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Vertical distribution and migration of planktonic polychaete larvae in Onagawa Bay, north-eastern Japan

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Abstract Abe, H., Sato-Okoshi, W., Nishitani, G. and Endo, Y. 2014. Vertical distribution and migration of planktonic polychaete larvae in Onagawa Bay, north-eastern Japan. *Memoirs of Museum Victoria* 71: 1–9.

The planktonic larvae of polychaetes are one of the most numerous and diverse groups in coastal zooplankton; however, little is known about their larval dynamics and the factors that affect their vertical distribution. We investigated the vertical distribution and migration of planktonic polychaete larvae in Onagawa Bay, north-eastern Japan, particularly focusing on the dominant spionid larvae. In total, 14 families of planktonic polychaete larvae and 14 species or genera of spionid larvae were identified during our study. Their density greatly fluctuated according to season and depth, with the polychaete larvae generally distributed in the lower layers of the water column. Furthermore, trends in vertical distribution of spionid larvae varied between species. In winter and spring, larvae of *Polydora onagawaensis* were the most prevalent, with a wide range in vertical distribution. In summer and autumn, larvae of *Pseudopolydora achaeta* and *Prionospio* spp. were the most prevalent spionid larvae and were primarily distributed in the lower layers of the water column. Trends in larval vertical distribution varied as a result of differences in adult habitat; these variations would enable the larvae to efficiently recruit into their appropriate adult habitats. Spionid larvae did not show diel vertical migration. Larvae of two spionid taxa, *Pseudopolydora achaeta* and *Prionospio* spp., exhibited tidal vertical migration, with larvae appearing to avoid dispersal by moving to slower-flowing deeper water during flood and ebb tides. Although many previous studies assume that, because of their limited swimming capacity, polychaete larvae are passively dispersed within the water column, this study indicates that polychaete larvae can control their vertical distribution to some extent, and this small-scale vertical migration may be important as a retention mechanism for polychaete larvae.

Keywords polychaete larva, Spionidae, *Polydora*, *Pseudopolydora*, *Prionospio*, vertical distribution, vertical migration, larval retention

Introduction

Many marine invertebrates pass through a planktonic larval phase during their early life history. Historically, larval dispersal has typically been considered a passive process, and most larvae have been thought to be unable to control their horizontal dispersal (Chia et al., 1984; Scheltema, 1986), with a few exceptions such as some larval crustaceans (Luckenbach and Orth, 1992). However, the ability of larvae to control their vertical distribution in the water column has been well known and can have significant outcomes in terms of larval transport and horizontal distribution, because the current speed and direction generally vary with depth (Young, 1995; Hill, 1998; Metaxas, 2001).

Tidal vertical migration patterns have been observed, particularly in estuarine invertebrate larvae (Carriker, 1951; Cronin, 1982). Tidal currents move faster at the surface layers and slower at the bottom layers because of the friction at the bottom layers. Therefore, larvae can be transported towards the sea or shore or remain within the estuary by migrating to the surface or bottom layers, respectively, in synchronisation with tidal cycles (Forward and Tankersley, 2001; Tankersley et al., 2002; Gibson, 2003). These larval behaviours related to relocation are also known as ‘selective tidal stream transport’ (Greer Walker et al., 1978).

Diel vertical migration is also well known for many planktonic animals, including invertebrate larvae. Three patterns of diel vertical migration (DVM) have been observed for planktonic invertebrate larvae: (i) nocturnal (normal) DVM, with an ascent to a minimum depth at night and a descent to a maximum depth during the day; (ii) reverse DVM, with the ascent to a minimum depth during the day and the descent to a maximum depth at night; (iii) twilight DVM, with an ascent to the surface at sunset, a descent to deeper water around midnight, a second ascent to the surface in the early morning hours, followed by a final descent to deeper water at sunrise (Forward, 1988; Pearre, 2003). Although the latter two patterns are rare for invertebrate larvae (Young and Chia, 1987; Queiroga and Blanton, 2005), some larvae, particularly decapods, are sensitive to the diel light cycle (Forward et al., 1984). These behaviours occur in a wide range of planktonic animals and are considered to be predator avoidance behaviour because larvae alter their DVM patterns in the presence of predators (Bollens and Frost, 1991; Neill, 1992; Cohen and Forward, 2009).

In addition to the light and tidal cycles, gravity, temperature, oxygen, salinity, hydraulic pressure and chemicals from phytoplankton and predators are believed to influence larval vertical distribution and migration (Huntley and Brooks, 1982; Pires and Woollacott, 1983; Forward, 1988; Lass and Spaak, 2003). Furthermore, larval behavioural responses are also changeable depending on species, larval condition and feeding history (Thorson, 1946, 1964; Metaxas and Young, 1998a; Arellano et al., 2012). Mechanisms determining vertical distribution and migration of planktonic larvae are complex. Although the diverse vertical distribution and migration of many planktonic animals is well known, there is limited information about these behaviours in polychaete larvae.

Polychaetes are one of the major components of coastal macrobenthos in terms of species richness, density and total biomass (Ward and Hutchings, 1996). They play major roles in the marine food web and in the functioning of benthic communities by their activity in decomposition of organic matter and bioturbation (Aller, 1982; Tomiyama et al., 2005). The planktonic larvae of polychaetes are one of the most numerous and diverse groups of coastal zooplankton (Omel'yanenko and Kulikova, 2002). Despite the great importance of this group in marine ecosystems, the planktonic larval phase of polychaetes is still poorly understood.

Materials and methods

To reveal seasonal vertical distribution of planktonic polychaete larvae, sampling was performed from January to December 2012 at St. 1 (38°26'14.42" N 141°27'38.79" E; 21–23 m depth) in Onagawa Bay (fig. 1). Zooplankton samples were collected once a month from the surface down to 20 m in depth at 5-m intervals using an Iwaki MD-70R shipboard magnet pump (Iwaki Co., Ltd, Tokyo, Japan). A priming water tank and suction hose were connected to a magnet pump and were being primed seawater before pumping. The nozzle of the suction hose was attached to a 1.5-kg weight with wire and dropped to each depth. Approximately 100 L of seawater was pumped up onto the boat and filtered through a hand net with a mesh size of 110 μm, and the plankton samples were fixed with 5% neutralised formaldehyde solution. Planktonic polychaete larvae were identified and counted under a stereomicroscope. Vertical profiles of temperature and salinity were determined using a CTD RINKO-Profiler (JFE Advantech Co., Ltd, Kobe, Japan).

Chlorophyll (Chl) *a* concentration was measured once per month. Water samples were collected from the surface down to 20-m depth at 5-m intervals with a 5-L Van Dorn water sampler. Subsamples of 128 mL were taken at each depth and pre-filtered through 200-μm mesh onto a GF/F filter (average pore size 0.7 μm). After filtration, each filter was immediately covered by a quantitative filter and aluminium foil to protect it from light. Chl *a* was extracted from each filter by immersion in 90% acetone for 24 h in the dark at –20°C , and fluorescence was determined with a Turner Designs fluorometer by the method demonstrated by Yentsch and Menzel (1963).

Diel and tidal vertical distribution of planktonic polychaete larvae were examined by sampling at 0-, 5-, 10-, 15- and 20-m depths at 3-h intervals over a 21-h period. Zooplankton samples were collected at 8:00, 11:00, 14:00, 17:00, 20:00 and 23:00 on 20 August 2012 (spring tide) and 2:00 and 5:00 on 21 August 2012 (half tide) and treated in the same manner as has been described above. Vertical profiles of temperature, salinity and Chl fluorescence values were determined using a CTD RINKO-Profiler.

In order to analyse the relationships between larval and Chl vertical distribution, a weighted mean depth (WMD) for each vertical profile was calculated using the following equation (Rollwagen-Bollens et al., 2006):

$$\mathrm{WMD} = \frac{\Sigma(A_i \cdot Z_i)}{\Sigma(A_i)} ,$$

where i is each depth sampled, A is the density of polychaete larvae (individuals m^{-3}) or chlorophyll a concentration (μg L^{-1}), and Z is the sampling depth (m). Pearson's product–moment correlation coefficient (r) and associated significant probability (P) were calculated to examine the relationship between larval and Chl vertical distribution.

The significance of differences in larval vertical distribution of the dominant *Pseudopolydora achaeta* and *Prionospio* spp. in daytime vs. night-time and flood and ebb vs. high and low tide during the 21-h investigation were tested using the statistical test for differences in vertical plankton distributions in the presence of patchiness when replicate samples were available (Beet et al., 2003). Samples taken at different times were pooled into two sets of observations, daytime and night-time, and flood/ebb and high/low tide, and considered as replicates. Plankton profiles collected at 5:00 on 21 August were treated as night-time profiles because it was just after daybreak. The null hypothesis, that the shapes of the depth profiles of mean abundance are the same under all conditions (i.e. daytime, night-time, flood/ebb tide, and high/low tide) was tested using the following test statistic (Paul and Banerjee, 1998):

$$\mathrm{B} = \mathrm{n} \textstyle\sum_{i=1}^{T} \sum_{j=1}^{D} \dfrac{(\bar{Y}_{ij} - \hat{\mu}_{ij})^2}{\hat{\mu}_{ij}(1 + \hat{c}\hat{\mu}_{ij})} ,$$

where T and D are the number of conditions and depths, respectively, $\bar{Y}_{ij}$ is the average density of n replicates for condition

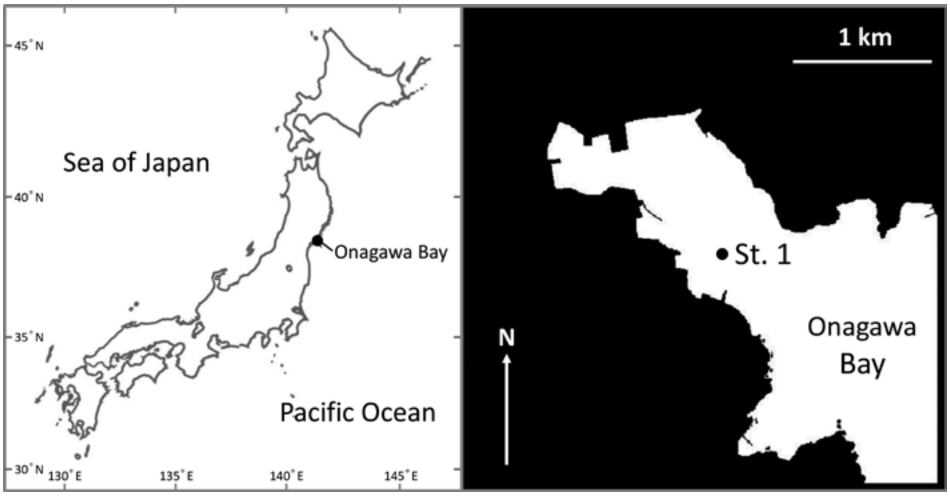

Figure 1. Location of the sampling station in Onagawa Bay.

i at depth *j*, and $\hat{\mu}_{ij}$ and $\hat{c}$ are the maximum likelihood (ML) estimates of the mean (μ_{ij}) and dispersion coefficient (c_{ij}) under the null hypothesis, respectively. The ML estimates, test statistic B, and its corresponding *P*-values under the null hypothesis were obtained using MATLAB software (MathWorks Japan, Tokyo, Japan), as described by Beet et al. (2003).

Results

Seasonal vertical distribution of planktonic polychaete larvae

Water temperature ranged from 4.4 to 25.9°C, with lowest temperatures at the 20-m depth in March and highest at 0-m depth in September. Thermal stratification in the water column began in April and lasted until September. The differences in temperature between the top and bottom waters were 2–5°C in these months. In other seasons, the water column was vertically well mixed. Salinity ranged from 28.4 to 34.7 but was generally stable at approximately 33–34. An episodic decrease in surface salinity in April was a consequence of heavy rainfall. Except for the 0-m depth, salinity was almost the same in all layers of the water column.

Chl *a* concentration varied from 0.18 to 11.71 μg L^{-1}, with marked seasonal and vertical variations (fig. 2). The lowest value was recorded at 20-m depth in June and the highest at 10-m depth in April. Typical of the annual pattern in temperate waters, there was a large spring phytoplankton bloom throughout the water column in February and another in April (fig. 2). High Chl *a* concentrations were also observed in the bottom water in January, July and August, and at 0 m in September. The Chl *a* concentration was very low in March, June, November and December.

The density of planktonic polychaete larvae fluctuated from 0 to 6240 individuals (ind.) m^{-3} and varied greatly according to season and depth (fig. 2). The lowest density was recorded at 0-m depth in February and March, and the highest density was recorded at 5-m depth in May. Larvae belonging to 14 families were identified. Spionidae was the most dominant family for most months (68.2%), followed by Phyllodocidae (11.6%) and Polynoidae (5.7%). In general, polychaete larvae were very sparse at the surface (0-m depth) and were distributed in the lower layers of the water column (fig. 2). This trend in vertical distribution was primarily observed in dominant spionid larvae, as well as in the larvae of Phyllodocidae and Terebellidae. In contrast, Serpulidae larvae tended to be located in the upper layers of the water column. There was slight correlation between weighted mean depth of planktonic polychaete larvae and Chl concentration during the study period from January to December 2012, but this correlation was not significant ($r = 0.44$, $P = 0.149$; $n = 12$).

The density of planktonic spionid larvae fluctuated from 0 to 5680 ind. m^{-3}, and also differed greatly depending on season and depth (fig. 3). The lowest densities were recorded at 0-m depth in February, March and December, and the highest density was recorded at 5-m depth in May. Larvae belonging to 14 species/genera were identified. *Pseudopolydora achaeta* was the dominant species (36.7%), followed by *Polydora onagawaensis* (30.6%) and *Prionospio* spp. (10.7%). During the period from January to June, larvae of the spionid *P. onagawaensis* were dominant. They did not show specific trends with regard to vertical distribution and tended to be distributed at a wide range of depths. During summer, larvae of *Pseudopolydora achaeta* and *Prionospio* spp. were the dominant species/genus and tended to be distributed in the lower layers of the water column.

Diel and tidal vertical distribution of planktonic polychaete larvae

Water temperature ranged from 18.0 to 23.5°C, with the lowest temperature near the bottom and the highest at the surface. There was thermal stratification, and a stable thermocline was observed between 0- and 5-m depths for the entire period. Salinity ranged from 32.3 to 33.9 and was stable around 33.0 to 34.0, except in the surface water at 11:00 on 21 August. Except for the 0-m depth, salinity was almost the same in all layers of the water column. Chlorophyll fluorescence values

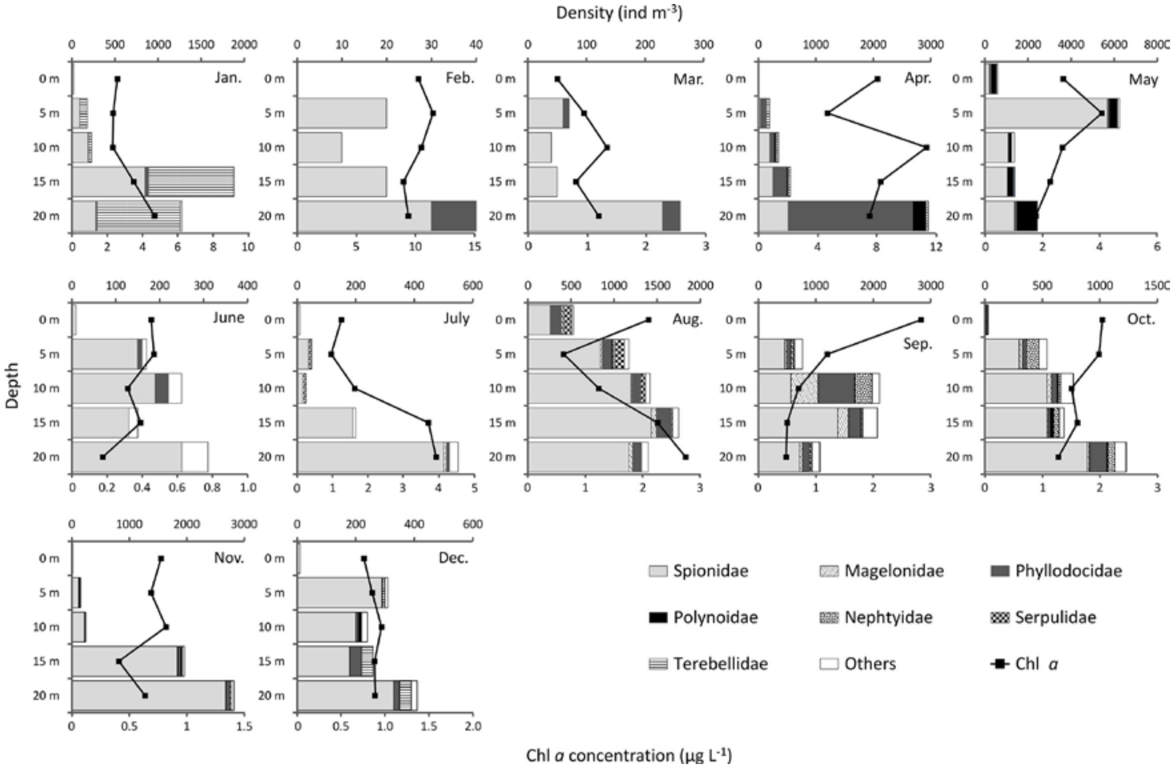

Figure 2. Vertical distribution of each family of planktonic polychaete larvae (upper axes) and chlorophyll *a* concentration (μg L^{-1}) (lower axes) at St. 1 in Onagawa Bay from January to December 2012.

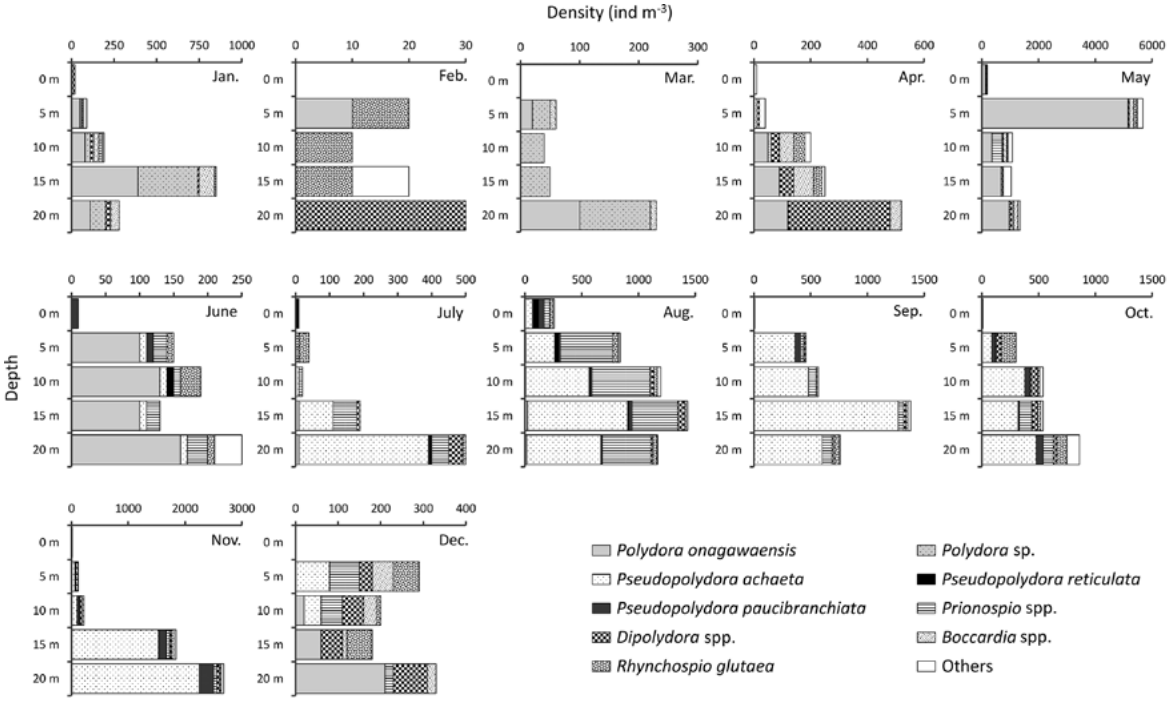

Figure 3. Vertical distribution of each species or genus of planktonic spionid larvae at St. 1 in Onagawa Bay from January to December 2012.

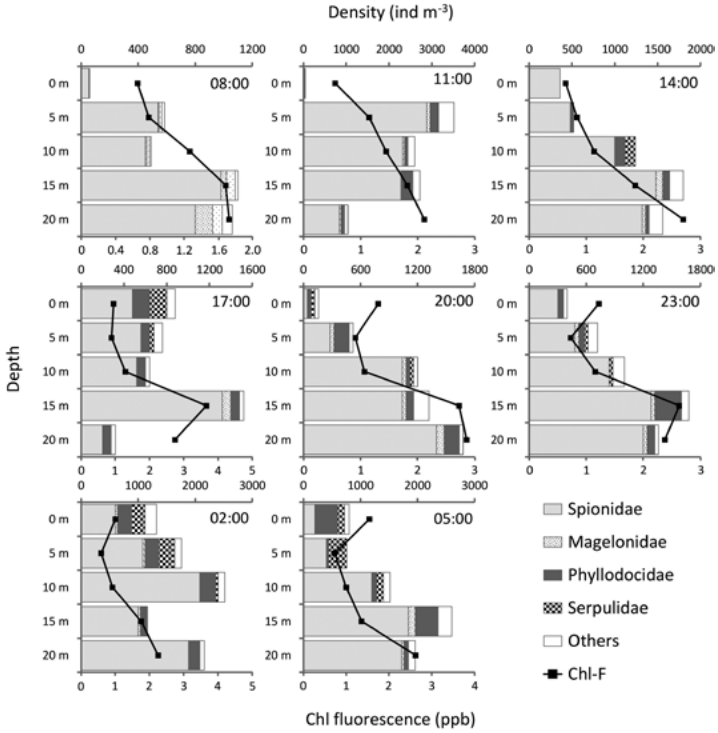

Figure 4. Diel changes in vertical distribution of planktonic polychaete (upper axes) and chlorophyll fluorescence (ppb) (lower axes) larvae at St. 1 in Onagawa Bay from 8:00 a.m. on 20 August to 5:00 a.m. on 21 August, 2012.

ranged from 0.6 to 3.7 ppb, with the lowest value at 0-m depth at 11:00 and the highest at 15-m depth at 17:00 (fig. 4). The maximum chlorophyll levels were found deeper in the water column all throughout the day.

The density of planktonic polychaete larvae fluctuated from 40 to 3520 ind. m^{-3} and varied greatly according to depth (fig. 4). The lowest density was recorded at the 0-m depth at 11:00, and the highest density was recorded at the 5-m depth at 11:00. Larvae belonging to 11 families were identified on 20 and 21 August. Spionidae was the dominant family at all times (78.9%), followed by Phyllodocidae (9.3%) and Serpulidae (3.6%). The larvae of Spionidae and Magelonidae were almost absent at the surface (0-m depth) and tended to be distributed in the lower layers of the water column. In contrast, the larvae of Serpulidae tended to be distributed in the upper layers of the water column.

Planktonic spionid larval densities ranged from 30 to 2880 ind. m^{-3} (fig. 5). The lowest density was at 0-m depth at 11:00 and the highest density at 5-m depth at 11:00. Larvae belonging to 11 species/genera were identified. *Pseudopolydora achaeta* and *Prionospio* spp. were the dominant species/genera (49.9% and 38.3%, respectively). In general, spionid larvae were sparse at the surface (0 m) and tended to be distributed in the lower layers of the water column. However, the highest density was recorded at the 5-m depth at 11:00 because of the extremely high density of *Prionospio* spp. (2040 ind. m^{-3}). The larvae of *Pseudopolydora achaeta* and *Prionospio* spp. tended to distribute slightly shallower during high and low tide and deeper during flood and ebb tide, especially in daylight hours (fig. 6). However, there were no statistically significant differences in the vertical distribution of *Pseudopolydora achaeta* and *Prionospio* spp. during the day vs. night (B = 1.39, $P > 0.05$ and B = 8.23, $P > 0.05$, respectively), or flood/ebb vs. high/low tide (B = 1.38, $P > 0.05$ and B = 3.20, $P > 0.05$).

Discussion

Vertical distribution of planktonic polychaete larvae

Polychaete larvae in Onagawa Bay generally tend to be distributed at higher densities in the lower layers of the water column and sparser densities at the surface (figs 2 and 4). In Onagawa Bay, the close timing between the phytoplankton blooms and the occurrence of planktonic polychaete larvae had been observed previously, and most planktonic polychaete larvae have tended to synchronise with summer phytoplankton increases and fall blooms (Abe et al., 2011). Because the phytoplankton increase near the surface during summer and autumn in Onagawa Bay, it was previously assumed that a photopositive response brought larvae up towards the phytoplankton-rich surface waters, as indicated by Thorson (1946; 1964) during summer and autumn in Onagawa Bay (Abe et al., 2011). However, the results of this study contradicted this assumption, because they indicated that polychaete larvae tended to be distributed in the lower layers rather than the

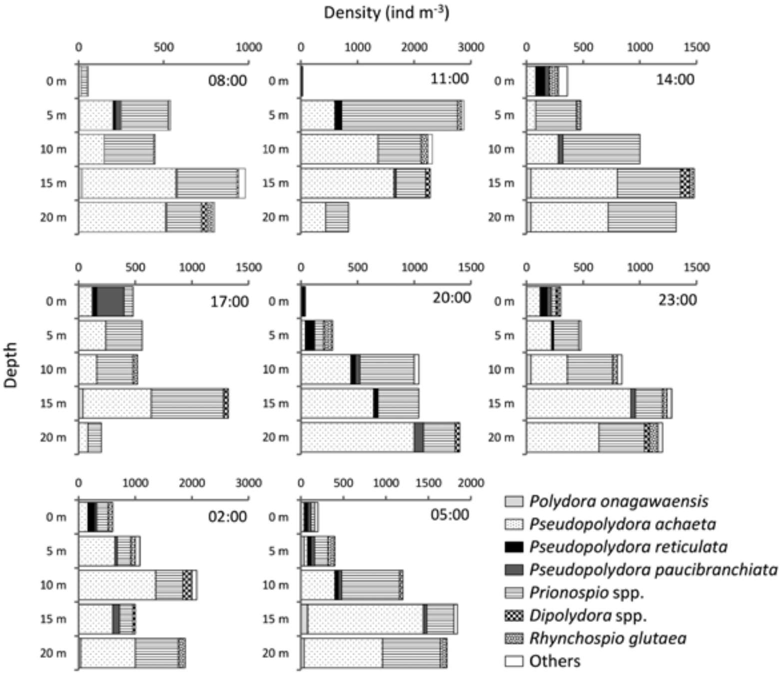

Figure 5. Diel changes in vertical distribution of planktonic spionid larvae at St. 1 in Onagawa Bay from 8:00 a.m. on 20 August to 5:00 a.m. on 21 August 2012.

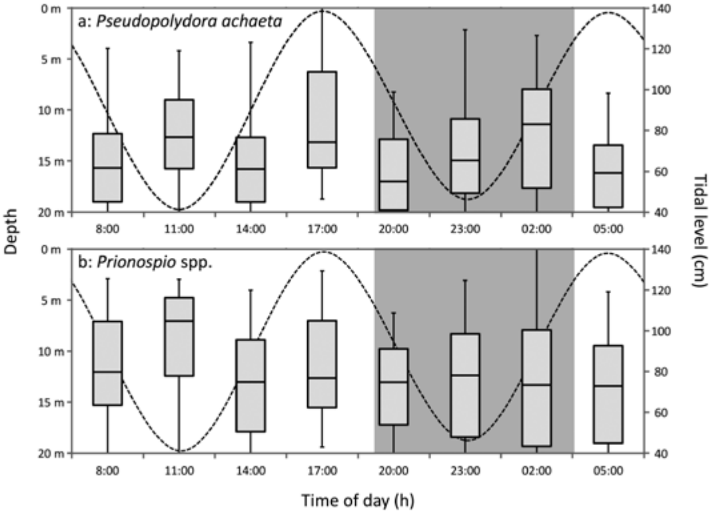

Figure 6. Box plots of vertical distribution of two spionid larvae: a, *Pseudopolydora achaeta* and b, *Prionospio* spp. The central line in the box represents the median, the upper and lower boundaries of the box represent the quartiles, and the vertical bar represents the 95% range of larval distribution (left axes). The dashed wavy lines and dark shaded areas represent the tidal level (right axes) and night-time, respectively.

surface layers, even in summer and autumn. The previously documented positive phototactic response of spionid larvae (Blake and Woodwick, 1975; Levin, 1986) was easily observed in this study, as the live larvae clearly moved towards the light source during microscope observation. However, this photopositive behaviour did not result in vertical migration in the field, as we found spionid larvae distributed primarily in the lower layers. The majority of young larvae of the benthic invertebrates were reported to be positively phototactic under laboratory illumination (Thorson, 1946) but have been observed to avoid very strong light and often to be absent from the surface layers of the sea (Russell, 1927; Thorson, 1964). The results of our study appear to be consistent with these reports. However, the results of our 21-h survey showed that the vertical distribution of spionid larvae did not vary between daytime and night-time (figs 4–6); therefore, strong light intensity cannot be the explanation for the scarcity of spionid larvae at the surface. In other studies, polychaete larvae have been found in higher densities at the bottom of the water column (Wilson, 1982; Ambrogi et al., 1989; Yokoyama, 1995; Schlüter and Rachor, 2001). Distribution of polychaete larvae in the bottom layers of the water column may be a common phenomenon in many marine waters.

In contrast to most of the polychaete larvae that were present in the lower layers of the water column, only Serpulidae larvae, one of the predominant intertidal animals in Onagawa Bay, tended to be distributed in the upper layers of the water column (figs 2 and 4). Thorson (1964) generalised that the larvae of intertidal species are photopositive throughout their planktonic larval period and larvae of most subtidal species are initially photopositive but become photonegative before settlement. Although it is unknown if the difference in larval vertical distribution between intertidal and subtidal polychaetes is due to a difference in their phototactic response, the difference in larval vertical distribution may be reflected in their adult habitats.

The vertical distribution trend of spionid larvae differed from species to species in this study. The larvae of *Pseudopolydora achaeta* and *Prionospio* spp. tended to be distributed in the lower layers of the water column (figs 3 and 5), whereas *P. onagawaensis* larvae showed no specific trends in vertical distribution and were distributed at a wide range of depths (fig. 3). *Polydora onagawaensis*, a recently described species from Onagawa Bay (Teramoto et al., 2013), is a shell-boring polychaete, and adults inhabit the shells of molluscs distributed in the intertidal zone as well as those suspended in deeper water for aquaculture in Onagawa Bay. It is possible that the larval distribution of *P. onagawaensis* is determined by the habitat in which the larvae were produced and hatched, and their wide range of vertical distribution has a role in larval recruitment to the vertically wide range of adult populations. The larvae of *Pseudopolydora reticulata* and *Rhynchospio glutaea* tended to be distributed in the surface and middle layers of the water column, respectively (figs 3 and 5). Adults of *Pseudopolydora reticulata* and *R. glutaea* are commonly distributed in the soft bottom sediments of intertidal and shallow subtidal zones (Radashevsky and Hsieh, 2000; Zhou et al., 2010). Shallower distribution of these larvae was also consistent with the area in which they were produced and probably assists with larval recruitment to adult populations. Larval vertical distribution may be influenced by the water layer in which hatching occurred (Pearse, 1994).

Some invertebrate larvae have been observed to alter their swimming behaviour in response to the presence and quality of food patches (Raby et al., 1994; Metaxas and Young, 1998b; Burdett-Coutts and Metaxas, 2004). In this study, although there was no significant correlation, a similar trend in vertical distribution between polychaete larvae and Chl *a* concentration was observed in several months (fig. 2). It is considered that various factors influence larval vertical distribution, so it would be difficult to detect a clear correlation between larval and Chl vertical distribution. However, the observed trend may indicate that the vertical distribution of Chl regulates the vertical distribution of polychaete larvae to some extent in Onagawa Bay.

Diel and tidal vertical migration of planktonic polychaete larvae

The phenomenon of DVM widely occurs in many marine zooplankton taxa (Rawlinson et al., 2004), including polychaete larvae (Garland et al., 2002). However, no difference was observed in the vertical distribution of polychaete larvae between the light and dark hours over the 21-h sampling period in Onagawa Bay (figs 4–6). Polychaete larvae did not show DVM in this study indicates that the light condition was not very important for larval vertical distribution of polychaete larvae. This was consistent with the results of seasonal vertical distribution of spionid larvae in this study.

It is well known that some invertebrate larvae show a tidal vertical migration pattern (Cronin, 1982). In this study, although there was no significant relationship between larval vertical distribution and tidal cycle, the larvae of *Pseudopolydora achaeta* and *Prionospio* spp. tended to be distributed at slightly shallower depths during high and low tide and at greater depths during flood and ebb tide, especially in daylight hours (fig. 6). In general, tidal currents are faster at the surface layers and slower at the bottom layers. Therefore, these larval tidal migrations were considered to avoid dispersal by moving to slower-flowing deeper water during flood and ebb tide. Tidal vertical migration has also been reported in the larvae of the colony-forming polychaete *Sabellaria alveolata*; the larvae of *S. alveolata* tended to migrate closer to the surface during flood tide and nearer to the bottom during ebb tide, promoting a net landward transport of larvae (Dubois et al., 2007). Although the swimming capacity of polychaete larvae is often limited, and vertical migration was small, this vertical migration may be important as a retention mechanism for polychaete larvae.

Some larvae are reported to vary their DVM behaviour throughout ontogeny (Neill, 1992). Although ontogenic migration is not a general feature in polychaete larvae, ontogenic larval migration has been reported in two polychaete species, *Pectinaria koreni* and *Owenia fusiformis* (Lagadeuc et al., 1990; Thiebaut et al., 1992), and these ontogenic migrations are believed to be important for larval retention in the estuarine and coastal environments. Larval vertical migration is well known for decapod larvae, bivalve larvae and gastropod larvae (Cronin, 1982; Forward et al., 1984; Forward and Tankersley, 2001; Gibson, 2003; Rawlinson et al., 2004; Lloyd et al., 2012). Meanwhile, many studies assume a passive dispersal of polychaete larvae within the water column (Banse, 1986; Stancyk and Feller, 1986; Levin, 1986; Kingsford et al., 2002). There is very little information on the vertical distribution and vertical migration of polychaete larvae throughout the world, and this study indicates the need for additional knowledge about the vertical migration of polychaete larvae.

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