Feeding, somatic condition and survival of sand lance *Ammodytes* sp. larvae in Mutsu Bay, Japan

Nobuaki Nanjo[1,3] · Tetsuya Takatsu[1] · Kazuo Imura[1,4] · Kingo Itoh[2] · Yuuhei Takeya[1,2] · Toyomi Takahashi[1]

Correspondence: Tetsuya Takatsu

takatsu@fish.hokudai.ac.jp

Tel/Fax: +81–138–40–8822

Nobuaki Nanjo

nobuaki.nanjo@pref.toyama.lg.jp

Kazuo Imura

imuimu@amber.plala.or.jp

Kingo Itoh

kingo_ito@aomori-itc.or.jp

Yuuhei Takeya

yuuhei_takeya@aomori-itc.or.jp

Toyomi Takahashi

t-tkhs@fish.hokudai.ac.jp

[1] Graduate School of Fisheries Sciences, Hokkaido University, 3–1–1, Minato, Hakodate, Hokkaido 041–8611 Japan

[2] Local Independent Administrative Institution Aomori Prefectural Industrial Technology Research Center Fisheries Research Institute, 10, Tsukidomari, Moura, Hiranai, Aomori 039–3381 Japan

[3] Toyama Prefectural Agricultural, Forestry and Fisheries Research Center Fisheries Research Institute, Takatsuka, Namerikawa, Toyama 936–8536 Japan

[4] Fisheries Affairs Division Department of Industrial Promotion Rumoi Subprefectural Bureau Hokkaido Government, Suminoe, Rumoi, Hokkaido 077–8585 Japan

Abstract

To clarify the recruitment process of sand lance *Ammodytes* sp., we investigated larval condition factor, relative gut fullness (*%GF*), prey abundance and oceanographic structure in Mutsu Bay, Japan, in 1999–2001. *Ammodytes* sp. larvae, which were collected by horizontal hauls of Motoda nets and a ring net at 1, 10, 20, 30 and 40 m depths, were mainly distributed at 10–30 m. Larvae at the first feeding time until 12 mm in body length (BL) fed predominantly on copepod nauplii, whereas large larvae of 12.1–14.0 mm BL fed on a mixture of copepod nauplii, copepodites and appendicularians from late February to April. A path analysis showed that difference in water density between 35- and 5-m depths negatively affected naupliar abundance at 10–30-m depth (standardised path coefficient β=−0.71, p=0.005 for 3.3–8.0-mm body length (BL) larvae and β=−0.78, p<0.001 for 8.1–12.0-mm BL larvae). Naupliar abundance positively affected *%GF* of *Ammodytes* sp. larvae (β=0.75, p<0.001 for 3.3–8.0-mm BL larvae and β=0.66, p<0.001 for 8.1–12.0-mm BL larvae), whereas it was negatively affected by water temperature (β=−0.45, p=0.008 for 3.3–8.0-mm BL larvae and β=−0.56, p=0.002 for 8.1–12.0 mm BL larvae) and temperature effect was weak compared with that of naupliar abundance. In turn, *%GF* positively affected larval somatic weight (β=0.91, p<0.001 for 6.0-mm BL larvae and β=0.70, p=0.005 for 10.0-mm BL larvae). The recruitment failure in 1999 was likely caused by a reduced condition factor, which resulted from low naupliar abundance. In contrast, the abundances of nauplii and *Oithona similis* copepodites were high in 2000 and 2001. It is possible that the higher recruitment success in 2001 was because of the higher water temperatures in Mutsu Bay sustaining faster growth of the larvae than in 2000 under the high prey abundance conditions.

Key words *Ammodytes* · Copepoda · Gut fullness · Nauplius · Pycnocline · Sand lance larva · Somatic condition

Introduction

The Pacific sand lance, previously known as *Ammodytes personatus*, but has recently been divided into two species, *A. japonicus* and *A. heian* [1], is found around Honshu Island, Japan, and is well-utilised commercially. The commercial landings of the former *A. personatus* (hereafter referred to as *Ammodytes* sp.) fluctuate annually in and around Ise Bay, Japan [2], and so it is possible that the recruitment of these fish may be mainly controlled by survival during the early life stages, as is the case for other marine fish. Hjort [3] suggested that a cause of fluctuations in larval mortality was starvation at first feeding (the 'critical period hypothesis'), whereas Cushing [4] suggested that the survival rates of larvae increase when they encounter high prey densities (the 'match-mismatch hypothesis'). Both hypotheses focus on starvation that occurs near the time when larvae first begin to feed. However, first-feeding larvae of *Ammodytes* sp. around Japan can consume both external nutrition (by feeding) and internal nutrition (from yolk) with high starvation tolerance [5, 6], suggesting that starvation may not be a direct cause of larval mortality [7]. Houde [8] suggested that larval mortality is affected by predation rather than starvation; hence, fast-growing larvae that are vulnerable to predation for a shorter time have higher survival rates (the 'stage-duration hypothesis' and 'growth-predation hypothesis') [9, 10, 11].

In Tsugaru Strait and the mouth of Mutsu Bay, *Ammodytes* sp. spawn adhesive demersal eggs from January to February [12, 13] (Fig. 1). In 1998–2002, the peak abundance of larvae with a yolk sac was found from mid-March in the mouth of the bay [14, 15, 16, 17]. The Tsugaru Warm Current (TWC) [18] transports most of the hatched larvae to the inner part of the bay, with pelagic larvae mainly being distributed in West Bay. Larvae without yolk sacs have a wide range of body lengths and are found in the southern part of West Bay in March and April [19]. Settled juveniles are then distributed across shallow coastal areas near the mouth of the bay, where they are caught commercially by dip nets with fishing lamps [19]. However, the recruitment process of *Ammodytes* sp. is currently unclear, particularly with regard to the sensitive periods and factors affecting the survival rate during the early life stages in the mouth of the West Bay of Mutsu Bay. Therefore, in this study, we investigated inter-annual changes in the digestive tract contents, feeding activity, relative body weight, prey abundance and quality and oceanographic structure in Mutsu Bay to better understand the biotic and abiotic factors that affect the recruitment success of *Ammodytes* sp.

Fig. 1

Materials and methods

Field surveys

Sampling was conducted aboard the T/S *Ushio-maru* and a commercial fishing boat in Mutsu Bay during the daytime from late March to mid-May in 1999 and 2000 and from late February to mid-May in 2001 (Fig. 1; Table 1). The sampling area was divided into three regions: the bay mouth, West Bay and East Bay, with the latter two regions being defined as the inner part of the bay. To investigate the vertical distribution and diet of *Ammodytes* sp., we collected individuals by horizontal hauls with both a ring net (0.8-m diameter, 2.7-m length and 0.33-mm mesh size) at 1, 10, 20 and 30 m depths and Motoda (MTD) closing nets (0.56-m diameter, 2.0-m length and 0.33-mm mesh size) [20] at 1, 10, 20, 30 and 40 m depths, mainly at Sta. 20 (sea bottom depth: 52 m), this area contains individuals with a wider range of body sizes than those in the other northern stations in Mutsu Bay [19]. These nets were towed at a speed of 1.0 m/s for 5–10 min. We collected copepod copepodites and appendicularians by vertical hauls with a plankton net (0.45 m diameter, 1.8 m length and 0.10 mm mesh size) at Sta. 20 and Sta. 22. All nets were equipped with flowmeters. We sampled copepod nauplii by collecting 6.8 or 20 l of water in Van Dorn bottles at 1, 10, 20, 30 and 40 m depths at Sta. 20 and filtering this through a 40-μm mesh sieve. All specimens were immediately fixed in a 5% buffered formalin-seawater solution.

We recorded the water temperature and salinity from the surface to the sea floor using a conductivity-temperature-depth (CTD) instrument (SBE-19; Sea-Bird Electronics Inc., Bellevue, WA, USA). The surface temperature was measured using a bar thermometer (Watanabe Keiki Mfg. Co. Ltd, Tokyo, Japan) and salinity was measured using a salinometer (Portasal 8410; Guildline Instruments Ltd, Ontario, Canada). The water temperature and salinity data have previously been published in Imura et al. [21], and these were used to calculate the difference in density [$\sigma t=\rho$ (kg/m^3) – 1000] between 5- and 35-m depths at Sta. 20 to measure the stratification index of the water column (hereafter expressed without a unit).

Biological measurements and diet analyses of *Ammodytes* sp. larvae

A. japonicus and *A. heian* have similar morphological features and so can only be clearly distinguished using molecular approaches [1]. DNA sequencing analysis has confirmed that the juveniles of both species co-occur in the bay mouth of Mutsu Bay [22]. Therefore, because the larvae collected in Mutsu Bay in this study could not be identified to species based on their morphological features, we refer to the larvae as *Ammodytes* sp. throughout this report.

We sorted and identified larval fishes to species or genus by referring to Okiyama et al. [23] and counted the number of *Ammodytes* sp. larvae. We measured the notochord length of preflexion and flexion larvae of *Ammodytes* sp. and the standard length of postflexion larvae to the nearest 0.1 mm using an electric slide calliper under a stereoscopic microscope, with both measures being referred to as body length (BL) in this report. We classified the larvae into four BL size groups: 3.3–8.0, 8.1–12.0, 12.1–14.0 and 14.1–24.1 mm. We analysed the digestive tract contents from 37–113 randomly selected larvae collected at Sta. 20 on each sampling date except 13 April 2000, when all 25 larvae were used. In addition, we analysed the digestive tract contents of larvae that were collected using a ring net at Sta. 22 (44-m depth) on 27 March 1999 and using MTD nets at Stn. 31 (51-m depth) on 13 April 1999 (Fig. 1; Table 1) to confirm low feeding intensities (see “Results”). We identified the digestive tract contents to the lowest possible taxa and then counted and measured each prey type. We also measured the body weight (somatic weight, SW) of larvae without their digestive tracts (removed from the oesophagus to the anus) to the nearest 0.1-mg wet weight using an electric balance after blotting the larvae on filter paper for approximately 1 min. The larval digestive tract contents were expressed as a percent index of relative importance (*%IRI*), which was calculated from the percent frequency of occurrence (*%F*), percent numerical composition (*%N*) and percent volume composition (*%V*), as follows:

$$\%IRI = IRI_i \times 100 / \sum IRI_i \quad (1)$$

$$IRI_i = \%F_i \times (\%N_i + \%V_i) \quad (2)$$

$$\%F_i = m_i \times 100 / M \quad (3)$$

$$\%N_i = n_i \times 100 / \sum n_i \quad (4)$$

$$\%V_i = v_i \times 100 / \sum v_i \quad (5)$$

where m_i was the number of larval individuals that fed on prey taxon i, M was the total number of larvae examined (including larvae without food in their digestive tracts), n_i was the total number of individuals of prey taxon i in the larval digestive tracts and v_i was the total volume of prey taxon i.

We measured the prosome widths of the copepod nauplii (PW_n) and copepodites (PW_c) in the digestive tracts under a binocular microscope with a micrometer. To examine the volume of copepod nauplii in the larval digestive tracts (V_n), we assumed that the prosome depth of a nauplius was equal to PW_n and that the total length of a nauplius was twice as long as PW_n [24], i.e. that the nauplii were of ellipsoid shape with a volume of:

$$V_n = (4/3) \times 3.14 \times (PW_n/2)^2 \times 2 \times (PW_n/2) = 1.05 \times PW_n^{\ 3} \quad (6)$$

We then estimated the mean volume of copepod nauplii in the diet of each larva to compare feeding intensities between sampling dates. To examine the volume of copepod copepodites (V_c), we assumed that all copepodites in the digestive tracts were *Oithona similis*, because all identifiable copepodites were this species in this study (see "Results"). We estimated the prosome length (PL_c) and depth (PD_c) of *O. similis* copepodites from the regression equations PL_c=2.43×PW_c (n=78, r^2=0.62) and PD_c=0.779×PW_c (n=20, r^2=0.55), which were obtained from plankton net samples, and the calculation of the volume of copepodites referred to Nishiyama and Hirano [24] and Takatsu et al. [25], as follows:

$$V_c = \left[(4/3) \times 3.14 \times 2.43 \times 0.779 \times (PW_c/2)^3\right] / 0.944 = 1.05 \times PW_c^{\ 3} \quad (7)$$

If a particle was immeasurable due to collapse or digestion, we used the mean V_n and V_c in the same digestive tract. We estimated the volumes of other minor prey items from conversion formulae that utilised prey length [25].

Because the saturation volume of the gut increases with body length, we estimated relative gut fullness (*%GF*) to compare feeding intensities between sampling dates. For each larva, *%GF* was calculated as the percentage of the prey volume to the saturation volume. We estimated saturation volumes from the maximum volume of every 10 larvae [25] and then substituted these for larval BL in the regression formulae provided above.

Analysis of environmental factors

We identified subsamples (≥60 individuals) of copepod nauplii from the Van Dorn bottle samples to genus level (based on the literature cited in Takatsu et al. [26, 27]) and measured their PW_n. Naupliar volume was calculated individually using the equation (6), and the abundance of copepod nauplii in each Van Dorn bottle sample was expressed as a volume per litre (mm^3/l). The mean densities of *O. similis* copepodites and appendicularians collected in the water column at each sampling stations by vertical hauls with a plankton net were expressed as individuals per m^2. The mouth area of the plankton net (0.159 m^2) was calibrated for the filtration efficiency, which was the ratio of the true filtration distance estimated from the total number of flowmeter rotations to the length of wire out on each sampling date. The density of *Ammodytes* sp. larvae was expressed as the number of individuals per m^3. The weighted mean depth (*WMD*; m) and the weighted mean temperature (*WMT*; °C) in the larval habitat were calculated as:

$$WMD = \sum(d_j \times s_j) / \sum s_j \quad (8)$$

$$WMT = \sum(t_j \times s_j) / \sum s_j \quad (9)$$

where d_j was the sampling depth of the MTD tows, t_j was the water temperature and s_j was the larval density at a depth of j m.

Horizontal distribution of *Ammodytes* sp. larvae

To confirm the horizontal distribution of *Ammodytes* sp. larvae, we counted the number of larvae in ichthyoplankton samples that were collected in three regions (bay mouth, West Bay, East Bay) during the daytime from February to April 1989–1997 to investigate the spatial distribution of Pacific cod (*Gadus macrocephalus*) larvae and juveniles [27, 28]. Ichthyoplankton were collected using a non-closing beam-trawl net (2.0-m height and 2.5-m wide square mouth and 13–3.1–0.33-mm mesh in 1989 and 13–3.1–0.72-mm mesh in 1990–1997) aboard the T/S *Ushio-maru*. The beam-trawl net was towed at a net speed of 1.5 m/s for 10–15 min for horizontal hauls at the target depths (12–26-m depth range) in 1989–1993 and for 20–22 min for oblique hauls from 2 m above the sea floor to the surface in 1994–1997. The towing methods for the beam-trawl net are detailed in Takatsu et al. [27]. The volume of water filtered by the beam-trawl net was calculated from its effective mouth area (0.16 m^2 for both mesh

sizes), and we assumed that the filtration efficiency of the beam-trawl net for *Ammodytes* sp. larvae was 100%. The density of larvae was expressed as the number of individuals per 1000 m^3.

Recruitment abundance index

We extracted commercial landings data of *Ammodytes* sp. juveniles, which were captured from the coastal area of the bay mouth and the inner bay, from commercial landings data of Aomori Prefecture. We estimated the densities of larvae just after hatch per haul in the bay mouth and West Bay from four horizontal hauls at a 20-m depth using a larva net (1.3-m diameter, 5.4-m length and 0.45-mm mesh size) at a speed of 1.0 m/s for 10 min aboard the R/V *Seiho-maru* in March 1994–1995 and 1997–2001. Based on these data, we calculated the natural logarithmic ratio of commercial landings of juveniles (R) per larval density (S) as the recruitment per spawning stock [ln(RPS)] for each year.

Statistical analysis

The data were compared using one-way analysis of variance (ANOVA) and Scheffe's test for multiple contrasts [29, 30]. Non-parametric Kruskal–Wallis tests were also used to compare median values between three or more samples if the assumption of homogeneity of variance was rejected by the F_{max}-test on log(x + 1)-transformed data. Differences in the log(x + 1)-transformed densities of *O. similis* copepodites and appendicularians were compared using two-way ANOVA, with sampling period and sampling years. An *F*-test was used to compare differences between the slopes of the allometric growth equations for log-transformed BL and log-transformed SW of the larvae on each sampling date, and *G*-tests were used to compare the frequency of occurrence of larvae with empty digestive tracts and the percentage of sampling stations where larvae were collected between sampling areas. Significance levels were set at 0.05.

A path analysis [29] using the maximum likelihood method was conducted with Amos ver. 5.0 (SmallWaters Corporation, Chicago, IL, USA; now 'SPSS Amos', IBM Corporation, Armonk, NY, USA) to examine the interaction between abiotic and biotic factors, with the difference in water density (σt) between 35- and 5-m depths (stratification index) at Sta. 20 and *WMT* included as exogenous variables,

the mean abundance of nauplii at 10–30 m depths at Sta. 20, larval SW at 6.0- and 10.0-mm BL (estimated from allometric growth equations) and arcsine-transformed *%GF* included as endogenous variables. Path analysis techniques allow researchers to test the fit of the correlation matrix against two or more causal models, avoiding the need to use often misleading univariate analyses. Path model selection (i.e. whether indirect paths between non-neighbouring factors are inclusive or not) was based on goodness-of-fit statistics (e.g. r^2 for endogenous variables, the comparative fit index (*CFI*), the parsimony-adjusted comparative fit index (*PCFI*) and the root mean square of approximation (*RMSEA*)).

Results

Horizontal and vertical distributions of *Ammodytes* sp. larvae

In the present study, we confirmed that the horizontal distribution of the larvae during the daytime gradually extended from the bay mouth into West Bay, but rarely into East Bay (Fig. 2). Larvae were present at low densities in Mutsu Bay in late February 1991, 1992, and mid-February 1994. By contrast, the highest densities of larvae were recorded in the bay mouth in early March 1989 and early April 1991 and in West Bay in mid-April 1992 and late April 1995, 1996, and 1997. There was a significant difference in the percentage of sampling stations at which larvae were collected with the beam-trawl net between sampling areas (*G*-test: $p<0.001$), with a higher occurrence in the bay mouth (80%) and West Bay (62%) than in East Bay (27%) throughout the sampling period.

Fig. 2

Figure 3 shows the vertical distributions of *Ammodytes* sp. larvae collected by simultaneous horizontal hauls using MTD closing nets at Sta. 20 during the daytime. Larval densities were highest at 20-m depth on all sampling dates except 13 April 2000, when the highest density occurred at 30-m depth. Overall, relatively higher densities were found at 10–30-m depths. There was no significant difference in larval *WMD* between BL groups (Kruskal-Wallis test: $p=0.95$). Large numbers of larvae were collected at Sta. 20 in March and April 1999–2001; however, they were rare in May (17, 2 and 1 individuals on 15 May 1999, 13 May 2000 and 7 May 2001, respectively; Table 1). The total BL range was 3.3–24.1 mm; however, only 4.6% (143) of the individuals belonged in the 14.1–24.1 mm BL size class at Sta. 20

Fig. 3

during the study period till April. Therefore, we did not include the data from May or the 14.1–24.1-mm BL size class in the following analyses because the sample sizes were not large enough to compare the trends between sampling periods.

Larval digestive tract contents and relative gut fullness

The frequencies of larvae without food in their digestive tracts were low (4.7% in 1999, 4.2% in 2000, 3.2% in 2001) and did not significantly differ between years (*G*-test: $p=0.66$). The percent index of relative importance (*%IRI*) was larger for copepod nauplii (94.0–99.9% in 3.3–8.0-mm BL larvae, 72.8–98.4% in 8.1–12.0-mm BL larvae and 52.6–82.4% in 12.1–14.0-mm BL larvae) than for other prey items throughout the sampling periods, with the exception of 12.1–14.0-mm BL larvae on 10 April 2001 (32.8%; Table 2). Eight genera of copepod nauplii were identifiable in the digestive tracts, with *Oithona* (59.4% of individuals and 44.2% of the volume), *Centropages* (21.9% and 21.1%), *Pseudocalanus* (11.2% and 26.8%) and *Paracalanus* (7.1% and 5.5%) predominating, and *Acartia*, *Calanus*, *Microsetella* and *Oncaea* making a small contribution (0.03–0.26% and 0.05–2.03%). The mean prosome width of *Pseudocalanus* nauplii was significantly larger (113 μm) than the other three major nauplii (76.6–82.0 μm; Scheffe's test for multiple contrasts: $p<0.001$). As the larval BL increased, the *%IRI* of copepod copepodites also increased (0–2.0% in 3.3–8.0-mm BL larvae, 0.0–15.5% in 8.1–12.0-mm BL larvae and 6.5–49.9% in 12.1–14.0-mm BL larvae). All identifiable copepodites in the digestive tracts were *Oithona similis*. In the 8.1–12.0-mm BL and 12.1–14.0-mm BL larvae, the *%IRI* of appendicularians were occasionally high on a few sampling dates (26.3% on 26 April 2000 and 13.5% on 10 April 2001 in 8.1–12.0-mm BL larvae, and 35.8% on 24 April 1999 in 12.1–14.0-mm BL larvae). Thus, ≤12.0-mm BL larvae fed mainly on copepod nauplii, whereas 12.1–14.0-mm BL larvae fed on a mixture of copepod nauplii, copepodites and appendicularians. Invertebrate eggs and tintinids were also found but these were rare (≤5.1 and ≤0.7%, respectively) even in small larvae (Table 2).

Table 2

Relative gut fullness (*%GF*; Fig. 4) and the volume of nauplii per larva (Fig. 5) were used to compare the feeding intensities for 3.3–8.0-mm BL and 8.1–12.0-mm BL larvae between sampling periods (the data for 8.1–12.0-mm BL larvae on 27 February 2001 were omitted because only one larva was obtained). The median *%GF* in the 3.3–8.0 mm BL and 8.1–12.0 mm BL size classes was relatively higher on 28

Fig. 4

Fig. 5

March 2000, 13 April 2000, 27 February 2001, 13 March 2001 and 29 March 2001 (31–73 and 26–64%, respectively) than on the other sampling dates (8–14 and 8–19%; Fig. 4), as was the mean total volume of all naupliar taxa per larva (34.3–71.2×10^{-4} mm^3/larva and 118–172×10^{-4} mm^3/larva cf. 6.3–20.9×10^{-4} mm^3/larva and 24.3–59.1×10^{-4} mm^3/larva; Fig. 5). In the four or five sampling dates with high *%GF* and naupliar volumes, *Oithona* nauplii (43–72% in 3.3–8.0-mm BL larvae and 20–58% in 8.1–12.0-mm BL larvae) and *Pseudocalanus* nauplii (7–34% in 3.3–8.0-mm BL larvae and 25–45% in 8.1–12.0-mm BL larvae) occupied a relatively high percentage of the volume.

In 1999, the larvae that were sampled at Sta. 20 had a relatively low *%GF* and naupliar volume. To confirm these low feeding intensities, we analysed the *%GF* and naupliar volumes in larvae that were collected from Sta. 22 on 27 March and Sta. 31 on 13 April 1999. These also generally contained low levels for each (7% and 17.2×10^{-4} mm^3/larva at Sta. 22, 22% and 16.8×10^{-4} mm^3/larva at Sta. 31 for 3.3–8.0 mm BL larvae and 13% and 27.7×10^{-4} mm^3/larva at Sta. 22 for 8.1–12.0 mm BL larvae), although higher values were found for the 8.1–12.0 mm BL size range at Sta. 31 (36% and 151×10^{-4} mm^3/larva).

Larval somatic condition

Allometric growth curves (the relationship between BL and SW) were estimated for each sampling date to assess variation in body condition (Fig. 6). There was a significant difference between the slopes of the regression lines (*F*-test: $p<0.001$). The estimated SW values for 6.0 mm BL larvae were heavier on 28 March 2000 (0.40 mg), 13 April 2000 (0.46 mg) and 29 March 2001 (0.34 mg), but lighter on 27 March 1999 (0.21 mg), 13 April 1999 (0.20 mg) and 26 April 2000 (0.20 mg) (we did not estimate SW on 10 April 2001 because no larvae in this size range were collected). The estimated SW values for 10.0 mm BL larvae were heavier on 28 March 2000 (2.1 mg), 13 April 2000 (2.3 mg), 13 March 2001 (2.0 mg) and 10 April 2001 (2.1 mg), but lighter on 27 March 1999 (1.2 mg), 13 April 1999 (1.4 mg) and 26 April 2000 (1.4 mg) (we did not estimate SW on 27 February 2001 because only one larva was sampled, which was 9.2-mm BL) (Table 2).

Fig. 6

Abundance of copepod nauplii, *O. similis* copepodites and appendicularians in the environment

The mean abundances of copepod nauplii per unit volume at 10–30-m depths were relatively higher in 2000 and 2001 (43–66×10^{-3} mm^3/l and 30–69×10^{-3} mm^3/l, respectively) than in 1999 (18–36×10^{-3} mm^3/l; Fig. 7). Mean abundances was particularly high on 13 April 2000 and 29 March 2001 (66×10^{-3} and 69×10^{-3} mm^3/l, respectively), but was low on 27 March 1999 and 13 April 1999 (18×10^{-3} and 20×10^{-3} mm^3/l, respectively). *Oithona*, *Centropages*, *Pseudocalanus* and *Paracalanus* nauplii made up a large proportion of all nauplii in the environment.

Fig. 7

The densities of *O. similis* copepodites collected by vertical hauls with a plankton net (0.10-mm mesh size) from late March to mid-May were significantly different between sampling years (two-way ANOVA: p=0.002), but did not significantly differ between sampling dates (p=0.22; Fig. 8). The mean densities of *O. similis* copepodites were low in 1999 (2.0×10^4 ind./m^2) but high in 2000 (7.4×10^4 ind./m^2) and 2001 (15.6×10^4 ind./m^2; Scheffe's multiple contrasts: p=0.002 between 1999 and 2000 + 2001, and p=0.37 between 2000 and 2001).

Fig. 8

The densities of appendicularians collected by vertical hauls with a plankton net from late March to mid-May were not significantly different between sampling years (two-way ANOVA: p=0.98) or sampling dates (p=0.22; Fig. 8).

Abiotic environment

The water density (σ_t) was calculated at 35- and 5-m depths at Sta. 20, based on the temperature and salinity data provided in Imura et al. [21]. There was a large difference in water density between these depths (stratification index) in March and April 1999 (0.63–1.02), but only a small difference in 2000 and 2001 (0.00–0.27 and 0.00–0.19, respectively). An obvious pycnocline was observed at around 15-m depth in March and April 1999, with a low temperature-reduced saline water mass distributed near the surface layer and a high temperature-saline water mass near the bottom [21]. By contrast, no obvious pycnocline was formed in 2000 and 2001, and so the water masses were almost homogenised vertically.

The *WMT*s for 3.3–8.0 mm BL and 8.1–12.0 mm BL larvae collected from late March to late April in 2001 were slightly higher than for those in 1999 and 2000 (Fig. 9).

Fig. 9

Path analysis

A path analysis was conducted to estimate the effect of environmental factors on larval feeding intensities and condition factor. Data for the 3.3–8.0-mm BL size class on 10 April 2001 were omitted because only larvae that were ≥6.5-mm BL were available and the degree of accurancy was insufficient with body weight estimated from the allometric growth curve based on the 6.0-mm BL size class. Similarly, data for the 8.1–12.0-mm BL larvae on 27 February 2001 were excluded from the analysis because only one larva (9.2-mm BL) was collected in this range (Table 2).

The best model based on goodness-of-fit statistics is shown in Fig. 10. In the 3.3–8.0-mm BL larvae, the stratification index negatively affected the abundance per unit volume of all nauplii at 10–30-m depth (standardised path coefficient β=−0.71, p=0.005), and explained 50% of the variance in naupliar abundance (r^2=0.50). The abundance of all nauplii positively affected larval relative gut fullness (arcsine-transformed *%GF*: β=0.75, p<0.001), while the *WMT* negatively affected larval *%GF* for the 3.3–8.0 mm BL size class (β=−0.45, p=0.008), with these two terms explaining 77% of the variance in *%GF*. In turn, *%GF* positively affected larval somatic weight at 6.0 mm BL (β=0.91, p<0.001), explaining 83% of the variance. Because the covariance between the stratification index and *WMT* was insignificant (p=0.85), this interaction was excluded from the model. Models that included indirect paths between non-neighbouring factors (e.g. between the stratification index and *%GF*, or *WMT* and larval SW) were not selected due to poor goodness-of-fit statistics.

Fig. 10

A similar result was obtained for the 8.1–12.0 mm BL size class, with the stratification index negatively affecting the abundance of all nauplii (β=−0.78, p<0.001) and explaining 62% of the variance in naupliar abundance. The abundance of all nauplii also positively affected arcsine-transformed *%GF* (β=0.66, p<0.001), while *WMT* negatively affected *%GF* (β=−0.56, p=0.002), with these parameters explaining 75% of variance in *%GF*. In turn, *%GF* positively affected larval somatic weight at 10.0-mm BL (β=0.70, p=0.005), explaining 49% of the variance. Again, the covariance between the stratification index and *WMT* was insignificant (p=0.90), and so this interaction was excluded from the model.

Relationship between commercial landings of juvenile *Ammodytes* sp. and the density of larvae

Fig. 11

Figure 11 shows the recruitment abundance index ln(RPS) in 1994–1995 and 1997–2001. Of the years in which larval condition was analysed, the index exhibited lowest value in 1999 (7.17), followed by that in 2000 (9.55), and the highest in 2001 (11.16).

Discussion

Copepod nauplii were the primary prey for *Ammodytes* sp. larvae at the first feeding time until 12-mm BL, when *Ammodytes* sp. switched to feeding on a mixture of copepod nauplii, *Oithona similis* copepodites and appendicularians in Mutsu Bay. Copepod eggs (recorded as invertebrate eggs) and tintinnids were also found in the digestive tracts, but these were rare even in small larvae. In Ise Bay and its mouth, *Ammodytes* sp. larvae start to feed on copepod eggs [6] and/or tintinnid ciliates [31] just after hatching, but copepod nauplii are the primary prey [6, 32]. Therefore, the larvae may depend largely on copepods as prey items through the waters. This study provides the first description of the genus composition of copepod nauplii in the digestive tracts of *Ammodytes* sp. larvae and shows that *Oithona* nauplii were predominant. *Pseudocalanus* nauplii constituted the second highest proportion of the larval diet per unit volume and exhibited a larger body size than the other nauplii. There were differences in the genus composition (in terms of number and volume) between sampling periods, but these two genera occupied relatively higher percentages whenever the relative gut fullness (*%GF*) and mean volume of copepod nauplii in the diet were high. Therefore, these nauplii may be important food sources for supporting *Ammodytes* sp. larvae under favourable prey conditions in Mutsu Bay.

The path analysis showed that a higher abundance of copepod nauplii in the less-stratified water column and subsequently higher larval condition factor, and lower water temperatures in the water column led to a higher *%GF* of larvae. Similarly, Wright and Bailey [33] showed that a high abundance of micro-zooplankton (copepod nauplii and copepodites) resulted in a high growth rate in *Ammodytes marinus* larvae and suggested that the onset of prey production may be an important contributory factor to year-class variability. Low temperatures reduce the gut fullness of some fish larvae (e.g. Nakagami [34]). However, the reverse is true for *Ammodytes* sp. larvae in Mutsu Bay, as larval relative gut fullness (*%GF*) would not be particularly restricted by the temperatures experienced (5.4–9.2°C) and low water

temperatures may reduce the digestion and evacuation rates and sustain a high prey abundance in the larval diet. In other words, this high *%GF* under the low temperature might not mean high energy intake. In addition, the path analysis showed that arcsine-transformed *%GF* of *Ammodytes* sp. was strongly affected by naupliar abundance in environment (β=0.75 and 0.66) compared with temperature (β=−0.45 and −0.56). Similarly, Buckley et al. [35] suggested that mortality of 30 days old larvae of sand lance *Ammodytes americanus* was strongly influenced by plankton density but not temperature (5–9°C).In this study, the abundance of copepod nauplii was low in 1999, but high in 2000 and 2001. The low naupliar abundance in 1999 may have been caused by the formation of a pycnocline, which was shaped by saline TWC water entering the bay beneath a low-salinity water mass near the surface that resulted from the large amount of precipitation that fell in Autumn 1998 [21, 36]. This pycnocline prevented vertical mixing of the nutrients from the sea bottom with the surface waters, which may have had a negative effect on the production of copepod nauplii.

The recruitment index ln(RPS) was the lowest in 1999 in the present study. It has previously been shown that the larvae of this species have a high starvation tolerance and so would not die of starvation directly [5, 6]. However, starvation or poor nutrition could affect the risk of predation by reducing the larval swimming speed or ability to escape [37]. In addition, unfavourable growth conditions can prolong the duration of the larval stage, increasing the time that larvae are vulnerable to predation [8]. Thus, the recruitment failure in 1999 was likely caused by increased predation on the larvae due to a reduced condition factor, which resulted from the low naupliar abundance following the formation of a pycnocline. Similarly, Buckley et al. [35] also observed a high larval growth rate of *A. americanus* in the laboratory when plankton densities were high. In contrast, the naupliar abundance was high in 2000 and 2001, and thus, the larvae had good nutrition, but ln(RPS) was higher in 2001 than in 2000. This difference could not be explained by the abundance of *O. similis* copepodites in the water column from late March to April, which was similar in 2000 and 2001. There is limited knowledge of the relationship between water temperature and growth rate in *Ammodytes* sp. larvae in the laboratory (0.12 mm/day at 6.5°C [38]; 0.23 mm/day at 10.1°C [7]), but fish larvae generally tend to exhibit high growth rates under high water temperature within the tolerable range and abundant food (e.g. Wright and Bailey [33], Buckley et al. [35], and Laurence [39, 40]). Therefore, it is possible that higher water temperatures in Mutsu Bay in 2001 sustained faster growth of the larvae, leading to a higher recruitment success than in

2000 under the high prey abundance conditions.

Here we demonstrated that naupliar and copepodite abundances are important for recruitment success in *Ammodytes* sp. larvae not only at the first feeding time but also throughout the pelagic period. In addition, recruitment may be affected by water temperature through its impacts on the growth rate. The findings outlined in this paper were partly collected to evaluate the stock of *Ammodytes* sp. in Mutsu Bay as it is thought that both *A. japonicus* and *A. heian* are among the fishes that are caught by fishing boats in this bay [22]. Therefore, further research is required to investigate the difference in early life history between *A. japonicus* and *A. heian*, particularly with regard to their survival processes.

Acknowledgements The authors thank Haruo Ogi, Tosikuni Nakatani, John R. Bower of Hokkaido Univ. and Tatsuki Yoshinaga of Kitasato Univ. who have made valuable suggestions. Thanks are also expressed to Mituaki Akabane, Yunosuke Sugisawa and late Johji Odagiri of the Local Independent Administrative Institution Aomori Prefectural Industrial Technology Research Center Fisheries Research Institute for supporting our samplings. Thanks are due to the captain and crew of the T/S *Ushio-maru* of Hokkaido University Faculty of Fisheries for their cooperation on board in collecting the samples. We express our gratitude to the students of our laboratory in 1999–2001. This work was supported by JSPS KAKENHI Grant Number15780129 to T. Takatsu.

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Figure captions

Fig. 1 Location of Mutsu Bay (**a**) and the sampling stations with isobaths (**b**). The sampling area was divided into three regions: the bay mouth (*M*), West Bay (*W*) and East Bay (*E*), with the latter two regions treated as the inner part of the bay

Fig. 2 Horizontal distribution of *Ammodytes* sp. larvae collected with a beam-trawl net in Mutsu Bay. Larvae were collected by horizontal hauls at 12–26-m depth in 1989–1993 and by oblique hauls from 2 m above the sea floor to the surface in 1994–1997

Fig. 3 Vertical distribution of *Ammodytes* sp. larvae by body length (BL) class collected with Motoda (MTD) nets (56-cm diameter) at Sta. 20 in Mutsu Bay

Fig. 4 Median relative gut fullness (*%GF*) of *Ammodytes* sp. larvae by body length (BL) class (3.3–8.0-mm BL and 8.1–12.0-mm BL). Data from samples with <4 larvae are omitted

Fig. 5 Mean volume of copepod nauplii in the digestive tracts of *Ammodytes* sp. larvae (3.3–8.0-mm body length (BL) and 8.1–12.0-mm BL). Data from <4 larvae are omitted

Fig. 6 Allometric growth curves of *Ammodytes* sp. larvae by sampling date calculated using the least square method. Somatic weight (SW) is the wet body weight excluding the digestive tract (27 Mar. 1999: $SW=4.2\times10^{-4}\times BL^{3.46}$, $r^2=0.87$; 13 April 1999: $SW=2.6\times10^{-4}\times BL^{3.71}$, $r^2=0.96$; 24 April 1999: $SW=9.0\times10^{-4}\times BL^{3.25}$ $r^2=0.92$; 28 March 2000: $SW=13\times10^{-4}\times BL^{3.22}$, $r^2=0.93$; 13 April 2000: $SW=15\times10^{-4}\times BL^{3.19}$, $r^2=0.97$; 26 April 2000: $SW=2.0\times10^{-4}\times BL^{3.84}$, $r^2=0.96$; 27 February 2001: $SW=18\times10^{-4}\times BL^{2.72}$, $r^2=0.61$; 13 March 2001: $SW=2.6\times10^{-4}\times BL^{3.89}$, $r^2=0.84$; 29 March 2001: $SW=12\times10^{-4}\times BL^{3.16}$, $r^2=0.81$; 10 April 2001: $SW=6.1\times10^{-4}\times BL^{3.54}$, $r^2=0.96$; all: $p<0.001$)

Fig. 7 Vertical distribution of copepod nauplii (volume per litre) collected with a Van Dorn bottle at Sta. 20, Mutsu Bay. Naupliar volume was estimated based on an assumed ellipsoidal shape using the equation $V=1.05\cdot PW^3$, where V is the estimated volume and PW is the prosome width. Mean naupliar volumes were calculated for 10–30-m depth

Fig. 8 Mean densities of *Oithona similis* copepodites and appendicularians collected by vertical hauls with a plankton net (0.10-mm mesh size) at Sta. 20 and Sta. 22, Mutsu Bay

Fig. 9 Seasonal change in the weighted mean water temperature (*WMT*; °C) associated with vertical distributions of *Ammodytes* sp. larvae of 3.3–8.0-mm body length (BL) and 8.1–12.0-mm BL at Sta. 20, Mutsu Bay

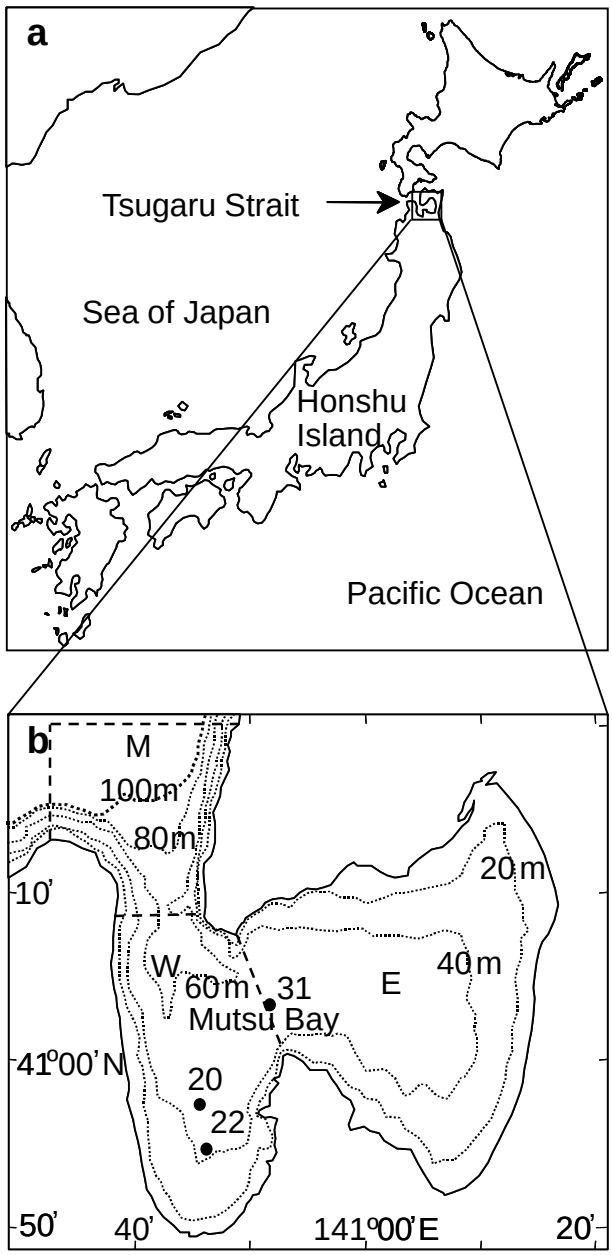
Fig. 10 Path models of the interaction between environmental and larval parameters [3.3–8.0-mm body length (BL) larvae: comparative fit index (*CFI*): 0.812, parsimony-adjusted *CFI* (*PCFI*): 0.487, root mean square of approximation (*RMSEA*): 0.330; 8.1–12.0 mm BL larvae: *CFI*: 0.865, *PCFI*: 0.519, *RMSEA*: 0.228]. *Numerals alongside arrows* indicate the standardised path coefficients (β), while those above the boxes represent the squared multiple correlations (r^2). There were no significant correlations between exogenous variables [weighted mean water temperature (*WMT*) and the stratification index (difference in σ_t)] for either BL class

Fig. 11 Recruitment per spawning stock for *Ammodytes* sp. in Mutsu Bay in 1994–1995 and 1997–2001. This recruitment index was calculated as the ratio of commercial landings (metric tonnes) of settled juveniles from the bay mouth per the inner bay to the mean density of *Ammodytes* sp. larvae (ind./m^3) as detected by R/V *Seiho-maru* in the bay mouth and West Bay in March

陸奥湾におけるイカナゴ属仔魚の摂餌，栄養状態と生残

南條暢聡，髙津哲也，伊村一雄（北大院水），伊藤欣吾（青森水総研），
竹谷裕平（青森水総研，北大院水），高橋豊美（北大院水）

1999–2001 年 2–4 月に陸奥湾で採集されたイカナゴ属仔魚は，主に水深 10–30 m 層に分布し，主にかいあし類ノープリウスを捕食し，体長 12 mm を超える大型仔魚は *Oithona similis* と尾虫類も捕食していた。パス解析の結果，水深 35 m 層と 5 m 層の海水密度差が大きいほど環境中のノープリウスの豊度は低く，体長 6 mm と 10 mm の仔魚の体重は軽かった。1999 年には，鉛直混合と栄養塩の供給が妨げられた結果，ノープリウスの生産が妨げられ，イカナゴは加入に失敗したものと推定された。一方，餌豊度が高かった 2001 年と 2000 年には，高水温だった 2001 年の方が成長が速く，生残率が高かったものと考えられた。

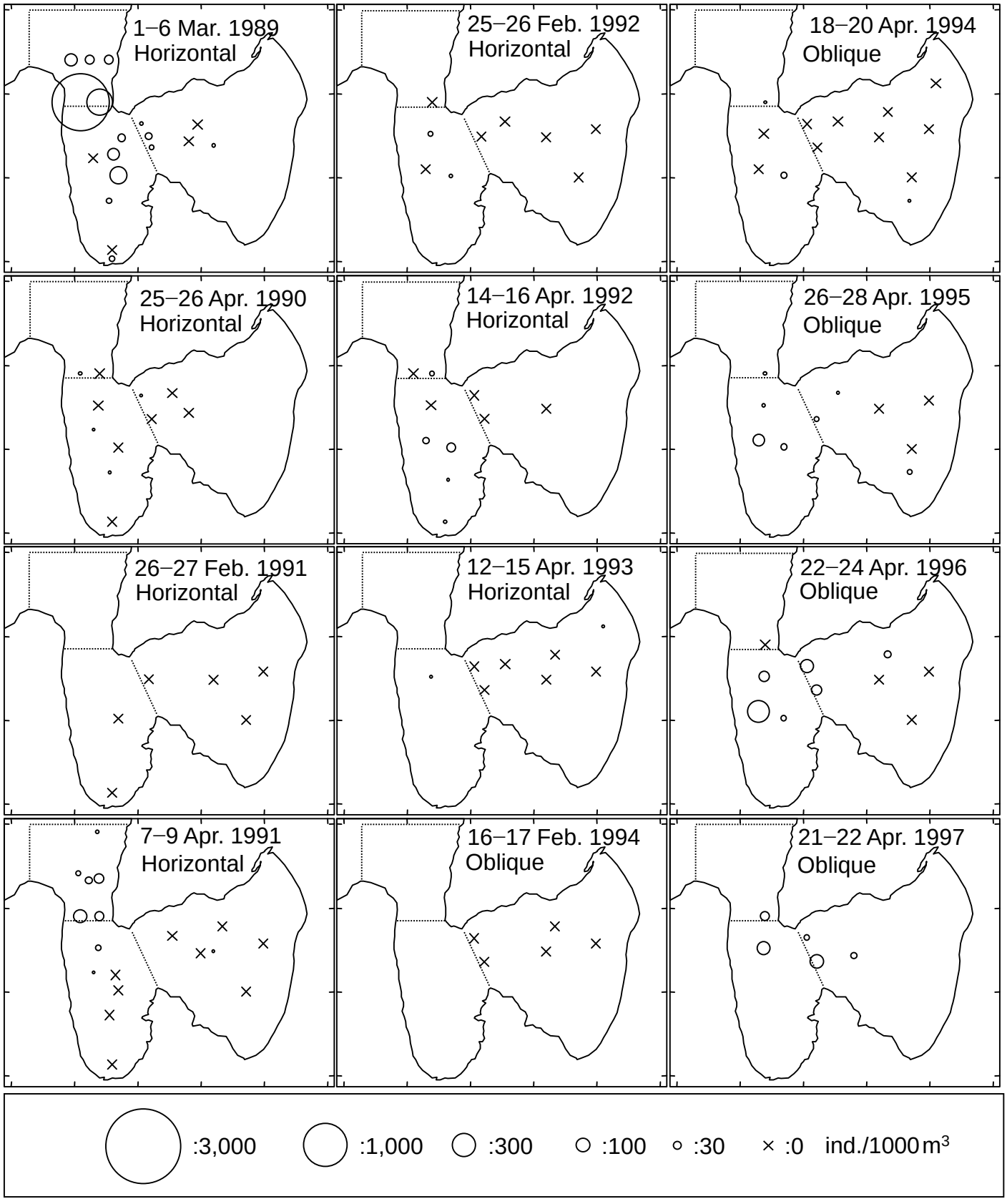


Nanjo et al., Fig. 1 84 mm

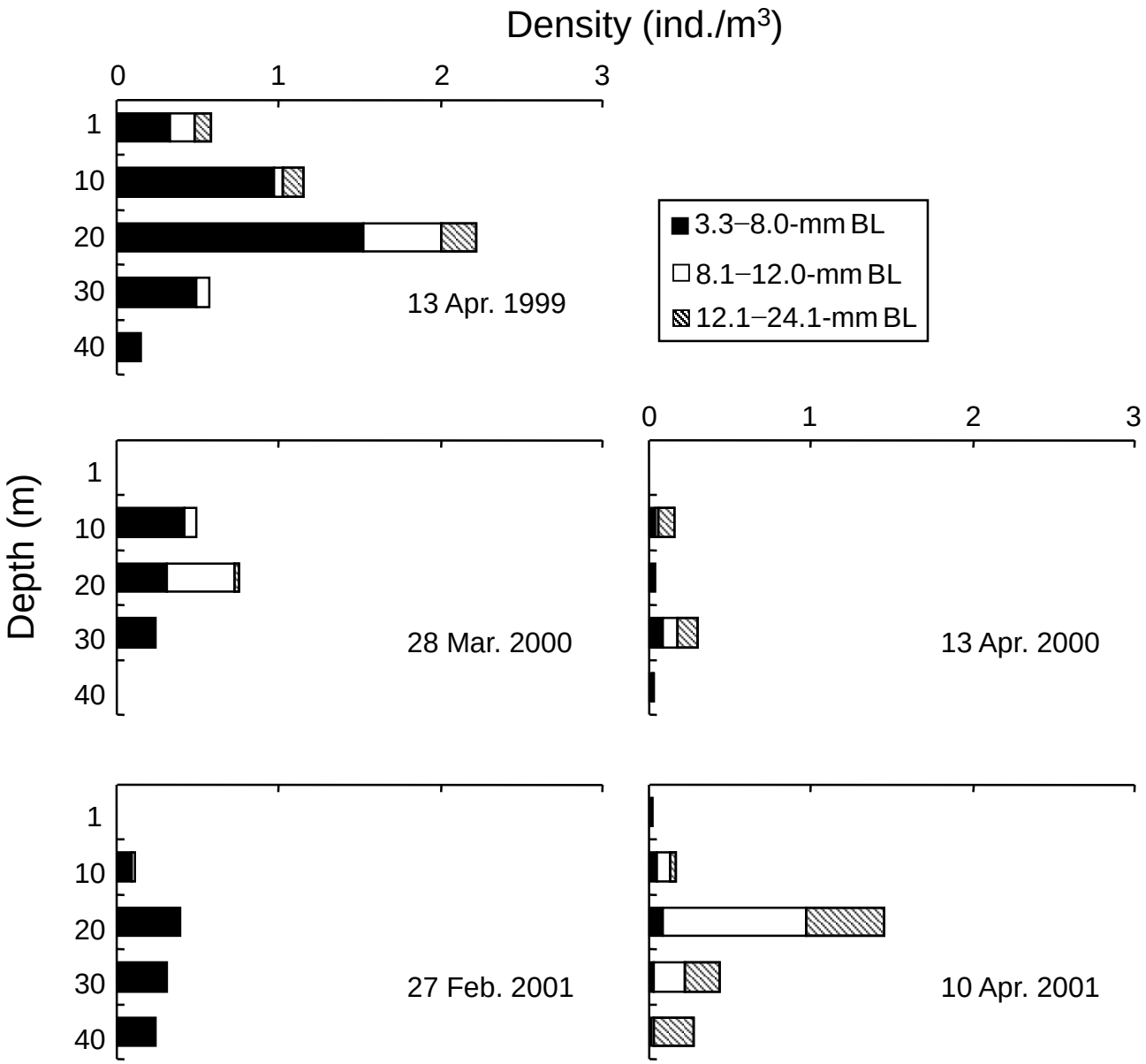
Table 1 Number of biological samples collected at Sta. 20, Sta. 22 and Sta. 31 in Mutsu Bay

Date	Time	Research ship	Sampling gear	Number of tows or bottles	Number of *Ammodytes* sp. larvae collected
27 Mar. 1999	13:25–15:25	F	Ring net at Sta. 20	3	418 (0)
			Ring net at Sta. 22	2	319 (0)
			Van Dorn bottle at St	5	
			Plankton net	2	
13 Apr. 1999	10:49–15:06	U	MTD nets at Sta. 20	5	1168 (20)
			MTD nets at Sta. 31	5	36 (4)
			Van Dorn bottle at Sta. 20	5	
			Plankton net at Sta. 20	1	
24 Apr. 1999	13:30–15:30	F	Ring net at Sta. 20	4	328 (3)
			Van Dorn bottle at Sta. 20	5	
			Plankton net	2	
15 May 1999	14:43–16:43	F	Ring net at Sta. 20	4	17 (3)
			Van Dorn bottle at Sta. 20	5	
			Plankton net	2	
28 Mar. 2000	08:39–09:49	U	MTD nets at Sta. 20	5	49 (0)
			Van Dorn bottle at Sta. 20	5	
			Plankton net	2	
13 Apr. 2000	13:40–14:50	U	MTD nets at Sta. 20	5	34 (9)
			Van Dorn bottle at Sta. 20	5	
			Plankton net	2	
26 Apr. 2000	12:13–14:13	F	Ring net at Sta. 20	4	61(4)
			Van Dorn bottle at Sta. 20	5	
			Plankton net	2	
13 May 2000	12:24–14:24	F	Ring net at Sta. 20	4	2 (1)
			Van Dorn bottle at Sta. 20	5	
			Plankton net	2	
27 Feb. 2001	09:18–10:28	U	MTD nets at Sta. 20	5	89 (0)
			Van Dorn bottle at Sta. 20	5	
			Plankton net	2	
13 Mar. 2001	07:45–09:45	F	Ring net at Sta. 20	4	398 (0)
			Van Dorn bottle at Sta. 20	5	
			Plankton net	2	
29 Mar. 2001	07:30–09:30	F	Ring net at Sta. 20	4	96 (0)
			Van Dorn bottle at Sta. 20	5	
			Plankton net	2	
10 Apr. 2001	10:02–11:12	U	MTD nets at Sta. 20	5	444 (102)
			Van Dorn bottle at Sta. 20	5	
			Plankton net	2	
26 Apr. 2001	08:45–10:45	F	Ring net at Sta. 20	4	3 (1)
			Van Dorn bottle at Sta. 20	5	
			Plankton net	2	
7 May 2001	09:15–11:15	F	Ring net at Sta. 20	4	1 (0)
			Van Dorn bottle at Sta. 20	5	
			Plankton net	2	

F, a commercial fishing boat; U, T/S *Ushio-maru*
Samples were collected with a plankton net at both Sta. 20 and Sta. 22 on all dates except 13 Apr. 1999.
The number of larvae in the 14.1–24.1-mm body length (BL) size class is shown in parentheses; these numbers are included in the totals



Nanjo et al., Fig. 2 84 mm



Nanjo et al., Fig. 3 84 mm

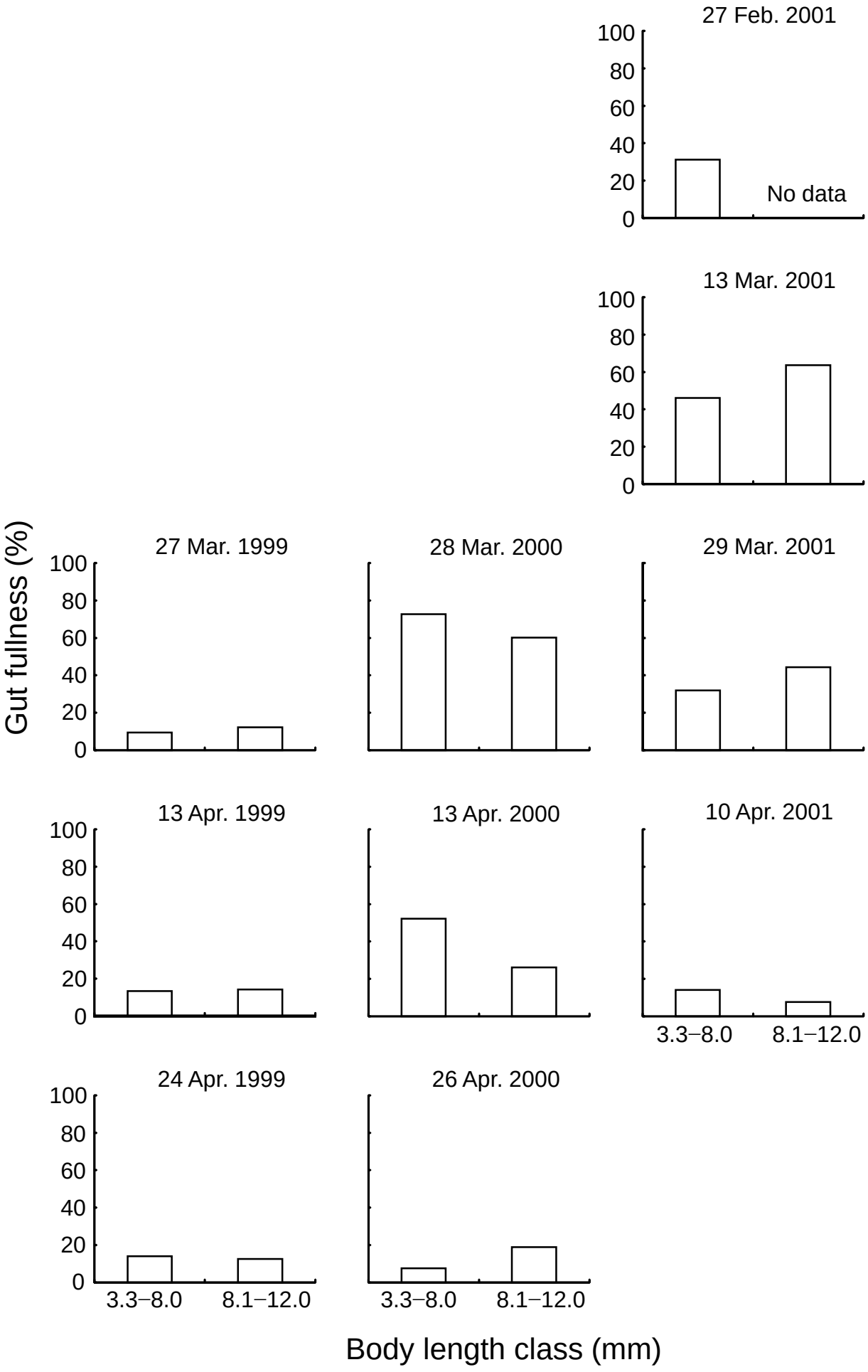
Table 2 Percent index of relative importance (*%IRI*) of prey on which *Ammodytes* sp. larvae fed by body length (BL) class at Sta. 20, Mutsu Bay

3.3–8.0-mm BL	1999			2000			2001			
Taxon	27 Mar.	13 Apr.	24 Apr.	28 Mar.	13 Apr.	26 Apr.	27 Feb.	13 Mar.	29 Mar.	10 Apr.
Tintinnina	<0.1	0.7	<0.1	0	0	0	<0.1	0	0	0
Rotatoria	0	0.5	0	0	1.4	0	<0.1	<0.1	<0.1	0
Cladocera	0.1	0	0	0	0	0	0	0	<0.1	0
Copepoda (nauplius)	94.0	98.5	99.9	98.1	98.0	96.7	99.4	97.8	98.2	96.3
Copepoda (copepodite)	0.1	0	0	1.2	0.7	0	0.2	2.0	0.1	0
Invertebrate egg	3.6	0.2	<0.1	0.1	0	0	<0.1	<0.1	0	0
Appendicularia	2.3	0	0	0.6	0	3.2	0.4	0.1	1.6	3.7
Bivalvia (larva)	0	0.2	0	0	0	0.1	0	0	0	0
Number of larvae examined	24	49	41	22	4	13	60	73	36	7

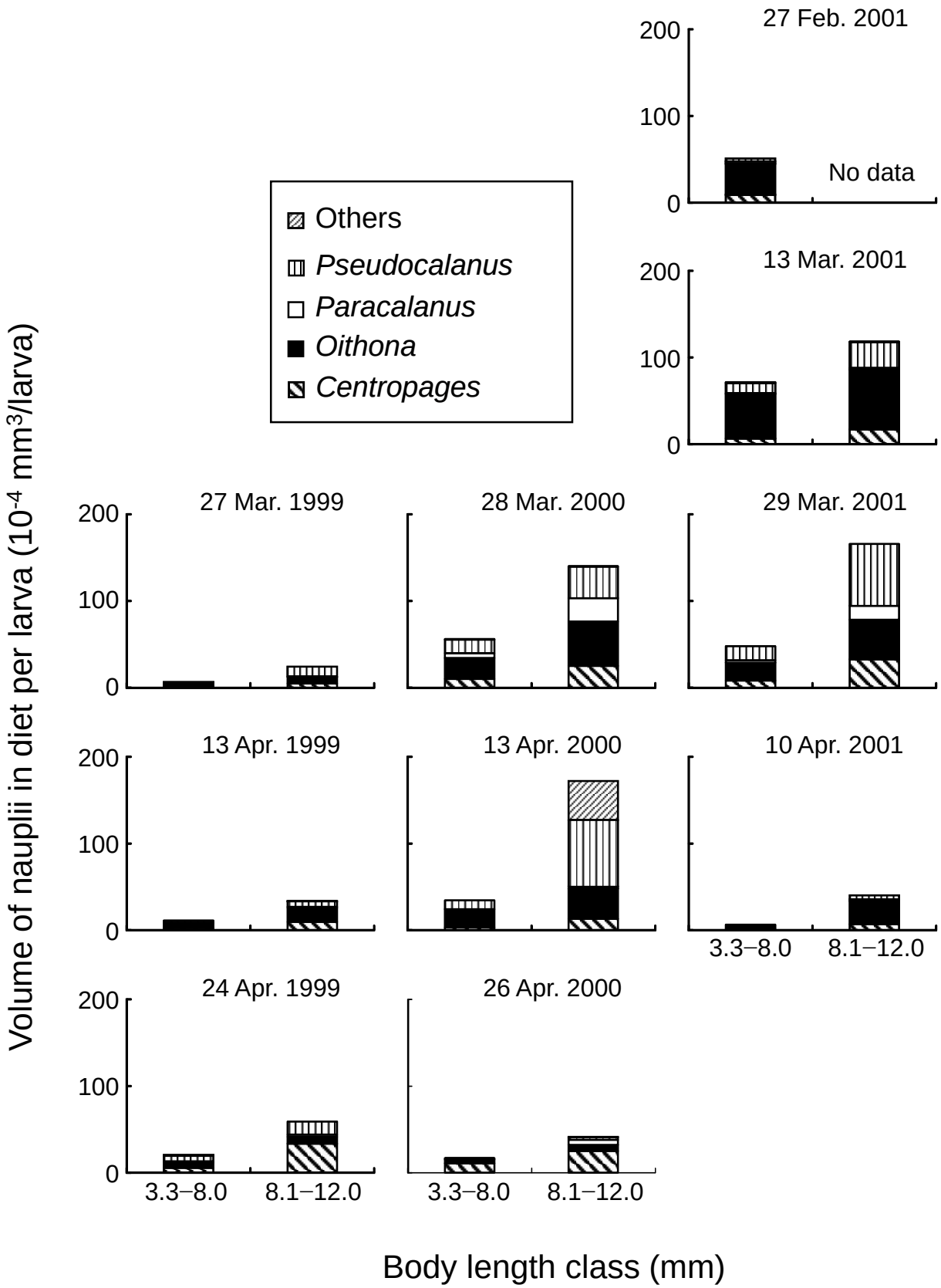
8.1–12.0-mm BL	1999			2000			2001			
Taxon	27 Mar.	13 Apr.	24 Apr.	28 Mar.	13 Apr.	26 Apr.	27 Feb.	13 Mar.	29 Mar.	10 Apr.
Tintinnina	0	0.1	0	0	0	0		0	0	0.1
Rotatoria	0	<0.1	0	0	0	0		0	0	0
Cladocera	0.1	0	0	0.1	0	0.5		0	0	0
Copepoda (nauplius)	85.1	98.4	96.8	84.4	94.6	72.8		78.3	76.6	82.2
Copepoda (copepodite)	9.5	0.9	<0.1	11.5	5.3	0.3		13.7	15.5	0.3
Invertebrate egg	5.1	0.5	0.1	<0.1	0.1	0.1		<0.1	0	0.2
Appendicularia	0.3	0	3.0	3.9	0	26.3		8.0	7.9	13.5
Bivalvia (larva)	0	0.1	0	<0.1	0	<0.1		0	0	3.6
Number of larvae examined	50	41	29	14	7	30	(1)	13	4	43

12.1–14.0-mm BL	1999			2000			2001			
Taxon	27 Mar.	13 Apr.	24 Apr.	28 Mar.	13 Apr.	26 Apr.	27 Feb.	13 Mar.	29 Mar.	10 Apr.
Tintinnina		0.2	0		0					<0.1
Rotatoria		0	0		0					0
Cladocera		0	0		3.2					0
Copepoda (nauplius)		82.4	57.6		52.6					32.8
Copepoda (copepodite)		12.4	6.5		44.1					49.9
Invertebrate egg		0.8	0.1		0					3.1
Appendicularia		4.0	35.8		0.1					4.1
Bivalvia (larva)		0.2	0		0					10.1
Number of larvae examined	(2)	23	4	(1)	14	(3)				38

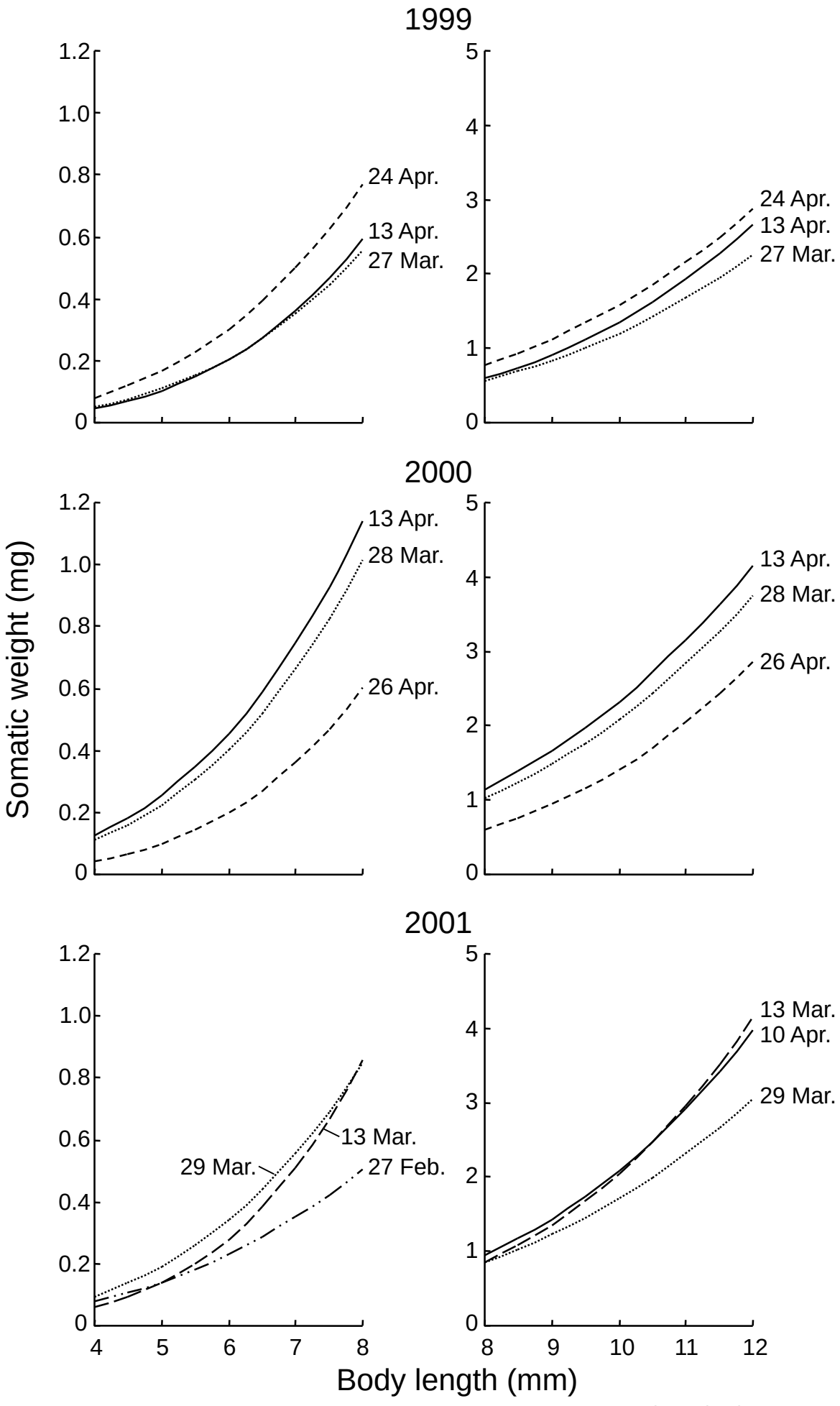
Only data that were obtained from ≥4 larvae are shown



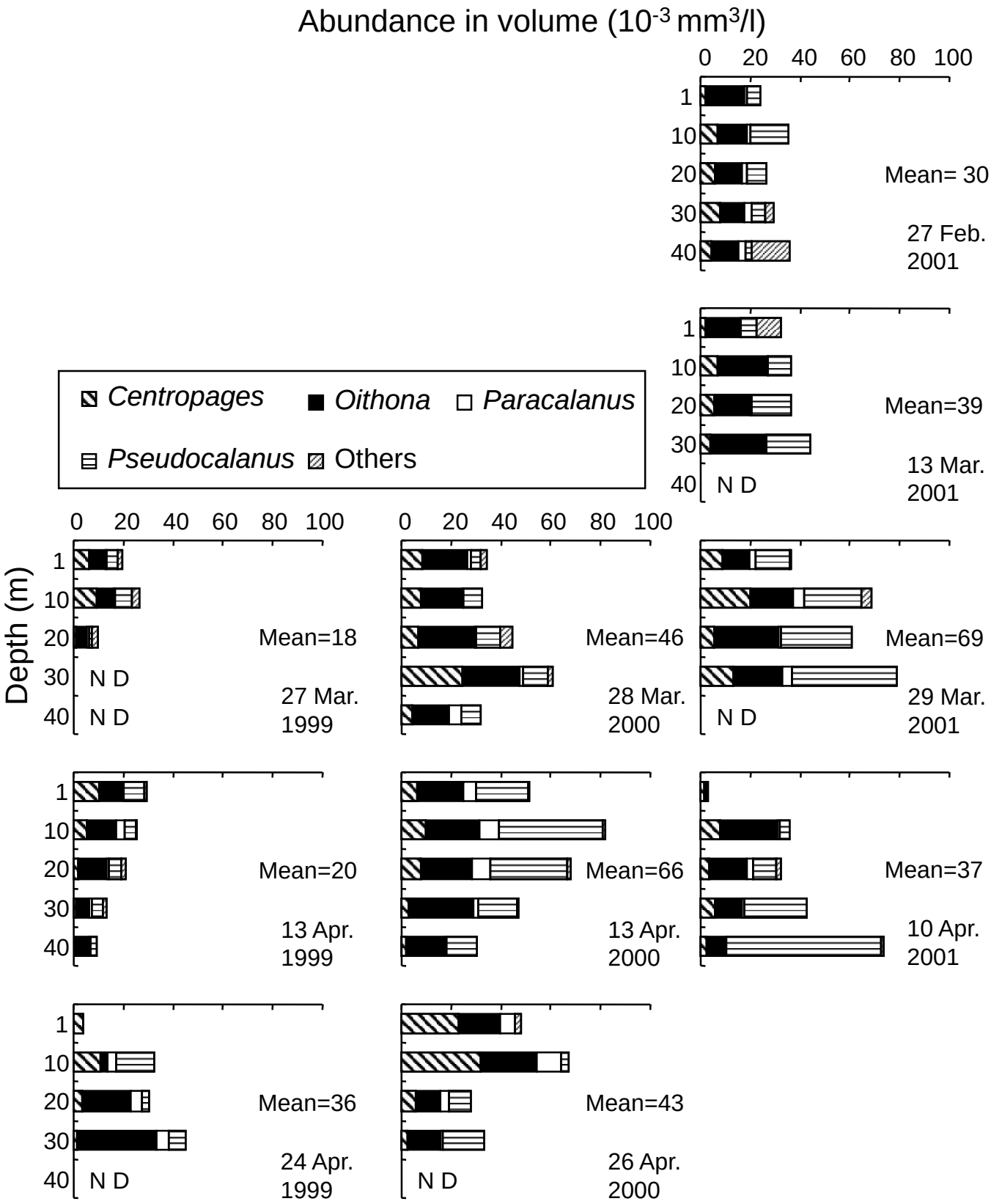
Nanjo et al., Fig. 4 84 mm



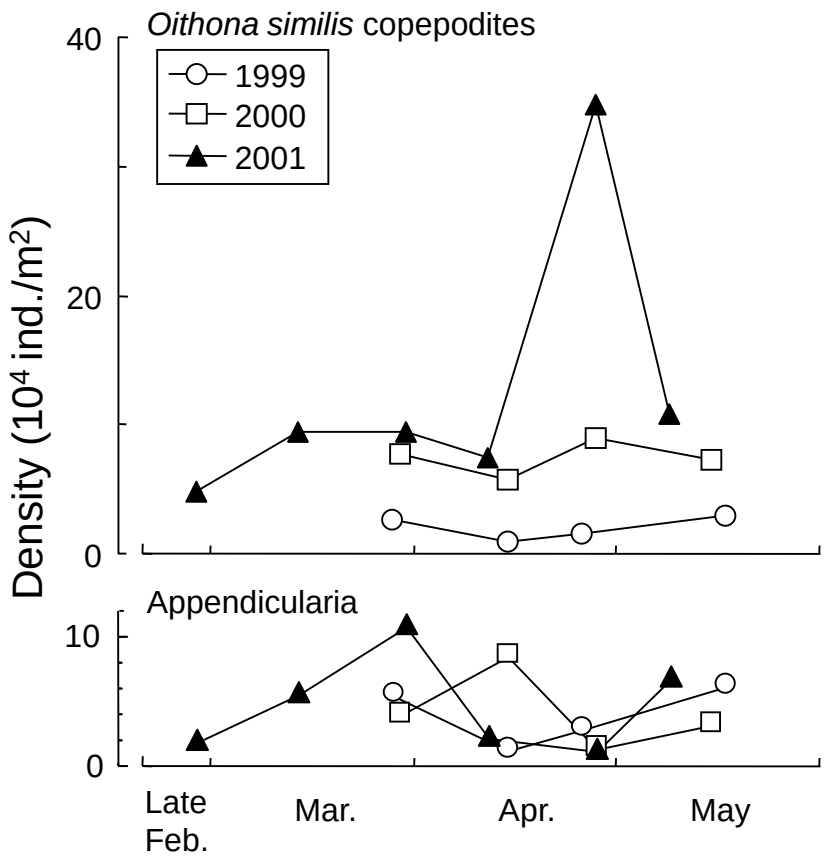
Nanjo et al., Fig. 5 84 mm



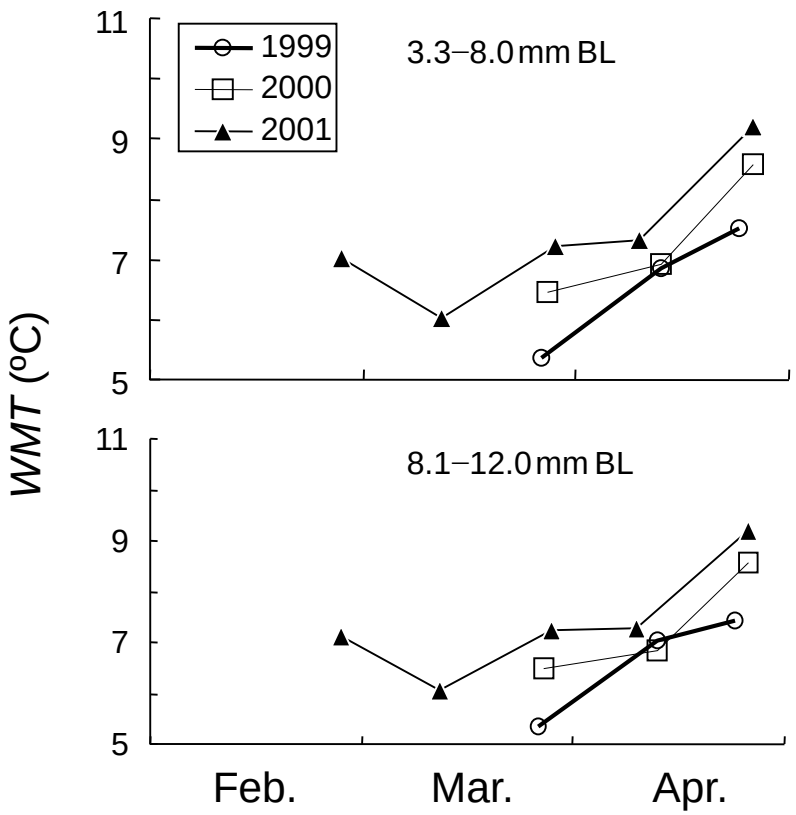
Nanjo et al., Fig. 6 84 mm



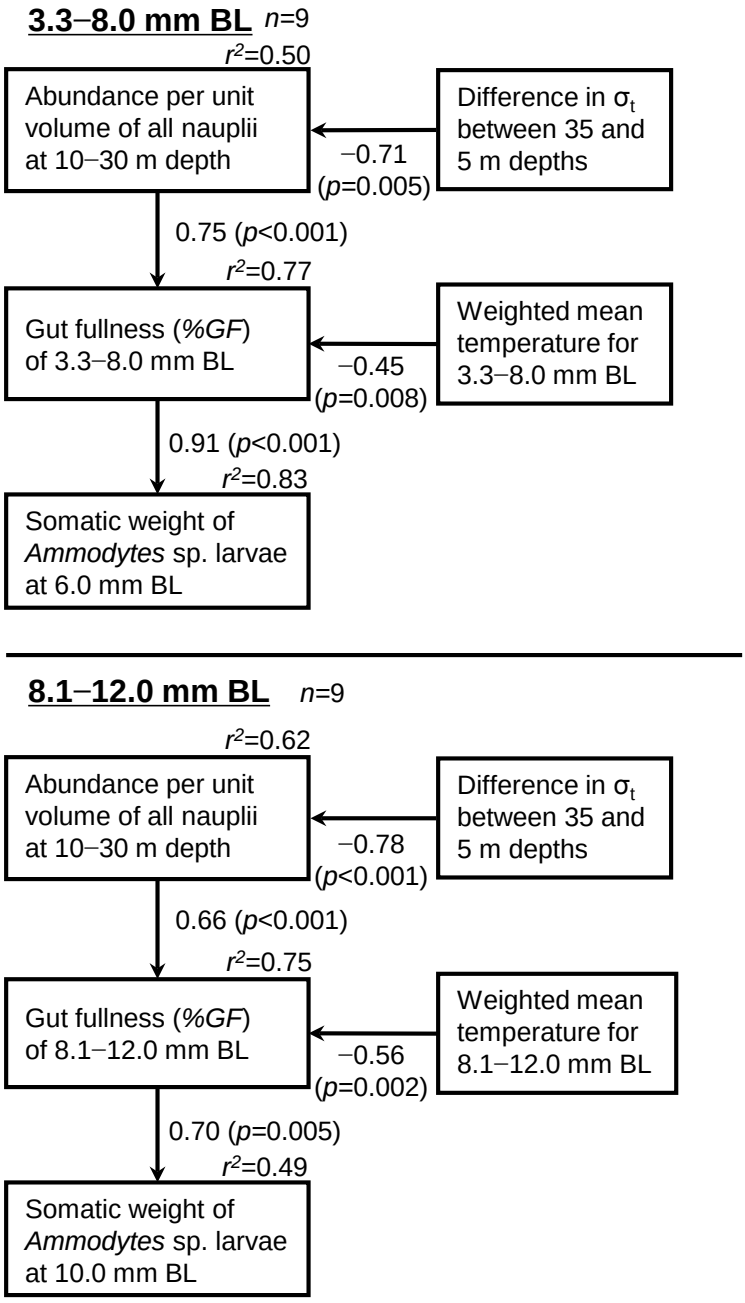
Nanjo et al., Fig. 7 84 mm

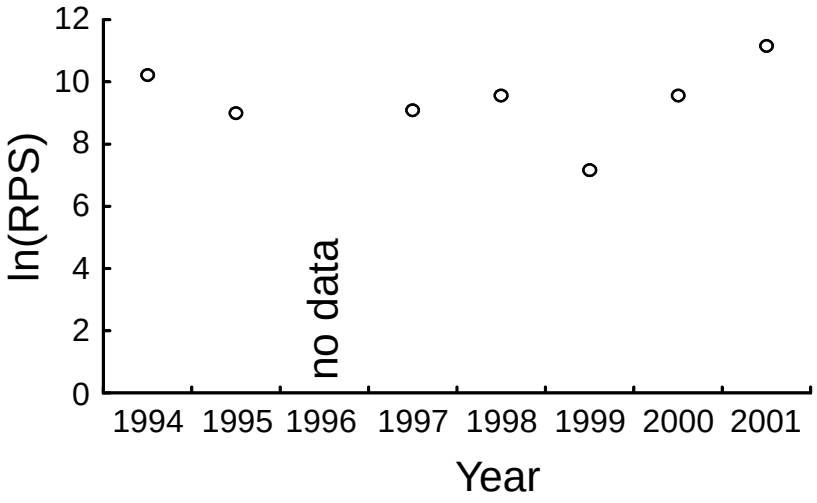


Nanjo et al., Fig. 8 84 mm



Nanjo et al., Fig. 9 84 mm


3.3–8.0 mm BL n=9
r²=0.50
Abundance per unit volume of all nauplii at 10–30 m depth
Difference in σt between 35 and 5 m depths
−0.71 (p=0.005)
0.75 (p<0.001)
r²=0.77
Gut fullness (%GF) of 3.3–8.0 mm BL
Weighted mean temperature for 3.3–8.0 mm BL
−0.45 (p=0.008)
0.91 (p<0.001)
r²=0.83
Somatic weight of Ammodytes sp. larvae at 6.0 mm BL
8.1–12.0 mm BL n=9
r²=0.62
Abundance per unit volume of all nauplii at 10–30 m depth
Difference in σt between 35 and 5 m depths
−0.78 (p<0.001)
0.66 (p<0.001)
r²=0.75
Gut fullness (%GF) of 8.1–12.0 mm BL
Weighted mean temperature for 8.1–12.0 mm BL
−0.56 (p=0.002)
0.70 (p=0.005)
r²=0.49
Somatic weight of Ammodytes sp. larvae at 10.0 mm BL



Nanjo et al., Fig. 11 84 mm