Seasonal changes in the density and vertical distribution of nauplii, copepodites and adults of the genera *Oithona* and *Oncaea* (Copepoda) in the surface water of Toyama Bay, southern Sea of Japan

TAKASHI TAKAHASHI^{1*} & ISAMU UCHIYAMA²

¹ Jouetsu Environmental Science Center, 1666 Shimomonzen, Jouetsu Niigata 942–0063, Japan

² Toyama Prefectural Fisheries Research Institute, 364 Nakatsuka, Namerikawa, Toyama 936–8536, Japan

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Abstract: In this study, we examined seasonal changes in the vertical population density of each developmental stage (nauplius and copepodite) of *Oithona* and *Oncaea* species in the surface water of Toyama Bay from 1997 to 1999. Furthermore, we investigated the detailed vertical distribution (0 m, 25 m and 50 m depth) of the naupliar stages, which are regarded as an important food source for fish larvae. Major changes in the community structure of nauplii, which occurred at different sampling depths and in different seasons, are considered to have been influenced by the occurrence of adults and changes in the hydrographic conditions, including temperature and water currents. In winter to early summer (January to June) nauplii of *Oithona similis* and *Oithona atlantica*, copepodites and adults, were abundant, while those of *Oithona plumifera*, and other species of *Oithona* and *Oncaea* showed a higher density between August and December.

During the spring season, when many fish larvae appeared, *O. similis* nauplii occurred at higher densities of more than 10^5 indiv. m⁻³ in the upper layer (0 m and 25 m depth) than those of *O. atlantica*. The weighted mean depth of *O. atlantica* nauplii was significantly deeper than that of *O. similis* nauplii. The respective vertical distributions of the nauplii of *O. atlantica* and *O. similis* were similar to the distributions of adults. *Oithona similis* nauplii are suggested to be a potentially important food item for fish larvae in spring because of their high density and similar vertical distribution to many fish larvae.

Key words: *Oithona*, *Oncaea*, seasonal abundance, Toyama Bay, vertical distribution

Introduction

The abundance of copepod nauplii encountered by early stage larvae of marine fish can significantly affect fish survival and development (Ikewaki & Sawada 1991). Higher rates of larval development have been related to encountering high density patches of copepod nauplii (Oozeki & Zenitani 1996). Various studies have concluded that increased rates of development in fish larvae lead to lower mortality from predation due to more rapid development of the sensory organs (e.g. Shepherd & Cushing 1980). Because the overall density of copepod nauplii is low in the open ocean, the probability of the survival of fish larvae has been suggested to be associated with the distribution of high-density naupliar patches (Laurence 1974, O'Connell

& Raymond 1970, Sawada 1996).

Investigations of copepod nauplii, however, often fail to grasp the factors that influence their availability to fish larvae. The species composition of high densities of nauplii is clearly one of those factors. But, so far, the species of nauplii have not been determined, and, in most cases, high-density naupliar patches are only identified at the family or order level. The ecology of different species of nauplii within the same family varies greatly and requires detailed investigation. The species-level population and community structures of copepod nauplii within patches also require investigation. The relationship between the ecology of the species forming high-density naupliar patches and the factors affecting such patch occurrences also need to be examined.

Fish larvae, e.g. the Japanese sardine *Sardinops melanostictus* (Temminck & Schlegel) and the anchovy *Engraulis*

* Corresponding author: Takashi Takahashi; E-mail, takutaku@jo-kan.or.jp

japonicus Temminck & Schlegel are abundant in Toyama Bay, southern Sea of Japan, from May to July (Ito 1961, Hayashi 1990, Goto 1998). During the larval stage, sardines and anchovies prey mainly on *Oithona* and *Oncaea* nauplii (Hirakawa & Goto 1996, Hirakawa et al. 1997). In Toyama Bay, sardines and anchovies are usually found at depths less than 25 m (Hayashi 1990). If the distribution depth of nauplii is species specific, we must clarify which species of nauplii are dominant at the depths where many of the fish larvae of commercial species are distributed.

Hirakawa et al. (2004) concluded that nauplii of *Oithona similis* Claus were the most dominant in their study based on the fact that adults of the species were abundant concurrently and the size of each naupliar stage matched that of this species. However, they did not identify the nauplii at the species level on the basis of morphological characteristics. Takahashi & Uchiyama (2007) have recently described a method for identifying *Oithona* nauplii in Toyama Bay. They showed that *O. similis* is a major contributor to the high population density of *Oithona* nauplii. However, Takahashi & Uchiyama (2007) did not investigate the vertical distributions of nauplii of other species. In this paper we examine the vertical distributions of nauplii, and copepodite species of *Oithona*, *Oncaea* and others. We also discuss the factors that influence the characteristic vertical distributions of nauplii, and their availability as food for fish larvae.

Materials and Methods

Six naupliar (N1–6) and six copepodite (C1–6) stages of *Oithona* and *Oncaea* were collected in the central region of Toyama Bay (Stn. 8) from January 1997 to December 1999 (Fig. 1). Samples were taken once or twice per month. Water samples were taken with van Dorn bottles (10 L) at depths of 0 m, 25 m and 50 m, filtered through a 0.02 mm mesh net and fixed in 3–5% formaldehyde. High densities of copepod nauplii were found at depths of less than 50 m (Sawada 1996, Hirakawa et al. 2004).

All *Oithona* copepodite stages were identified at the species level and counted for each entire sample (not split). *Oithona* and *Oncaea* adults (C6) and copepodites (inferred from the morphological characteristics of the adult stage) were identified to the species level according to keys to species provided by Ito (1997) and Nishida (1997). The cold-water and warm-water species were separated by their geographic distribution. The nauplius stages were identified and counted under a microscope in 1/15 to 1/20 aliquots of each sample. Nauplii for each genus were counted and identified using a key developed by Koga (1984). Nauplii of *Oithona similis*, *Oithona atlantica* Farran, *Oithona plumifera* Baird, and the other *Oithona* spp. and *Oncaea* spp. were differentiated according to the method of Takahashi & Uchiyama (2007). Small nauplii, with an N1-stage body length of <0.1 mm (*Oithona nana* Giesbrecht, *Oithona davisae* Ferrari & Orsi or *Oithona rigida* Gies-

Fig. 1. Map showing the sampling site (●) for this study in Toyama Bay, Sea of Japan.

brecht) were grouped together as congeners. It was very difficult to distinguish between nauplii of the genus *Oncaea* at species level, so those nauplii with a pair of long second segment antennules (Koga 1984) were identified as *Oncaea* nauplii.

The weighted mean depth (*WMD*) of nauplii was calculated according to the method outlined by Frost & Bollens (1992); that is, $WMD = (\sum n_s d_s) / \sum n_s$, where d_s is the sampling depth and n_s is the density (indiv. m⁻³) of the species *s*. Differences in mean *WMD* were compared using the Wilcoxon signed ranks test.

From January 1997 to October 1998, vertical profiles of temperature and salinity at Stn. 8 in Toyama Bay were measured during sampling using a CTD (MK3B, Neil Brown, SBE911, Seabird Co., Ltd.), and surface water salinity was measured with a salinometer (601MKIII, Yeo-kal, Autosal, Guildline Co., Ltd.). Over this period, chlorophyll-*a* in water samples from depths of 0 m, 25 m and 50 m was measured using the fluorescence method (Parsons et al. 1984). To observe large changes in the submarine climate, we investigated environmental factors between 0 m and 300 m. From November 1998 to December 1999, vertical profiles of temperature, salinity and fluorescence were measured simultaneously with a CTD (ACL200DK, Alec Co., Ltd.).

Results

Hydrography

From March to April during the three years of investigation, the lowest water temperature in the upper 50 m was 10°C (Fig. 2, upper panel). Each year, vertical mixing occurred in the upper 150 m from February to May and the

Fig. 2. Seasonal variations in temperature (upper), salinity (middle) and chlorophyll-*a* concentration (lower) at Stn. 8 in Toyama Bay (adapted from Takahashi & Uchiyama 2007).

concentration of chlorophyll-*a* increased to more than $1.0\text{--}4.0\ \mu\text{g L}^{-1}$ from February to May (Fig. 2, lower panel).

After May, water temperatures increased gradually. Surface water salinities were observed to be less than 33 PSU in May, June and August–October in 1997 and 1998 (Fig. 2, middle panel), which indicates the possible intrusion of river water between May and July (Nagata & Nakura 1993) or surface water of the Tsushima Warm Current (TWC) in August (Ogawa 1983). At this time, the chlorophyll-*a* concentration decreased rapidly to below $0.5\ \mu\text{g L}^{-1}$. However, in 1997, a higher concentration of chlorophyll-*a* ($>1.0\ \mu\text{g L}^{-1}$) was observed at the surface (0 m) after May, with the highest value ($5.1\ \mu\text{g L}^{-1}$) recorded in mid-July. During this season (mid-July) in 1997, water of low salinity (less than 33 PSU) was observed at the surface (0–5 m), which indicates the possible intrusion of river water from mid-June to July.

The water column became thermally stratified during summer. In August, the highest surface water temperature recorded was 28°C , and the water temperatures decreased gradually after September. Salinities that were consistently

Fig. 3. Seasonal variations in the total density of copepod nauplii (upper) and the genus composition (lower) at depths of 0, 25 and 50 m in Toyama Bay from January 1997 to December 1999.

greater than 34.2 PSU were observed at a depth of 10–100 m every year from June–August to December–January, which indicates the possible intrusion of core water from the TWC.

Seasonal changes in abundance and composition of nauplii of various genera

At 0 m the total copepod naupliar abundance increased from April to June each year, and the highest total abundance ($230 \times 10^3\ \text{indiv. m}^{-3}$) was recorded in June 1997 (Fig. 3 upper panel). Total naupliar abundance increased slightly from April to May in 1998 and 1999 but was lower than the 1997 value, with a maximum density of $80\text{--}100 \times 10^3\ \text{indiv. m}^{-3}$. It decreased to $20\text{--}30 \times 10^3\ \text{indiv. m}^{-3}$ after August in each year. *Oithona* nauplii were the most important component throughout the three years, and 55% of the highest total abundance in June 1997 consisted of nauplii of this genus (Fig. 3 lower panel). In May and September to October of almost every year, *Paracalanus* and *Clausocalanus* were also major naupliar components.

At a depth of 25 m the total copepod naupliar abundance increased in May and July 1997, with $190 \times 10^3\ \text{indiv. m}^{-3}$ in May and $198 \times 10^3\ \text{indiv. m}^{-3}$ in July (Fig. 3 upper panel). *Oithona* nauplii constituted 84% of the total in May (Fig. 3

lower panel). The total naupliar abundance did not increase during spring in 1998 and 1999. Between July and November in each year, *Oncaea* was a major naupliar component (13–77%). In June and July of almost every year, *Microsetella* was a major naupliar component (37–89%).

At a depth of 50 m the total copepod naupliar abundance increased from April to July 1997 (Fig. 3 upper panel). The second highest total density of nauplii ($75 \times 10^3 \text{ indiv. m}^{-3}$) occurred in April and the highest ($81 \times 10^3 \text{ indiv. m}^{-3}$) in July 1997. However, these higher densities were less than those recorded at 0 m and 25 m. *Oithona* nauplii constituted 42% of the highest density and 78% of the second highest (Fig. 3 lower panel). *Oncaea* and *Microsetella* were major naupliar components in the same months as at 25 m depth.

The highest total naupliar densities at 0 m and 25 m were greater than at 50 m, with the greatest density of *Oithona* nauplii ($160 \times 10^3 \text{ indiv. m}^{-3}$) being observed at 25 m in 1997. However, in 1998 and 1999 the greatest density ($24\text{--}60 \times 10^3 \text{ indiv. m}^{-3}$) decreased. *Oithona* and *Oncaea* nauplii, which were examined in detail in this study, were the most important component, constituting more than 50% of the mean total naupliar density per sample throughout the three consecutive years (50% at 0 m, 57% at 25 m and 55% at 50 m; Fig. 3, lower panel).

Seasonal changes in abundance and composition of naupliar and copepodite stages of each species

The maximum density of nauplii was almost ten times the density of copepodites and adults for each species over the three years.

Oithona similis. The nauplii occurred almost continuously throughout the year, except in August and September (Fig. 4). The nauplii had higher density peaks at 0 m and 25 m than at 50 m in April and June, with the greatest value (over $10^5 \text{ indiv. m}^{-3}$) in June 1997. At 0 m and 25 m depth, *Oithona similis* nauplii were the main naupliar component during the whole survey period, comprising >50% (0 m) and ca. 33% (25 m) of the total density of *Oithona* and *Oncaea* nauplii (Fig. 5). In 1997, at 0 m, 93% of the greatest naupliar abundance was made up of *O. similis* nauplii. Copepodite and adult densities of this species were greater at 0 m and 25 m than at 50 m as was also the case for nauplii (Fig. 4). Increases in the density of *O. similis* copepodites and adults occurred in the same seasons as those of nauplii. The greatest densities of *O. similis* copepodites and adults ($13\text{--}16 \times 10^3 \text{ indiv. m}^{-3}$) were observed in 1998, although for nauplii it was in 1997.

Oithona atlantica. The nauplii had higher density peaks at 25 m and 50 m than at 0 m (Fig. 4), with the highest density ($10\text{--}60 \times 10^3 \text{ indiv. m}^{-3}$) from February to May. After

Fig. 4. Seasonal variations in the densities of nauplii, copepodites and adults of five taxa at depths of 0, 25 and 50 m in Toyama Bay from January 1997 to December 1999.

June, however, the density decreased in all three years. Between December and July, *O. atlantica* nauplii were the main naupliar component at 25 m and 50 m (Fig. 5). At 25 m, *O. atlantica* nauplii were the second most abundant taxonomic component, constituting 30%, and were the most dominant at 50 m, constituting approximately 34% of the total density of *Oithona* and *Oncaea* nauplii over the three consecutive years. *O. atlantica* copepodites and adults were found in the same season and at the same depth as nauplii (Fig. 4). The greatest density of *O. atlantica* copepodites and adults (6×10^3 indiv. m^{-3}) was observed at 25 m in 1999, whereas the greatest density of nauplii was observed in 1997.

Oithona plumifera. The naupliar abundance was greatest at a depth of 25 m (Fig. 4), increasing from June to reach a maximum ($10\text{--}25 \times 10^3$ indiv. m^{-3}) between September and October each year. The nauplii of this species were not observed from January to May, when *O. atlantica* nauplii were abundant. The nauplii of these two species appeared simultaneously between June and August, and in December. At depths of 25 m and 50 m, from August to November, *O. plumifera* were the main component of total *Oithona* and *Oncaea* nauplii (Fig. 5). *O. plumifera* copepodites and adults occurred in the same season as the nauplii (Fig. 4), but their greatest densities were lower than those of other *Oithona* species.

Other *Oithona* spp. Naupliar abundance was greatest at 0 m (Fig. 4). In 1997, the naupliar abundance rapidly increased from early July to reach a maximum (80×10^3 indiv. m^{-3}) in the middle of July. This maximum naupliar density was mainly comprised of *Oithona nana*. Maximum densities in 1998 and 1999 were lower than in 1997, although the seasonal occurrences were the same. At 0 m, nauplii of other *Oithona* species were most dominant between August and September in each year (Fig. 5). At 25 m and 50 m, other *Oithona* species were sometimes the main component from August to November. In this study, the other *Oithona* copepodites and adults identified were from three species: *Oithona davisae*, *O. nana*, and *O. rigida*. The copepodites and adults of these other *Oithona* species occurred in the same seasons as the nauplii (Fig. 4).

Oncaea spp. The naupliar densities of *Oncaea* spp. increased from June to August–November, when the maximum density ($10\text{--}25 \times 10^3$ indiv. m^{-3}) was recorded, and then decreased after December (Fig. 4). *Oncaea* spp. were the main component from August to November at each depth (Fig. 5). Nauplii of *Oncaea* spp. were the second most important taxon, constituting 20% at 0 m and 21% at 25 m of the total *Oithona* and *Oncaea* nauplii. In this study, the *Oncaea* copepodites and adults were comprised of three species: *Oncaea media* Giesbrecht, *Oncaea venusta* Philippi and *Oncaea mediterranea* (Claus). *Oncaea* copepodites and adults occurred throughout the year, with the greatest density ($3\text{--}4 \times 10^3$ indiv. m^{-3}) observed in the same season as the nauplii (Fig. 4).

Fig. 5. Seasonal variations in the composition of nauplii of five taxa at depths of 0, 25 and 50 m in Toyama Bay from January 1997 to December 1999.

Vertical distribution of *Oithona* and *Oncaea* nauplii

From February to July, the WMD of *O. atlantica* nauplii was below 25 m (25.2–42.5 m, average 30.4 m), while that of *O. similis* nauplii was above 25 m (6.5–24.0 m, average 16.7 m) (Fig. 6). The WMDs of *O. atlantica* and *O. similis* nauplii were significantly different (Wilcoxon signed ranks test: $p < 0.01$). The WMDs of the warm-water *O. plumifera* and *Oncaea* nauplii were concentrated at about 25 m (*O. plumifera*: 23.9–31.8 m, average 28.9 m, *Oncaea*: 16.5–29.4 m, average 23.6 m). The WMDs of the nauplii of these two taxa were not significantly different (Wilcoxon signed ranks test: $p > 0.05$).

Discussion

Seasonal changes in abundance

In Toyama Bay, we found that *Oithona* and *Oncaea* nauplii were a significant proportion of the total copepod nauplii. *Oithona* and *Oncaea* species have a worldwide distrib-

Fig. 6. Seasonal changes in the weighted mean depths (WMDs) of the nauplii of four taxa (*Oithona atlantica*, *O. similis*, *O. plumifera* and *Oncaea* spp.) in Toyama Bay from January 1997 to December 1999. Vertical lines represent ± 1 SD.

Fig. 7. Schematic diagram showing seasonal occurrence (averaged over three years) of the nauplii of three *Oithona* species and *Oncaea* nauplii in the layers where they were the main naupliar component (in the direction of the arrows) in Toyama Bay. Horizontal broken lines show average WMDs for each species. Top bars show the water mass characteristics.

ution (Paffenhöfer 1993), and the genus *Oithona* has already received much attention (Gallienne & Robins 2001, Castellani et al. 2005a). In this study, *Oithona* and *Oncaea* nauplii occurred over the three years, constituting more than 50% of the average total copepod naupliar density.

Figure 7 shows the seasonal occurrence (averaged over three years) of the three nauplii of the *Oithona* species and of *Oncaea* nauplii in the layers with high naupliar densities (in the first and second highest density layers, with an average naupliar density of $>1 \times 10^3$ indiv. m^{-3}). *Oithona similis* and *Oithona atlantica* nauplii were abundant between January and July, during which time the vertically mixed water column gradually became vertically stratified. There is a clear segregation in the vertical distribution of these two cold-water naupliar species in Toyama Bay: *O. similis* and

O. atlantica occurred in the region of 0–25 m and 25–50 m, respectively. *Oithona plumifera* and *Oncaea* nauplii were abundant between August and December when an intrusion of the TWC and high water temperatures occurred (Naganuma 2000). Hirakawa (1995) noted the influence of temperature on reproduction in *Oncaea venusta*, which reproduces actively at high temperatures (>20 – 25°C), but not at low temperatures ($<15^\circ\text{C}$). Increasing temperatures cause nauplii of warm-water species to appear in abundance.

Hirakawa et al. (2004) suggested that low salinity surface waters in the Sea of Japan in May and June were due to the in-flow of river water, which led to high chlorophyll-*a* concentrations and high densities of *O. similis* nauplii. The results of this study did not confirm the statistically signifi-

cant relationship between low salinity and either the high density of nauplii or the high concentration of chlorophyll-*a* (regression analysis $p > 0.05$). However, the maximum density of *O. similis* nauplii coincided with the highest chlorophyll-*a* concentration from June to July 1997. The increased concentration of chlorophyll-*a* has been reported to be caused by an increase in the density of flagellates, which are an appropriately sized food for *O. similis* nauplii in Toyama Bay (Taniguchi et al. 1997, Hirakawa et al. 2004). One of the reasons for the high density of *O. similis* may have been an increased density of flagellates, a food source for nauplii, which is suggested by the observed increase in chlorophyll-*a* concentration. However, we do not have any data on the cell density of flagellates per se.

Oithona similis is regarded as the most abundant and ubiquitous species of copepod in cold-water marine environments (e.g. Castellani et al. 2005a). The reason for its success is its continuous and constant rate of egg production throughout the year (Fransz & Gonzalez 1995, Castellani et al. 2005b), and its high rate of egg hatching in cold water (Nielsen et al. 2002). Based on laboratory experiments, hatching time in *O. similis* has been found to decrease with increasing water temperature between -1 and 20.5°C (Nielsen et al. 2002). In mid-June in Toyama Bay, the average surface water temperature recorded was about 20°C (19.8 – 20.3°C in 1997–1999). We propose that the density of *O. similis* nauplii was higher in mid-June in Toyama Bay because the life cycle progressed most rapidly during this period due to the fast growth of the nauplii.

Vertical distribution

Our study showed that the *WMD* of *O. atlantica* nauplii was greater than that of *O. similis* nauplii. Hirakawa et al. (2004) showed that the abundance of larger nauplii (body length > 0.2 mm) increased in layers below 50 m in unspecified nauplii from the two species *O. atlantica* and *O. similis* in Toyama Bay. Our conclusion from the present study is that the small *O. similis* nauplii (N1–N5 body length < 0.2 mm) were mainly distributed in the 0–25 m zone, whereas the larger *O. atlantica* nauplii (N3–N6 body length > 0.2 mm), were more abundantly distributed in the 25–50 m zone.

Morphologically similar *Oithona* adults that thrive in the same area tend to have different vertical distributions (Nishida & Marumo 1982). We propose that the same is true for *Oithona* nauplii, based on the observation that their distribution depth is the same as that of the adult females. It is likely that the vertical distribution of nauplii is influenced by the distribution of the adults for a number of reasons. For example, *Oithona* species are all egg-carrying and *Oithona* adults do not follow diel vertical migration patterns for reproduction (Zalkina 1970, Boxshall 1977, Ueda 1987). In neritic copepod nauplii, the vertical distribution changes seasonally, and this may be associated with breeding cycles and changing depth preferences of different

stages in the life cycle (Sekiguchi 1985, Ueda 1987, Uye et al. 1990). For *Oithona*, the adult stage of *O. atlantica* was primarily distributed in layers deeper than 500 m from summer to winter but was recorded at a depth of 60 m in March, which suggests an ontogenetic vertical migration (Takahashi & Hirakawa 2001). In this study, we found that the abundance of *O. atlantica* nauplii increased from February to April in the shallow layer (0–50 m depth), which also suggests ontogenetic migration of adult females. Sawada (1996) described the vertical distribution of copepod nauplii in Wakasa Bay: *Oithona* nauplii were distributed above a depth of 10 m and *Microsetella* nauplii were distributed at depths greater than 10 m. These generic differences in depth distribution indicate different optimal water temperatures for each genus. *Oithona similis* maintained a similar vertical distribution during both the day and night (with a median depth of 30 m) throughout the copepodite and adult stages in Fladen Ground, Norway (Eiane & Ohman 2004). In Toyama Bay, the maximum density of *O. similis* adults occurred at 10–30 m in May (Hirakawa et al. 2004), a similar depth to that observed for *O. similis* nauplii (0–25 m) in this study. The vertical distributions of *O. atlantica* and *O. similis* adults were similar to those of the nauplii of the same species, in the present study.

In Toyama Bay, the Japanese sardine, anchovy and *Hyporhamphus sajori* (Temminck & Schlegel) larvae which prey mainly on *Oithona* nauplii are distributed between 0 m and 25 m (Hirakawa & Goto 1996, Hirakawa et al. 1997, Oya et al. 2002). These fish larvae occur in Toyama Bay from May to July when *O. similis* is at the maximum density. During this period, larvae and eggs of these fish species are distributed between 0 m and 25 m, as are *O. similis* nauplii. We believe therefore that *O. similis* nauplii may be a good food source for these fish larvae, owing to their high density of occurrence and their similar vertical distributions, and this ensures a high likelihood of fish larvae encountering them as a potential food source.

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