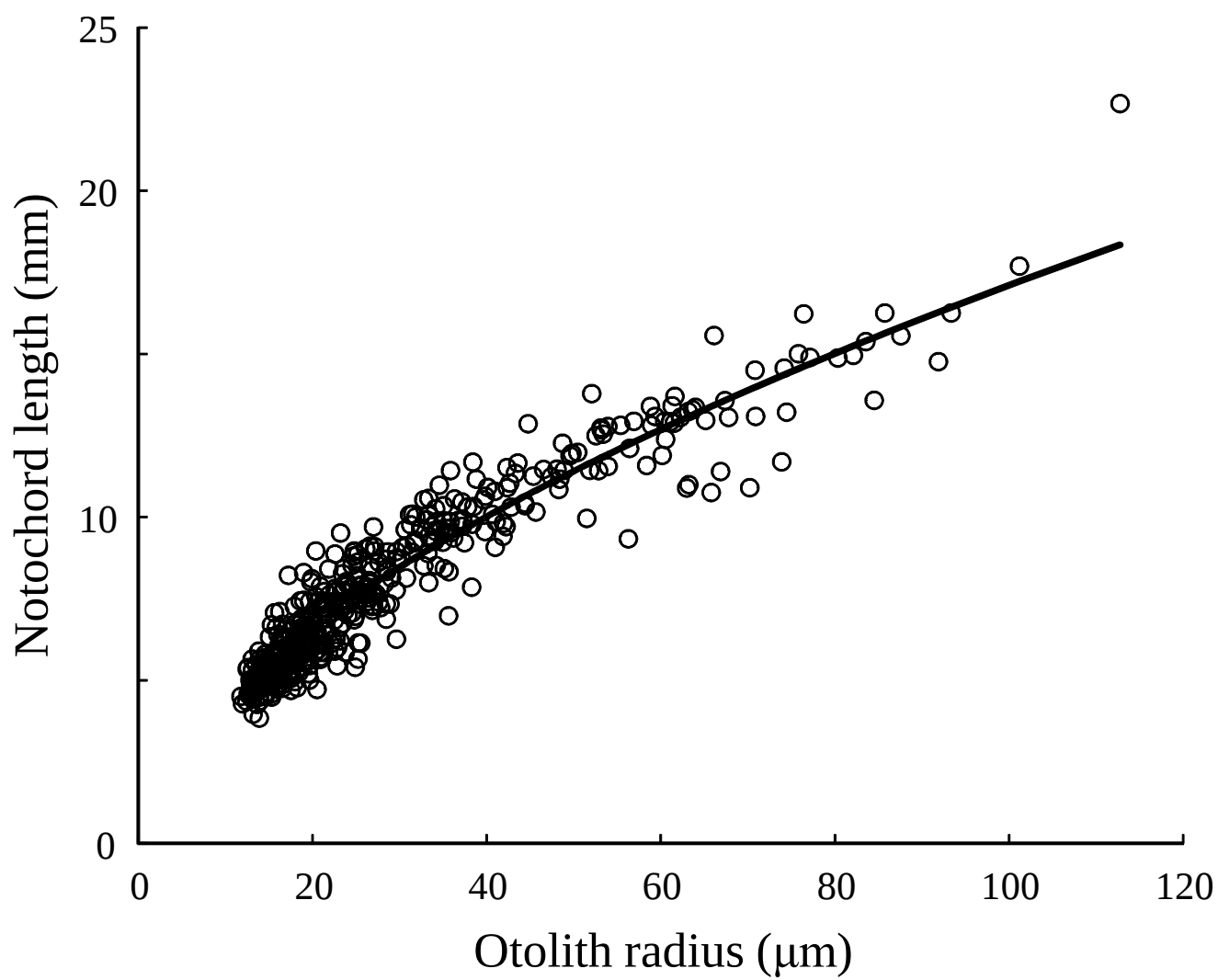
Kano et al. Figure 2



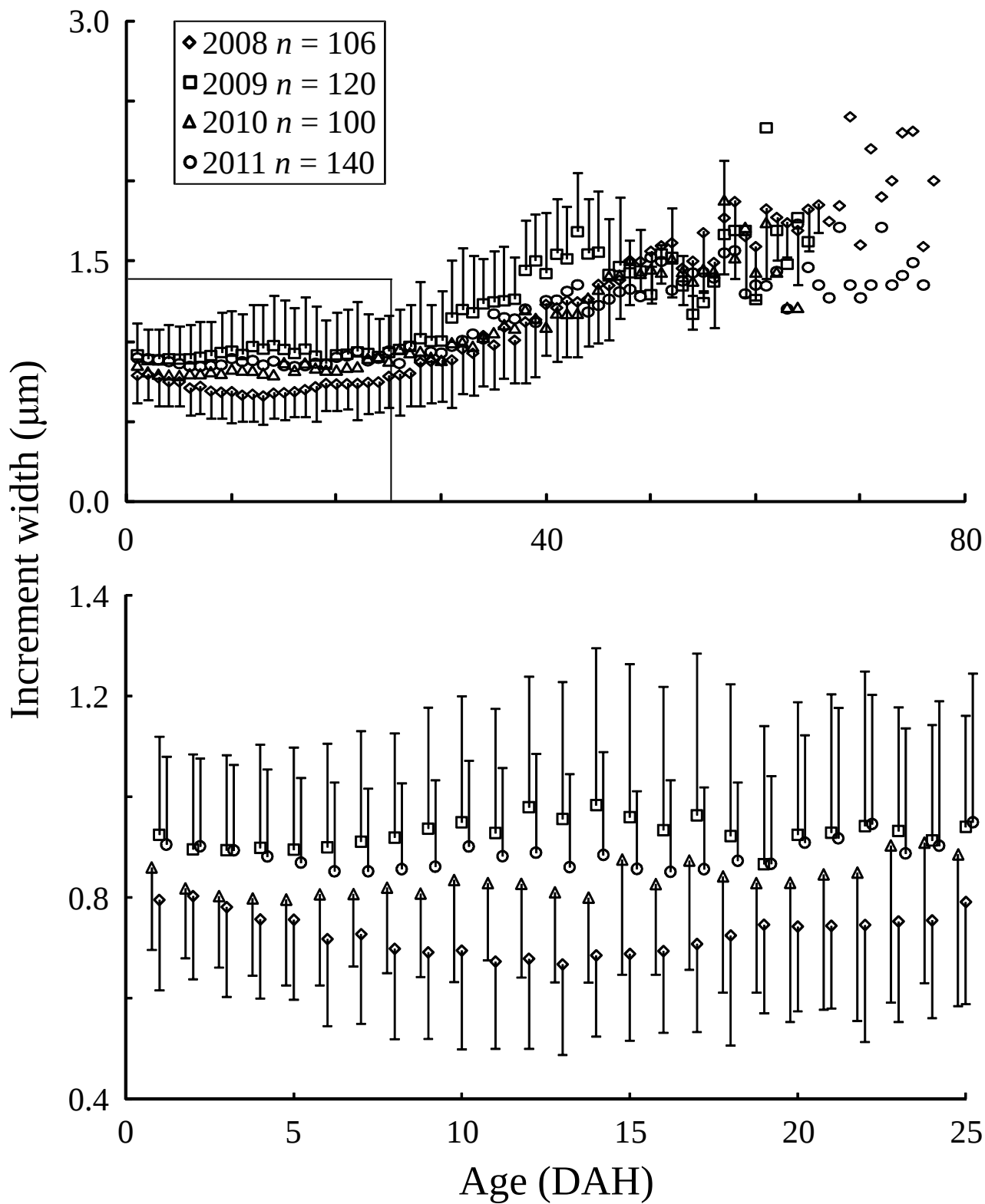
Kano et al. Figure 3



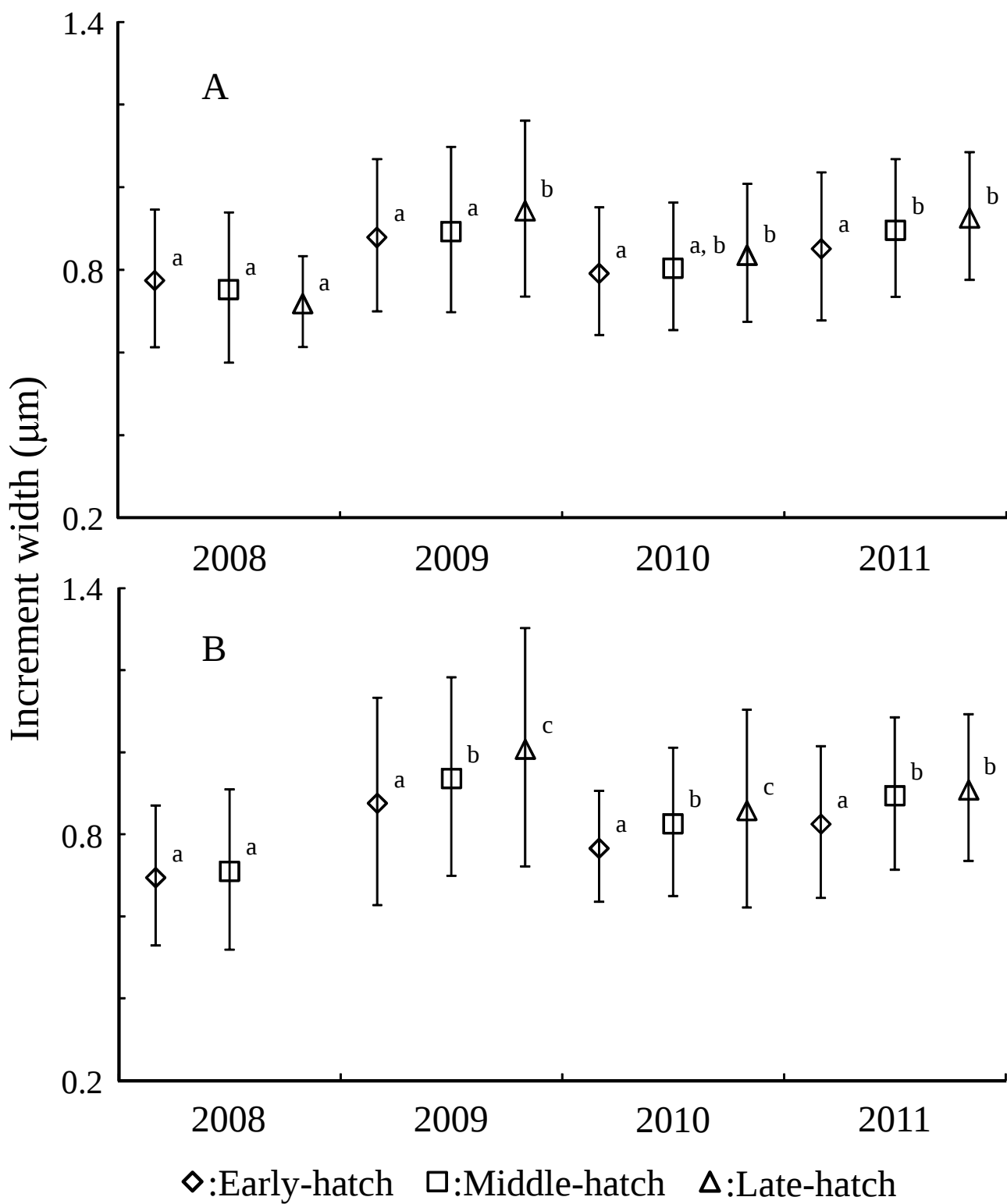
Kano et al. Figure 4



Kano et al. Figure 5



Kano et al. Figure 6



Kano et al. Figure 7