

Morphology of the naupliar stages of some *Oithona* species (Copepoda: Cyclopoida) occurring in Toyama Bay, southern Japan Sea

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Abstract: Adults of *Oithona atlantica*, *Oithona plumifera* and *Oithona similis* occurred throughout the year in Toyama Bay (0–500 m), but in the surface layers (0–50 m), the adults of *O. atlantica* and *O. plumifera* were observed in Toyama Bay during different seasons. Based on the differences in adult distribution, *O. atlantica* nauplii were found in samples collected during spring (April to May) while *O. plumifera* were found in samples collected during autumn (September to October). Identification of *O. atlantica* and *O. plumifera* nauplii and comparisons of their morphological differences were based on this temporal separation. Nauplii of *O. atlantica*, *O. plumifera* and *O. similis* differed in their ratio of body height (maximum length of dorsal-ventral axis) to length (H/L). This characteristic ratio was common to all naupliar developmental stages and is therefore useful as a basis for distinguishing between naupliar stages of the three species. The population and community structure and densities of these species of *Oithona* were investigated in the surface water layer (0–50 m depth) of Toyama Bay from 1997 to 1999. Major population structural changes occurred in different sampling seasons, and may have been influenced by changes in hydrographic conditions, including temperature and water current. In winter and spring (from February to June), many *O. similis* and *O. atlantica* nauplii appeared, and the former nauplii were more dominant. *Oithona similis* nauplii are suggested to may be the most important species as prey for fish larvae.

Key words: identification, naupliar stage, *Oithona*, seasonal density, Toyama Bay

Introduction

The high abundance of *Oithona* (Copepoda: Cyclopoida) nauplii observed in surface waters in Toyama Bay southern Japan Sea between spring and early summer each year (e.g. Iguchi & Tsujimoto 1997) is considered to be a good food resource for fish larvae in the area (Hirakawa & Goto 1996, Hirakawa et al. 1997). Although *Oithona* nauplii are dominant when copepod nauplii attain high densities, previous studies have failed to distinguish them to species level (Iguchi & Tsujimoto 1997, Hirakawa et al. 2004). The difficulty in identifying *Oithona* nauplii, due to their very small size and similar morphology, must be overcome if their population dynamics are to be investigated satisfactorily.

The present study compared the morphology of *Oithona* nauplii with reference to previous studies, having the following specific objectives: 1—investigation of the seasonal abundances of *Oithona* adults and estimation of the abun-

dance of *Oithona* nauplii when copepod nauplii attain high densities in Toyama Bay; 2—selection of species with a high density throughout the year, as we considered the nauplii of these species would be more abundant; 3—comparison of the morphology of each naupliar stage of the *Oithona* species that may be abundant in Toyama Bay throughout the year; and 4—in the discussion, a comparison of the results of the present study with those obtained previously (Björnberg 1972, Faber 1966, Gibbons & Ogilvie 1933, Oberg 1906, Rao 1958) in order to establish a systematic method for the identification of the naupliar stages of *Oithona* species.

Based on literature descriptions it was not possible to distinguish the nauplii of *Oithona atlantica* from those of *Oithona plumifera*, because they have been misidentified or incompletely described (Gibbons & Ogilvie 1933). Björnberg (1972) illustrated the N1 (first nauplius stage) of *O. plumifera* from a female reared in the laboratory and the remaining naupliar stages, which agreed with Gibbons and Ogilvie (1933) from plankton samples. Björnberg (1972)

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did not have nauplii of *O. atlantica* for comparison. In this study we observed that nauplii of the above two species were found to differ in the ratio of their body height (maximum length of dorsoventral axis) to length (along antero-posterior axis) and lateral body shape. This difference was common to naupliar developmental stages and therefore useful as a basis for distinguishing all naupliar stages of the two species. However, *O. atlantica* and *O. plumifera* potentially could be misidentified because based on the method detailed in this study the nauplii of the two species showed close similarities. In addition, other distinguishing characteristics were established. We refer to recent studies that have described the morphology of some caudal Oithonidae species (*Oithona ovalis*, *Oithona oligohalina*, *Oithona hebes* and *Dioithona oculata*) for which the species identification was confirmed for each development stage because of rearing under laboratory conditions (Fanta 1976, Fonseca & Almeida-Prado 1979, Zacarias & Zoppi-Roa 1981, Ferrari & Ambler 1992).

In the present study, we investigated the population, community structure and density of *Oithona* nauplii, copepodites and adults collected in the surface water layer (upper 50 m depth) of Toyama Bay from 1997 to 1999. Major naupliar population structures changed according to different sampling seasons, such changes possibly being influenced by changes in hydrographic conditions, including temperature and current. We discuss the role of nauplii of oithonid species in the diet of fish larvae in Toyama Bay and conclude that *Oithona similis* is the most important species as prey for fish larvae.

Materials and Methods

1) Relative abundance of *Oithona* adults

Identification of the *Oithona* species represented by the nauplii sampled was based on the co-occurrence with adult species (including late copepodite stages C5) in Toyama Bay. Two separate sampling procedures for adult *Oithona* were undertaken: 1—for large-sized species (adult female body length ≥ 1 mm) occurring in offshore and deep water; 2—for small-sized species (adult female body length ≤ 1 mm) occurring in coastal and shallow water. The life cycles of small-sized species may be shorter than those of large-sized species (Atkinson 1994). Based on this difference, the former were sampled at shorter intervals than the latter. Large-sized species (e.g. *Oithona atlantica*) were sampled once or twice per month from February 1997 to December 1999 by vertical tow (0–500 m depth) of a Norpac net (0.345 mm mesh) at three stations in Toyama Bay (Fig. 1). The small-sized species (e.g. *Oithona similis*) were sampled once or twice per week from March 1996 to March 1997 by vertical tow (0–5 m) of a Kitahara net (0.100 mm mesh) near the shore in Naoetsu Harbor and Himekawa Harbor (Fig. 1).

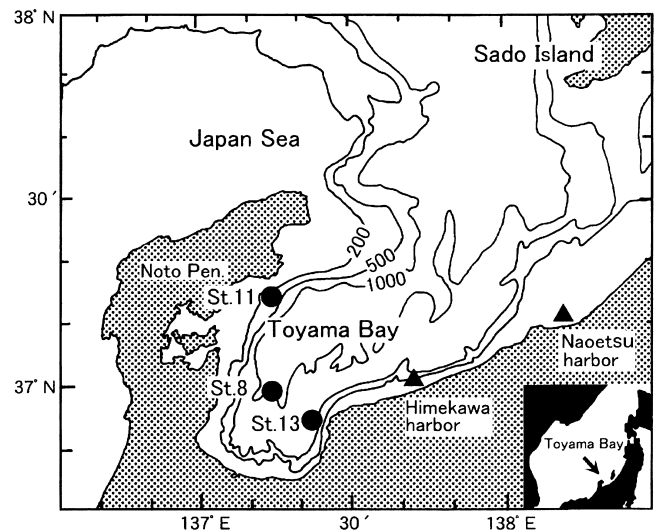


Fig. 1. Map showing the sampling sites and occurrence of *Oithona* species in Toyama Bay, Japan Sea. Solid circles (●) indicate stations at which large-sized species of *Oithona* (*O. atlantica*, *O. plumifera*, *O. longispina* and *O. setigera*) were sampled, solid triangles (▲) indicating stations at which small-sized species of *Oithona* (*O. similis*, *O. rigida*, *O. nana*, *O. brevicornis*, *O. davisae* and *O. simplex*) were sampled.

2) Morphological descriptions of nauplii of three *Oithona* species.

The cold-water species *O. atlantica* can reproduce in the low temperature water season in April and May (Takahashi & Hirakawa 2001). In September and October, *O. atlantica* adults were primarily distributed vertically in layers deeper than 300 m (Takahashi & Hirakawa 2001), and we inferred that the cold-water species *O. atlantica* did not reproduce in high temperature water. *Oithona plumifera* was dominant in the 0–50 m depth layer and we inferred that this species reproduced actively during the high temperature season. In September and October, *O. plumifera* was more abundant in the 0–50 m depth layer, while a few *O. atlantica* and other large *Oithona* species (eg. *Oithona longispina*) nauplii could contaminate the samples. Nauplii of *O. atlantica* and *O. plumifera* were collected by water sampler (10 L) from 0 m, 25 m and 50 m (mainly from 25 m) at St.8 in Toyama Bay on May to April and September to October 2000, respectively, and filtered through 0.02 mm mesh. In contrast, nauplii of *O. similis* were hatched from eggs spawned by adult females collected from Naoetsu Harbor from May to April 2000. These nauplii were cultured with the flagellates *Tetraselmis* and *Pavlova* (above 10^9 cells mL^{-1}), sampled daily for twenty days, and were used to describe the naupliar morphology. Nauplii were reared at a water temperature of 17.5 °C with a 12L : 12D light cycle.

Thirty individuals per developmental stage were used for the morphological descriptions. Body length (L) was measured from the anterior tip to the posterior end of the body in lateral view (Fig. 2). Body height (H) is the maximum

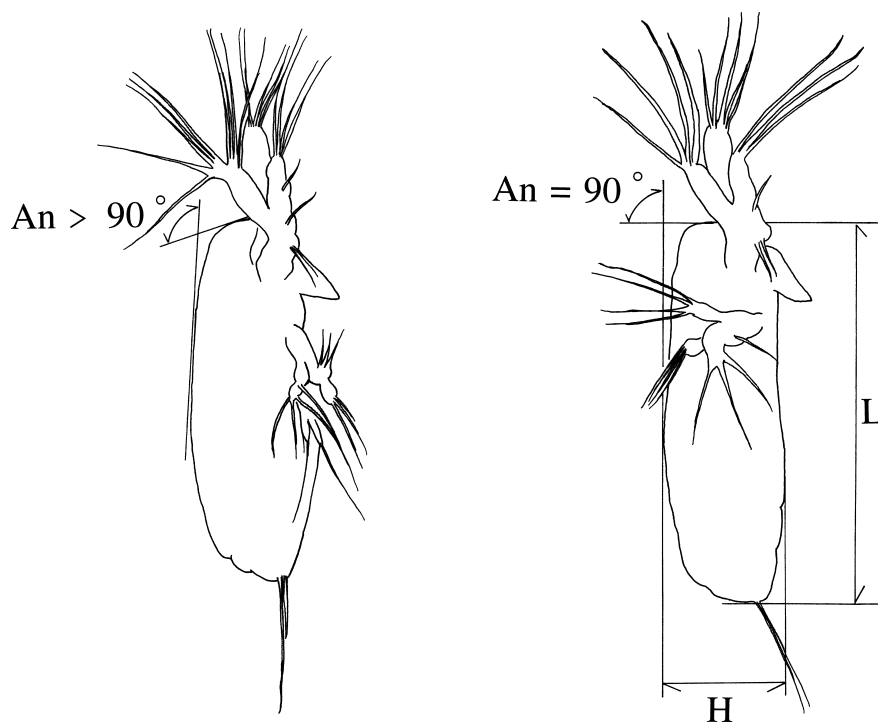


Fig. 2. Lateral views of *Oithona* nauplii. L, body length; H, body height. The angle between the dorsal line and the anterior tip boundary line were over 90-degrees (left: *Oithona atlantica*) and approximating 90-degrees (right: *Oithona plumifera*).

thickness of the dorsoventral axis in lateral view (Fig. 2). An ocular micrometer accurate to 0.001 mm was used for measurements. Differences in body length (L) average and the ratio of body height to body length (H/L) were compared using the students t-test. The very shallow rectangular lateral body shape of *O. plumifera* nauplii agrees closely with the account and sketch of *O. plumifera* given by Björnberg (1972). Body height is an important aid to generic identification, as noted for *Microsetella* (Koga 1984), but may also be important at the species level, as found here. The angle (An) between the dorsal line and the anterior tip boundary line was over 90-degrees (left: *O. atlantica*) and approximating 90-degrees (right: *O. plumifera*). Naupliar stages were designated as N1 to N6, appendages being denoted as A1=antennule; A2=antenna; Mn=mandible; Mx1=maxillule; CA=caudal armature. Accessory elements of appendages and CA constituted spines and setae, distinguishable by their apparent degree of flexibility (Huys & Boxshall 1991).

3) Changes in density of each developmental stage of 3 *Oithona* species in Toyama Bay.

Population and community structure of nauplii (N1–N6), copepodites (C1–C5) and adults (C6) of *Oithona* were investigated using samples collected in the central part (St. 8) of Toyama Bay, 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 0 m, 25 m and 50 m depths, filtered through a 0.02 mm mesh net

and fixed in 2–5% formaldehyde. All copepodite and adult *Oithona* stages were identified to species and the entire sample counted. Identification of the adult stage and copepodite stage (inferred from the morphological characteristics of the adult stage) of *Oithona* followed Nishida (1997), and cold-water and warm-water species were determined on the basis of their geographical distributions (Nishida 1997). Each sample was then concentrated to 20 ml. Depending on the density of copepods, three to five 1-ml subsamples were obtained by pipette after stirring, identification and counting were done on these subsamples. Nauplii of *Oithona* were identified and counted based on the morphological characteristics determined in this study. However, the morphology of *O. atlantica* and *O. plumifera* during N1–N3 stages were very similar. Furthermore, there is a possibility that nauplii of other large species (*Oithona longispina* or *Oithona setigera*) for which the morphological characteristics have not been reported in the literature may have contaminated the sample. Therefore, we can not conclusively rule out that other species were not contaminating the samples. In the N1–N3 stages of *O. atlantica* and *O. plumifera*, the number of individuals that had an ambiguous morphology were proportionally added to the totals in the ratio of individuals that had definite morphological characteristics. The small-sized *Oithona* nauplii with a body length of N1 stage of <0.1 mm: (*Oithona nana*, *Oithona simplex*, *Oithona davisae* or *Oithona brevicornis*) were included in the other *Oithona* spp.

From January 1997 to October 1998, vertical profiles of temperature and salinity at St.8 in Toyama Bay were mea-

Table 1. Frequency of occurrence of large-sized species (*Oithona plumifera*, *Oithona atlantica*, *Oithona longispina* and *Oithona setigera*) in Toyama Bay, and small-sized species (*Oithona similis*, *Oithona simplex*, *Oithona rigida*, *Oithona nana*, *Oithona brevicornis* and *Oithona davisae*) in Himekawa Harbor and Naoetsu Harbor.

Size	Species	Month																							
		J		F		M		A		M		J		J		A		S		O		N		D	
		e	m	e	m	e	m	e	m	e	m	e	m	e	m	e	m	e	m	e	m	e	m	e	m
large species ♀>1mm	● <i>Oithona atlantica</i>	cc	cc	cc	cc	ccc	ccc	ccc	ccc	ccc	ccc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
	○ <i>Oithona plumifera</i>	c	+	+	+	-	-	rr	-	rr	rr	r	r	r	c	c	c	+	+	+	+	+	+	c	+
	○ <i>Oithona longispina</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	rr	rr	rr	rr	rr	rr	rr	rr	rr	-	-
	○ <i>Oithona setigera</i>	rr	-	-	-	-	-	-	-	-	-	-	-	-	-	rr	rr	rr	rr	r	r	r	r	rr	rr
small species ♀<1mm	● <i>Oithona similis</i>	ccc	ccc	ccc	ccc	ccc	ccc	ccc	ccc	ccc	ccc	ccc	ccc	cc	r	rr	rr	+	+	+	r	c	cc	cc	
	○ <i>Oithona simplex</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	rr	r	c	+	rr	-	-	-	-	-	
	○ <i>Oithona rigida</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	r	rr	-	-	-	-	-	-	
	○ <i>Oithona nana</i>	rr	-	-	-	-	-	-	-	-	-	-	-	rr	+	c	cc	cc	c	c	r	c	c	rr	rr
	○ <i>Oithona brevicornis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	r	r	r	rr
	○ <i>Oithona davisae</i>	-	-	-	-	-	-	-	-	-	-	-	-	rr	+	rr	+	+	+	c	-	-	-	-	

Abbreviations used in this table. e: early in month, m: middle of month. ● cold-water species. ○ warm-water species. ccc - <90%, cc - 45–89%, c - 30–44%, + - 15–29%, r - 8–14%, rr - 2–7% and rrr - <2%.

sured during sampling using a CTD (MK3B; Neil Brown, SBE911; Seabird), and surface water salinity was measured with a salinometer (601MKIII; Yeo-kal, Autosal; Guildline). In this period, chlorophyll-a in water samples from 0m, 25m and 50m depths was measured using the fluorescence method (Parsons et al. 1984). From November 1998 to December 1999, vertical profiles of temperature, salinity and fluorescence were measured simultaneously with a CTD (ACL200DK, Alec).

Results

1) Relative abundance of *Oithona* adults

Ten *Oithona* species were found to occur around Toyama Bay. The two cold-water species, *Oithona atlantica* and *Oithona similis*, occurred throughout the year (Table 1), the former comprised more than 90% of the adults of large-sized species sampled from March to May. On the other hand, *O. similis* adults were most abundant from February to July, comprising more than 90% of the adults of small-sized species sampled in these months.

Seven warm-water species, *Oithona nana*, *Oithona longispina*, *Oithona setigera*, *Oithona simplex*, *Oithona rigida*, *Oithona brevicornis* and *Oithona davisae* occurred in summer and autumn, as well as for a limited period from July to January in the following year. These species together did not comprise more than 90% of the adult sample. Another warm-water species, *Oithona plumifera*, occurred towards the end of winter or early spring and was consistently present during summer and autumn.

2) Systematic morphological descriptions of nauplii of three *Oithona* species.

Nauplii of *O. atlantica*, *O. plumifera* and *O. similis* were considered to be the most common in Toyama Bay, in keeping with the high numbers of respective adults. Six naupliar stages were identified for each species (N1–N6).

Oithona similis nauplii (Fig. 3a–f, 4a–f, 5a–c)

Body length range: N1=0.111–0.123 mm; N2=0.136–0.150 mm; N3=0.156–0.168 mm; N4=0.179–0.194 mm; N5=0.196–0.210 mm; N6=0.217–0.279 mm; body length range mid-way between those of large (e.g. *O. atlantica* nauplii (N1: >0.125 mm)) and small species (e.g. *O. nana* (N1: <0.100 mm)).

Body shape in ventral view: N1–N2—egg-shaped (Fig. 3a–b); N3—egg-shaped with bluntly angular anterior end (Fig. 3c). N4—egg-shaped; anterior end quadrate (Fig. 3d); N5—pear-shaped with the posterior margin elongate and quadrate posterolaterally (Fig. 3e). N6—pear-shaped but more elongate with the posterior end narrowly extended (Fig. 3f).

Body shape in lateral view: N1–N2—egg-shaped; body height greater than in nauplii of other species (Fig. 4a–b); N3–N4—egg-shaped with posterodorsal aspect quadrate (Fig. 4c–d); N5—broadly egg-shaped; body height greater and dorsal surface rounded (Fig. 4e). N6—almost semi-circular; body height greater and dorsal surface more rounded than in N5 (Fig. 4f).

A1, A2 and Mn: N1–N6—segmentation and setation of appendages were similar to *O. atlantica* and *O. plumifera* nauplii (Fig. 3a–f).

Mx1: N1–N6—segmentation and setation of appendages

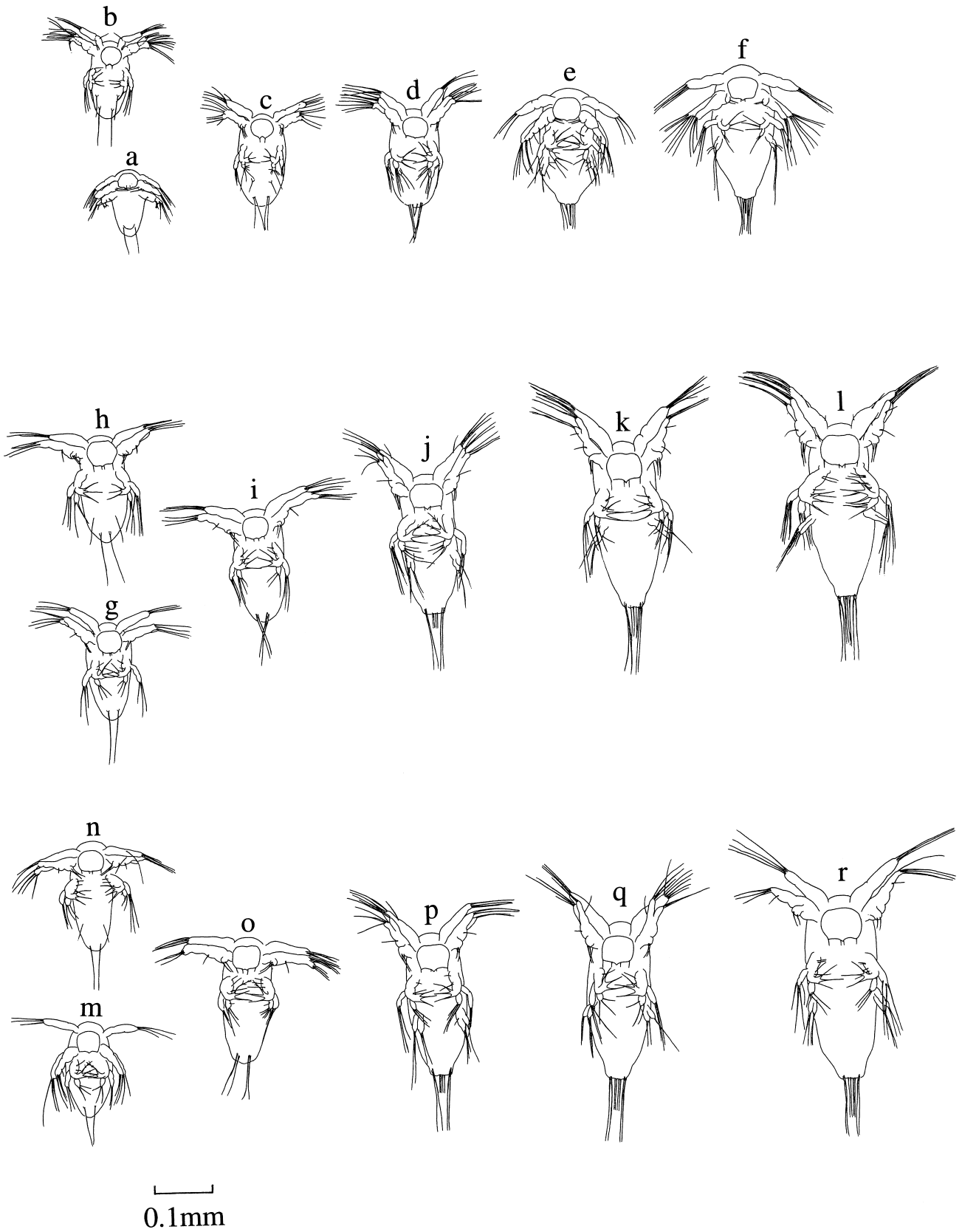


Fig. 3. Naupliar stages of *Oithona similis* collected from Naoetsu Harbor and reared in the laboratory: a–f; ventral views N1–N6. Naupliar stages of *Oithona atlantica* collected from Toyama Bay in 1997 March–April: g–l; ventral views N1–N6. Naupliar stages of *Oithona plumifera* collected from Toyama Bay in 1997 September–October: m–r; ventral views N1–N6.

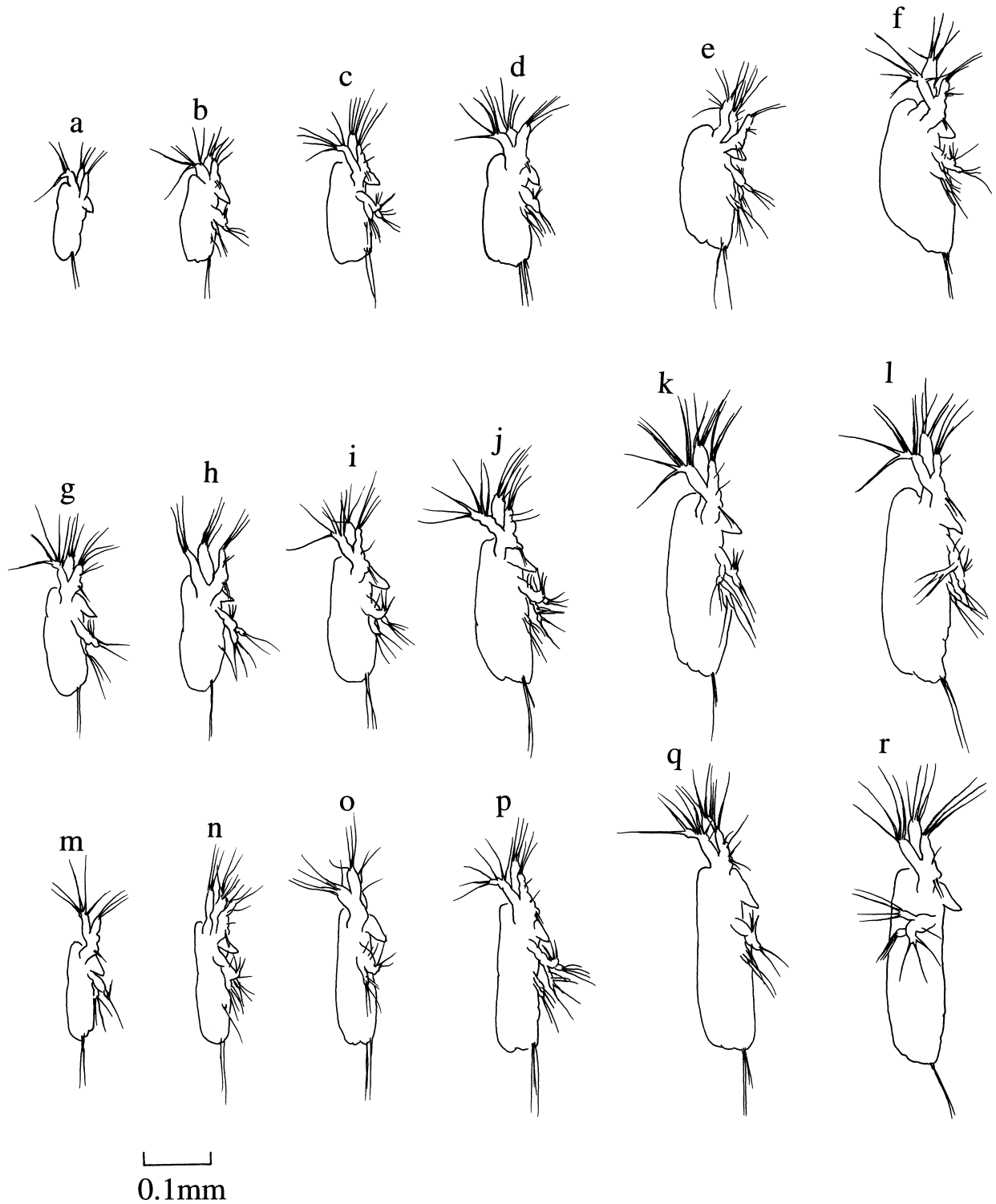


Fig. 4. Lateral views of *Oithona* nauplii (N1–N6). a–f, *Oithona similis* collected from Naoetsu Harbor in April and reared in the laboratory; g–l, *Oithona atlantica* collected from Toyama Bay in 1997 March–April; m–r, *Oithona plumifera* collected from Toyama Bay in 1997 September–October.

were similar to *O. atlantica* and *O. plumifera* nauplii (Fig. 3a–f).

CA: N1–N2—2 setae (Fig. 3a–b); N3—1 pair of setae on each side (Fig. 3c); N4—2 pairs of long outer setae and 2

short spines centrally, the latter pair differing considerably from the equivalent setae in the other two naupliar species (Fig. 3d, 5a); N5—2 pairs of outer setae, 2 spines and 2 small inner setae, the spines being about one-third the

length of those in N4 (Fig. 3e, 5b). N6—2 pairs of outer setae, 2 spines and 2 inner setae, the 2 spines being twice the length of those in N5 (shorter than the 2 outer pairs of setae) (Fig. 3f, 5c); N4–N6—outer setae lacking basal protrusions present in *O. atlantica* and *O. plumifera* nauplii (Fig. 5a–c).

Oithona atlantica (Fig. 3 g–l, 4 g–l, 5d–f)

Ranges of body length: N1=0.128–0.144 mm; N2=0.154–0.193 mm; N3=0.200–0.216 mm; N4=0.240–0.266 mm; N5=0.273–0.288 mm; and N6=0.291–0.299 mm.

Body shape in ventral view: N1—egg-shaped (Fig. 3g); N2–N4—elongate egg-shaped with posterior end squarish (Fig. 3h–j); and N5–N6—similarly elongate at posterior end (Fig. 3k–l).

Body shape in lateral view: N1–N2—egg-shaped (Fig. 4g–h); N3–N4—egg-shaped (Fig. 4i–j); N5–N6—egg-shaped with the dorsal face smoothly curved, and the angle (An) between dorsal line and anterior end boundary line separated to an obtuse angle of over 90-degree (Fig. 4k–l).

A1, A2 and Mn: N1–N6—segmentation and setation of appendages were similar to *O. plumifera* and *O. similis* nauplii (Fig. 3g–l).

Mx1: N1—absent (Fig. 3g); N2–N3 was a unilobed bud with 1 seta (Fig. 3h, 3i); N4–N6—was a bi-lobed bud (Fig. 3j–l).

CA: N1–N2—2 setae (Fig. 3g–h); N3—1 pair of setae on each side (Fig. 3i). N4—2 pairs of setae on lateral surface, and 4 short, setae of equal-length centrally (Fig. 3j, 5d); N5—2 pairs of long setae and 4 short of half-length of former, twice length of equivalent in N4 setae (Fig. 3k, 5e). N6—2 pairs of long setae and 4 short centrally-positioned setae, about two-thirds of former (Fig. 3l, 5f). N4–N6—(Fig. 5d–f) 1 pair of long outer setae on either side with a basal protrusion that was also observed in *O. plumifera* nauplii (not in *O. similis* nauplii).

Oithona plumifera (Fig. 3 m–r, 4m–r)

Body length range: N1=0.134–0.156 mm; N2=0.177–0.198 mm; N3=0.204–0.215 mm; N4=0.242–0.255 mm; N5=0.258–0.282 mm; N6=0.294–0.323 mm.

Body shape in ventral view: Same as in *O. atlantica* (Fig. 3m–r).

Body shape in lateral view: N1–N3—thin, somewhat rectangular, body height relatively thinner than *O. atlantica* nauplii, anterodorsally angular (Fig. 3m–o). N4–N6—anteriorly and posteriorly angular, giving a rectangular appearance; body height greater but thinner than *O. atlantica* nauplii, and the angle (An) between dorsal line and anterior end boundary line separated to an angle approximating 90-degrees (Fig. 3p–r).

A1, A2 and Mn: N1–N6—segmentation and setation of appendages were similar to *O. atlantica* nauplii (Fig. 3m–r).

Mx1: N1–N6—segmentation and setation of appendages were similar to *O. atlantica* nauplii (Fig. 3m–r).

CA: N1–N6—appearance of CA and number and length of setae as in *O. atlantica* nauplii in all naupliar stages.

3) Comparative morphological characteristics

The body length of *O. atlantica* naupliar stages was comparable to those of *O. plumifera*, but significantly larger than the naupliar stages of *O. similis* ($p < 0.05$). Because this feature is common to all naupliar stages of those species, it provides a good basis for separating nauplii of *O. similis* from those of *O. atlantica* and *O. plumifera*. In ventral view during naupliar development, the body shape of *O. atlantica* and *O. plumifera* nauplii changes from egg-shaped to more rectangular, elongate posteriorly and with more angular anterior and posterior margins (Fig. 3g–l, 3m–r). The body shape of *O. similis* nauplii changes from egg-shaped to pear-shaped, and then posteriorly elongated (Fig. 3a–f).

In ventral view, the body shape, appendages and CA of *O. atlantica* and *O. plumifera* nauplii were very similar, with the mandibular endopod bearing three stout, fork-like setae in all developmental stages (Fig. 3g–l, 3m–r). A careful ventral examination of N2 in the three species revealed a long fine seta under Mn; this seta is a bud of Mx1 (Fig. 3b, 3h, 3n). In N4–N6, the long outer setae of CA each had a small basal protrusion in *O. atlantica* and *O. plumifera* nauplii (Fig. 5d–f) but not in *O. similis* nauplii (Fig. 5a–c). This protrusion enables the distinction of co-occurring nauplii of *O. atlantica* and *O. similis*.

Morphological differences of the naupliar body shape in the three species were apparent from the lateral view in all developmental stages. The body length of *O. similis* nauplii was shortest, the height of the dorsoventral axis greater than in the other species; and the shape is rounded (Fig. 4a–f). By comparison, the body of *O. atlantica* nauplii is longer and the height of the dorsoventral axis is less; the over-all shape is egg-shaped (Fig. 4g–l). The body length of *O. plumifera* nauplii is similar to that of *O. atlantica* nauplii, however, in the lateral view the body height of *O. plumifera* nauplii is lower and more flattened; it is angular (quadrate) posterodorsally (Fig. 4m–r). Based on size (in terms of body height), the nauplii could be arranged in order (from smallest to largest) as: *O. similis*, *O. atlantica* and *O. plumifera*. Based on the angle (An) of the dorsal line, it was possible to distinguish in N4–N6 between *O. atlantica* and *O. plumifera* nauplii, but not in N1–N3.

The average ratio of body height to body length (H/L) of *O. similis* nauplii is 0.39–0.49 (Fig. 6), the ratio (H/L) increases with the developmental stage. The ratio of H/L overlapped to some degree in some stages. A significant difference ($p < 0.05$) in the ratio (except at the N1 stage) is evident between *O. similis* and *O. atlantica* nauplii. A significant difference ($p < 0.05$) also occurs between *O. atlantica* (0.32–0.38) and *O. plumifera* (0.29–0.34) nauplii.

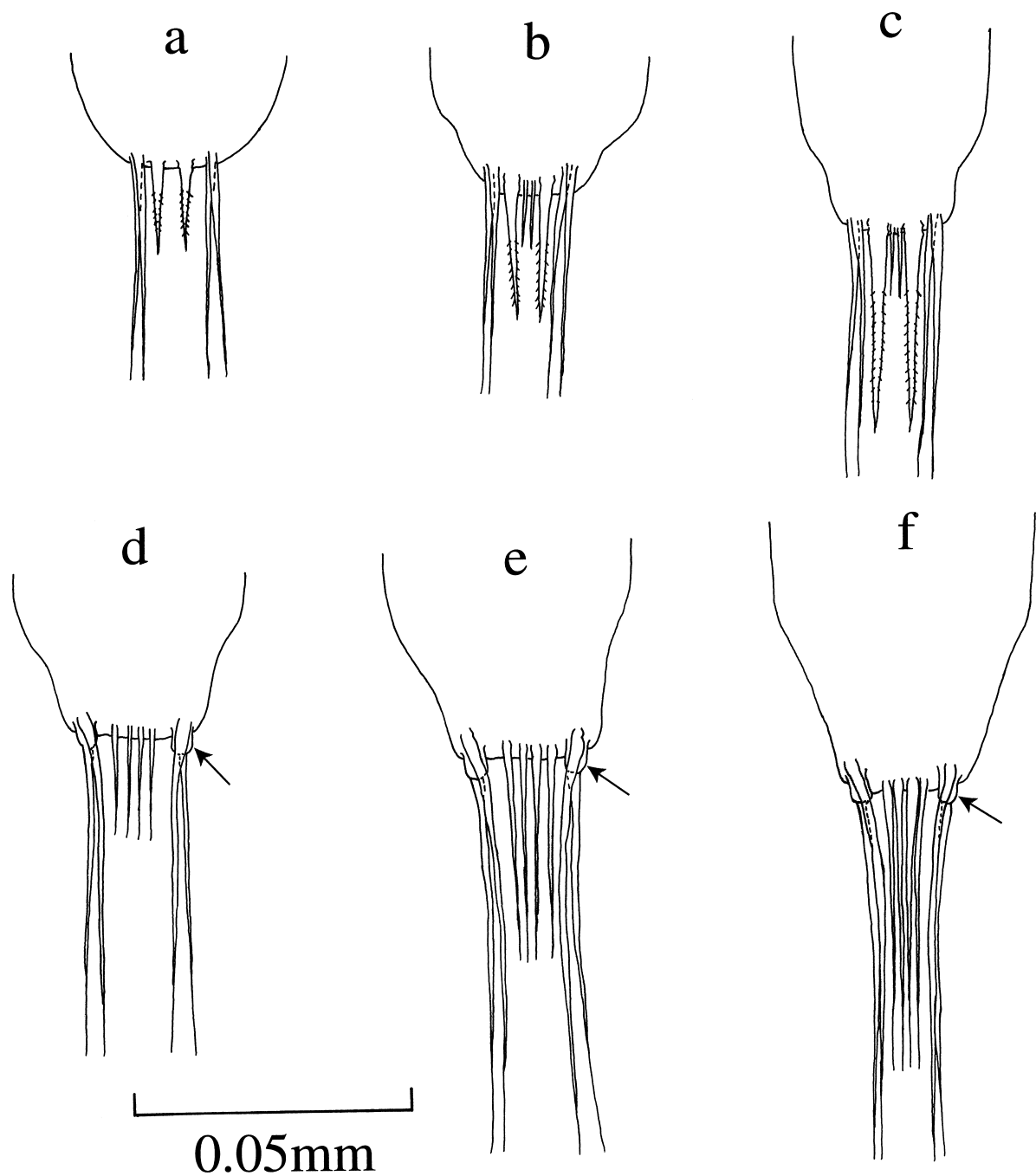


Fig. 5. Naupliar stages of *Oithona similis* collected from Naoetsu Harbor and reared in the laboratory; ventral views CA (=caudal armature) of N4–6, a–c. Nauplii of *Oithona atlantica* collected from Toyama Bay in 1997 March–April; ventral views CA (=caudal armature) of N4–N6, d–f. Arrows indicate protrusions of setae on the caudal armature.

4) Hydrography

During the three years of investigation, the lowest surface water (<50 m depth) temperature was 10°C, from March to April in each year, while vertical mixing occurred in the upper 150 m during this season (Fig. 7, upper panel). Water temperatures increased gradually after May, and the water column was thermally stratified during summer. The surface water temperature was highest at 28°C in August, and

decreased gradually after September.

Salinities higher than 34.2 psu were observed consistently in the 10–100 m depth range every year from June–August to December–January (Fig. 7, lower panel), indicating the intrusion of warm Tsushima current core water. Surface water salinities were less than 33 psu in May and June and after August in 1997 and 1998, indicating the intrusion of river water in May and June or surface water of the Tsushima Warm Current (TWC) in August (Ogawa

1983).

The concentration of chlorophyll-*a* was at the 1.0–4.0 $\mu\text{g L}^{-1}$ level between February and April, when vertical water

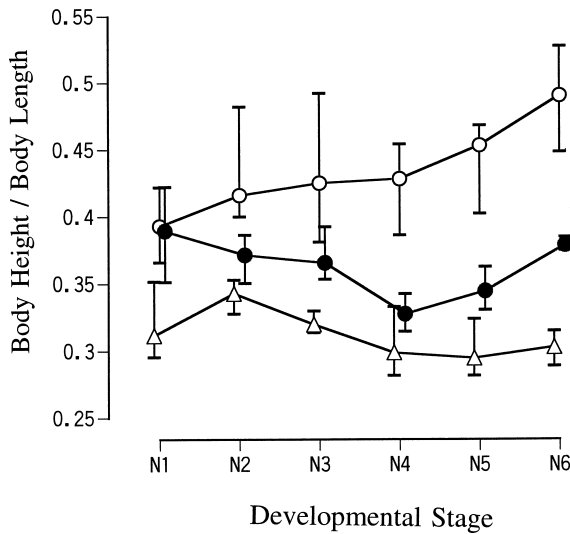


Fig. 6. Developmental changes in body height (maximum length of dorsal-ventral axis) to body length ratios in *Oithona similis* (○), *Oithona atlantica* (●) sampled in Mar. and Apr. and *Oithona plumifera* (△) sampled from September to November in Toyama Bay, Japan Sea. Vertical bars indicate ranges of body height to body length ratio (n=30).

mixing occurred (Fig. 8). After May, the concentration decreased rapidly to below $0.5 \mu\text{g L}^{-1}$. In 1997, a higher concentration of chlorophyll-*a* ($>1.0 \mu\text{g L}^{-1}$) was observed at the surface (0 m depth) after May, with the highest ($5.1 \mu\text{g L}^{-1}$) value recorded in mid-June, while the surface water chlorophyll-*a* concentrations remained constantly below $0.5 \mu\text{g L}^{-1}$ after May in 1998 and 1999.

5) Seasonal changes in numerical density of each developmental stage of 3 *Oithona* species

Oithona atlantica (Fig. 9): The nauplii of each stage (N1–N6) had higher densities ($3\text{--}15 \times 10^3 \text{ indiv. m}^{-3}$) occurring from February to June throughout the three years. After June, however, the densities decreased. High densities of both the adult and copepodite stages of this species occurred in February to June, linked to the occurrence season of nauplii. These variations in their densities were repeated each year, indicating a clear linkage in the occurrence of the adults and nauplii of *O. atlantica* nauplii.

Oithona plumifera: The population densities of each naupliar stage increased from June and reached a maximum ($3\text{--}10 \times 10^3 \text{ indiv. m}^{-3}$) between July and November. These variations in density were repeated each year. The nauplii of this species were not observed from January to May when *O. atlantica* nauplii were abundant. High adult and copepodite stage densities of this species occurred from

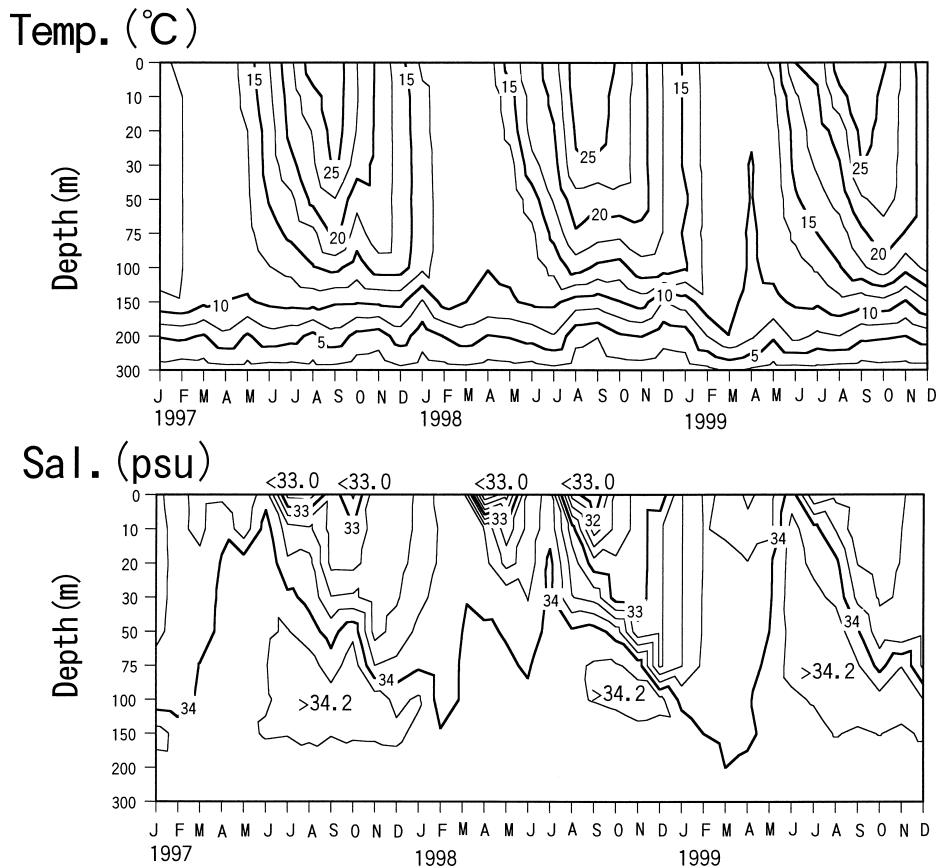


Fig. 7. Seasonal variations in temperature (upper) and salinity (lower) in Toyama Bay (Stn 8), from 1997 to 1999.

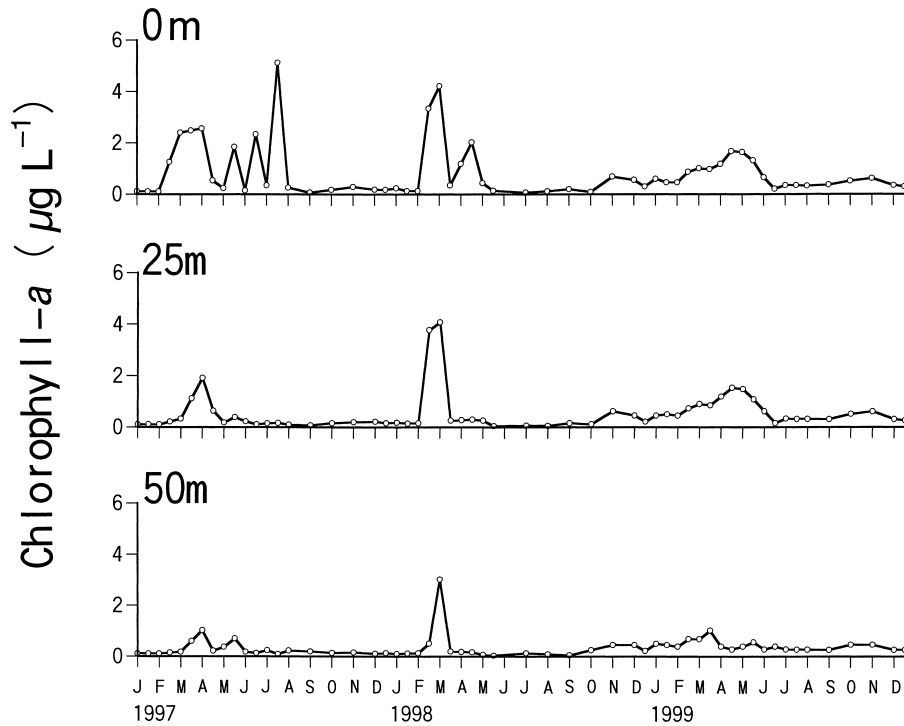


Fig. 8. Seasonal variations in chlorophyll-a concentration in Toyama Bay (Stn. 8).

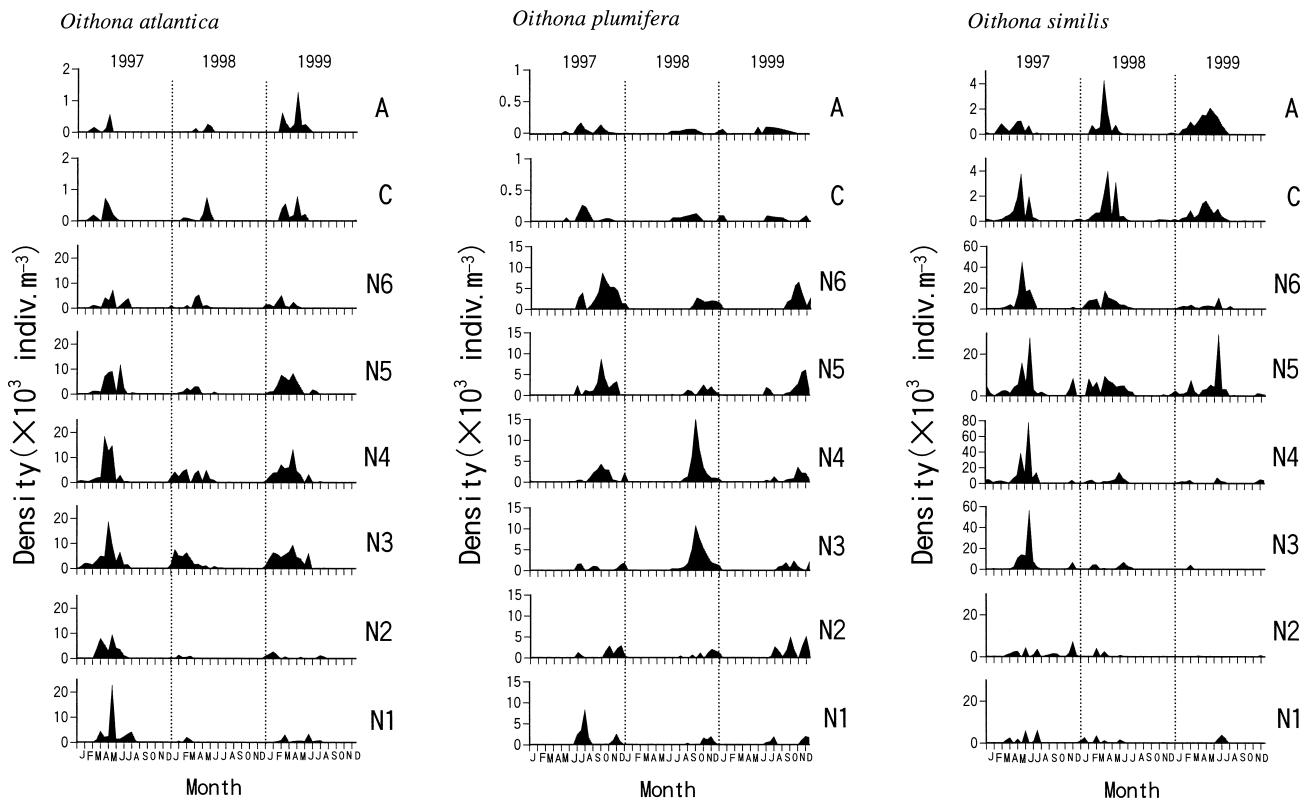


Fig. 9. Changes in stage-specific average density (indiv. m^{-3}) of three species of *Oithona* (*Oithona atlantica*, *Oithona plumifera* and *Oithona similis*) sampled in Toyama Bay (Stn. 8) from January 1997 to December 1999. The naupliar, copepodite and adult densities were calculated as three layer average densities $= (N_0d + N_{25d} + N_{50d})/3$. Where N_0 , N_{25} and N_{50} were the densities at 0 m, 25 m and 50 m depths for each sampling day (d).

July to October, the same as the naupliar occurrence season.

Oithona similis: Nauplii of each stage occurred throughout the year, but in September and October were a few. Densities of N3–N6 stages were high between April and June, with the highest density (over 60×10^3 indiv. m^{-3}) being observed in 1997. Adult and copepodites of this species occurred throughout the year except between September and November, and were higher between April and June, linked to the high density occurrence of nauplii.

The most abundant components of the *Oithona* nauplii population that occurred in Toyama Bay were *O. similis* nauplii, followed by *O. atlantica* nauplii throughout the three years. *Oithona similis* and *O. atlantica* nauplii had the highest composition ratio between January and July, whereas *O. plumifera* were more abundant between August and December. In 1997 between April and June, over 90% of the greatest naupliar density was comprised of *O. similis* nauplii.

Discussion

1) Seasonal dynamics of adult *Oithona* in the Japan Sea

Previous studies in areas of the Japan Sea that are influenced by the TWC (Ondo & Shimoda 1968, Abe et al. 1984, Koga 1984, Wada et al. 1984, Nishida 1985, Shim & Lee 1986, Hirakawa et al. 1990, Hirakawa & Ogawa 1996, Iguchi & Tsujimoto 1997, Iguchi et al. 1999) recognized fourteen *Oithona* species that were also observed in the vicinity of Toyama Bay in the present study (Table 2).

Four species, *Oithona fallax*, *Oithona tenuis*, *Oithona vivida* and *Oithona decipiens* were not recorded from Toyama Bay during this study: *Oithona fallax* has been sampled off Sado Island (Abe et al. 1984); *Oithona tenuis* in the western part of Wakasa Bay (Wada et al. 1984) and off Tottori Prefecture (Nishida 1985); *Oithona vivida* and *O. decipiens* also have been reported off Tottori Prefecture (Nishida 1985). The hydrographical distribution of the above four species extends to offshore tropical and subtropical waters (Nishida 1997) and it is likely that they migrate with the northwards movement of the TWC. Accordingly, the decrease in the number of species of *Oithona* northeast of Noto Peninsula is likely to be due to the decreased effect of the TWC on the local hydrography. Of the species observed in the present study, adults of the seven warm-water species (*Oithona longispina*, *Oithona setigera*, *Oithona simplex*, *Oithona nana*, *Oithona rigida*, *Oithona brevicornis* and *Oithona davisae*) were observed only from summer to autumn, probably having been transported northward by the Tsushima current during that season (Naganuma 2000). All of the immigrant species occur at low densities. Conversely, the most abundant *Oithona* species around Toyama Bay are cold-water species, e.g. *Oithona atlantica* and

Table 2. Oithonidae species associated with the Tsushima Warm Current in the Japan Sea, collected off Noto Peninsula (●): occurrence, C: cold-water species, W: warm-water species.

Species	North-east area of Noto Peninsula	South-west area of Noto Peninsula
C <i>Oithona similis</i>	●	●
W <i>Oithona fallax</i>	●	●
W <i>Oithona tenuis</i>		●
W <i>Oithona plumifera</i>	●	●
C <i>Oithona atlantica</i>	●	●
W <i>Oithona longispina</i>	●	●
W <i>Oithona setigera</i>	●	●
W <i>Oithona vivida</i>		●
W <i>Oithona simplex</i>	●	●
W <i>Oithona rigida</i>	●	●
W <i>Oithona nana</i>	●	●
W <i>Oithona brevicornis</i>	●	●
W <i>Oithona davisae</i>	●	●
W <i>Oithona decipiens</i>		●
Reference number	1)–3),7)	4)–10)

Reference number and sampling locality

- 1) Abe et al. 1984, coast of Sado Island
- 2) Iguchi & Tsujimoto 1997, Toyama Bay
- 3) Hirakawa et al. 1990, Toyama Bay
- 4) Wada et al. 1984, western Wakasa Bay
- 5) Iguchi et al. 1999, Wakasa Bay
- 6) Ondo & Shimoda 1968, Moroyose Bay
- 7) Nishida 1985, sea of Japan (offshore)
- 8) Hirakawa & Ogawa 1996, Tsushima Straits
- 9) Koga 1984, coastal waters off northwest Kyushu
- 10) Shim & Lee 1986, coastal waters off east Korea

Oithona similis, and cold-tolerant warmer water species that can persist during winter (e.g. *Oithona plumifera*). Recent studies have confirmed that *O. similis* is a dominant cold water copepod species world-wide, including in the North Sea (Nielsen & Sabatini 1996, Eiane & Ohman 2004), North Atlantic Sea (Maar et al. 2002, Castellani et al. 2005), Arctic (Nielsen et al. 2002) and Antarctic (Tanimura et al. 1997).

2) Comparison of morphological characteristics of *Oithona* nauplii at each developmental stage

The morphological development of naupliar stages of *Oithona* species recorded as adults from Toyama Bay have been investigated in a number of previous studies (Björnberg 1972, Faber 1966, Gibbons & Ogilvie 1933, Goswami 1975, Haq 1965, Murphy 1923, Oberg 1906, Rao 1958, Uchima 1979). However, there have been no studies on the morphological characteristics of *O. longispina* or *O. setigera* nauplii. Concerning the morphological characteristics of *Oithona* nauplii, the findings of the present and previous studies are compared in Tables 3 and 4. In the present

Table 3. List of diagnostic developmental stage characters of *Oithona* species collected in Toyama Bay. Common: indicates common to all species. Variable: indicates characters restricted to one or a few species.

Stage	Point	Characters	*) Reference number
NI	Common Variable	CA (=caudal armature)=1 paired setae (2 se.). All taxa were oval shape. Body height to body length ratio <i>Oithona similis</i> =0.37–0.42 <i>Oithona atlantica</i> =0.35–0.42 <i>Oithona plumifera</i> =0.29–0.36	1)–11) 11)
NII	Common Variable	1 paired spines (2 sp.) occur on Mx1 (rudiments represented). <i>Oithona atlantica</i> and <i>Oithona plumifera</i> elongated oval body shape. <i>Oithona nana</i> have 1 pair of spines on outer side of setae in CA.	1)–11) 6)11)
NIII	Common Variable	No characters apparent. Except <i>Oithona simplex</i> , 2 paired setae (4 se.) on CA.	1)–11) 1)–11)
NIV	Common Variable	New setae (se.) or spines (sp.) centrally on CA. Except <i>Oithona rigida</i> , Mx1 is a multi-lobed bud.	1)–11) 1)–11)
NV	Common Variable	Setae (se.) and spines (sp.) elongate, number increases centrally on CA. <i>Oithona rigida</i> , endopod and exopod of Mx1 clearly separate. <i>Oithona similis</i> pentagonally shaped.	1)–11) 9)11)
NVI	Common Variable	Posterior end of body well elongate. <i>Oithona similis</i> , <i>Oithona nana</i> , <i>Oithona brevicornis</i> and <i>Oithona davisae</i> , the rudiments of swimming legs occur lower part of body.	1)–11) 1)–8), 10)–11)

*) References: ¹⁾ Björnberg (1972), ²⁾ Faber (1966), ³⁾ Gibbons and Ogilvie (1933), ⁴⁾ Goswami (1975), ⁵⁾ Koga (1984), ⁶⁾ Haq (1965), ⁷⁾ Murphy (1923), ⁸⁾ Oberg (1906), ⁹⁾ Rao (1958), ¹⁰⁾ Uchima (1979), ¹¹⁾ This study

Table 4. Comparative list of selected diagnostic characters for *Oithona* species.

Characters	Species	NI	NII	NIII	NIV	NV	NVI	*) Reference number
Body length range (thousandths of mm)	<i>Oithona atlantica</i>	128–144	154–193	200–216	240–266	273–288	291–299	11)
	<i>Oithona plumifera</i>	134–156	177–198	204–215	242–255	258–282	294–323	11)
	<i>Oithona similis</i>	100–125	120–150	155–168	179–194	196–210	217–249	3)11)
	<i>Oithona simplex</i>	70	—	100	110	120	140	1)
	<i>Oithona rigida</i>	68	112	131	150	163	194	9)
	<i>Oithona nana</i>	50–85	85–100	100–110	110–125	130–145	150–175	6)
	<i>Oithona brevicornis</i>	90	100	110	120	130	150	5)
<i>Oithona davisae</i>	70–90	85–105	100–115	115–125	125–135	135–160	10)	
Number of setae (se.) or spines (sp.) on CA (=caudal armature)	<i>Oithona atlantica</i>	2se.	2se.	4se.	4se.+4se.	4se.+4se.	4se.+4se.	3)11)
	<i>Oithona plumifera</i>	2se.	2se.	4se.	4se.+4se.	4se.+4se.	4se.+4se.	1)11)
	<i>Oithona similis</i>	2se.	2se.	4se.	4se.+2sp.	4se.+2sp.	4se.+2sp.	2)3)8)11)
	<i>Oithona simplex</i>	2se.	2se.	2se.	2se.+2sp.	2se.+2sp.	2se.+2sp.	1)
	<i>Oithona rigida</i>	2se.	2se.	4se.	4se.+4sp.	4se.+4S	4se.+4sp.	9)
	<i>Oithona nana</i>	2se.	2sp.+2se.	2sp.+4se.	2sp.+4se.	2sp.+4se.	2sp.+4se.	1)6)7)
	<i>Oithona brevicornis</i>	2se.	2se.	4se.+2sp.	4se.+2sp.	4se.+2sp.	4se.+2sp.	4)5)
<i>Oithona davisae</i>	2se.	2se.	4se.+2sp.	4se.+2sp.	4se.+2sp.	4se.+2sp.	10)	

*) References: ¹⁾ Björnberg (1972), ²⁾ Faber (1966), ³⁾ Gibbons and Ogilvie (1933), ⁴⁾ Goswami (1975), ⁵⁾ Koga (1984), ⁶⁾ Haq (1965), ⁷⁾ Murphy (1923), ⁸⁾ Oberg (1906), ⁹⁾ Rao (1958), ¹⁰⁾ Uchima (1979), ¹¹⁾ This study

study, morphological characteristics that could be observed without dissection were emphasized, enabling more samples to be identified in a shorter time. Changes in morphological characteristics that could be used to identify the different developmental stages are shown when they are common for all species and also when variable (present in a few species) in different species. Changes in body size ranges, numbers of setae (se.) and spines (sp.) of the caudal armature (CA) are also recorded.

N1: CA composed of 1 pair of setae (2 se.) was common to each species. The endopod of the mandible was tipped with 3 long thick setae, being characteristic of many free-swimming cyclopoid nauplii. Nauplii with a body length greater than 0.125 mm were comprised of both *O. atlantica* and *O. plumifera*. The ratio of dorsoventral axis height to body length (H/L) of nauplii differentiates these two *Oithona* species at all developmental stages. *O. similis* nauplii were identified as having a mid-range body length (>0.100 mm and <0.125 mm). However, *O. rigida* and *O. nana* nauplii, with a body length less than 0.100 mm, cannot be distinguished because of the similarities in body shape and length, and lack of any other clear specific characteristic.

N2: Rudiments of Mx1 (unilobed bud with 1 seta) appeared under Mn in all of the species examined with body length greater 0.100 mm. Distinguishing characteristics of *O. atlantica*, *O. plumifera* and *O. similis* included body shape and body length (>0.120 mm) for same stage nauplii, in addition to a change in the ventral body shape. Koga (1984) described an elongate egg-shaped shape of Corycaeus nauplii, which is similar to that of *O. atlantica* and *O. plumifera* nauplii. *O. nana* nauplii can be identified by 2 outer spines on the outer sides of CA. Nauplii of the other four species cannot be identified by the methods given in this study.

N3: No morphological characters were found to be useful for identifications of this naupliar stage. Each species, except *O. simplex* has 2 pairs of setae (4 se.) on CA. *O. nana*, *O. brevicornis* and *O. davisae* nauplii bear 1 pair of spines (2 sp.) in the central part of CA, although *O. nana* can be distinguished from the two latter species on the basis of the spine number. However based on the methods detailed in this study the nauplii of *O. brevicornis* and *O. davisae* cannot be separated.

N4: In all taxa, the posterior part of the body remains elongate. Except for in *O. rigida*, the Mx1 is a multi-lobed bud. The nauplii of *O. atlantica*, *O. plumifera*, *O. similis*, *O. rigida* and *O. simplex* bear new spines and setae in the central part of CA, identification becoming more straightforward due to the increasing numbers of setae and spines on the CA of each nauplius.

N5: The setae and spines on the CA are elongate in all species, *O. similis* and *O. nana* nauplii bear a new pair of setae (2 se.) in the central part. Identification of *O. similis* is straightforward due to the entire body being characteristically pear-shaped.

N6: The lower part of the body is elongate in all species, the setae and spines on the CA being more elongated than in N5. *O. similis*, *O. nana*, *O. brevicornis* and *O. davisae* nauplii bear rudiment any swimming legs.

The key characteristics detailed above describe the morphological characteristics of *Oithona* nauplii observed around Toyama Bay, and only the N1–N3 stages of the smallest sized *Oithona* nauplii cannot be identified.

3) Seasonal changes in population density

Nauplii of the warm-water species *O. plumifera* were abundant from July to January when water temperatures were high. During this season, a large volume of TWC core water extended along the Japan Sea coast (Naganuma 2000). *Oithona plumifera* occurs abundantly in this warmer current (Hirakawa et al. 1992). Hirakawa (1995) noted the influence of temperature on reproduction in *Oncaea venusta*, a species that reproduces actively during the high temperature season (>20–25°C), but not at low temperatures (<15°C).

Nauplii of warm-water species did not appear in Toyama Bay during winter, when temperatures were low. Nauplii of the cold-water species, *O. atlantica* and *O. similis*, appeared from winter to spring, replacing the warm-water species. Reproduction of *O. atlantica* adults may increase in spring due to higher water temperatures, as indicated by the maximum density of *O. atlantica* nauplii recorded in May. The maximum density of *O. similis* nauplii (total of all stages) (230×10^3 indiv. m⁻³) was recorded in June 1997. In the present study, the *Oithona* nauplii densities were similar to those observed by Sawada (1996) in Wakasa Bay.

Worldwide, high nauplii densities (thousands $\times 10^3$ indiv. m⁻³) have been found to occur in estuaries, medium densities ($20\text{--}50 \times 10^3$ indiv. m⁻³) in coastal regions and low densities ($10\text{--}20 \times 10^3$ indiv. m⁻³) in the open oceans (Tanaka 1981). We concluded that the maximum density of *O. similis* nauplii recorded in the present study was very high for a coastal region. Hirakawa et al. (2004) inferred that *O. similis* nauplii significantly contributed to the high overall density of copepod nauplii in Toyama Bay, this species being distributed widely from cold-water areas in the Arctic and Antarctic to temperate areas, where it becomes dominant (Sabatini & Kiørboe 1994, Pane et al. 2004, Hopcroft et al. 2005, Werner 2005). Extensive sampling by Nishida & Marumo (1982) showed the highest densities of *O. similis* adults (3000 indiv. m⁻³) to occur offshore in the Japan Sea. It is likely, therefore, that *O. similis* nauplii are dominant throughout the entire Japan Sea.

In 1997, oscillating changes in chlorophyll-*a* concentrations were observed in the surface layer (0 m depth) over a long time period, from the February to July, and the highest concentration recorded was $5.1 \mu\text{g L}^{-1}$. However, vertical distribution and egg production of *O. similis* have not been reported to be correlated with chlorophyll-*a* concentrations (Maar et al. 2002). On the other hand, the density of *O. sim-*

ilis has been reported to be positively correlated with protozooplankton densities (Nielsen & Sabatini 1996), the former selectively feeding on ciliates in preference to other nano- and micro-plankton components (Castellani et al. 2005). Although we considered that the chlorophyll-*a* concentration did not directly reflect the quantity of food able to be ingested by *O. similis*, the former has been shown to influence the densities of protozooplankton (including ciliates) and bacteria (Iwamoto et al. 1994, Nakamura et al. 1994), implying that these food-web components in turn are influenced by the density of *O. similis* nauplii. *O. similis* was the most important species contributing to the high population density of *Oithona* nauplii in the surface layer of Toyama Bay. We infer that the low surface salinity observed in May and June caused by the intrusion of river water, the high chlorophyll-*a* concentration and the high density of *O. similis* nauplii were linked.

In the present study, we considered that *O. similis* was the most important species contributing to the high-densities of nauplii in spring. *Oithona* nauplii have been shown to be less susceptible to predation by fish larvae than *Paracalanus* nauplii (Funakoshi et al. 1983, Nakata 1990, Uye & Yamaoka 1990, Nakata 1997), the former having a flatter body shape than the latter, making them visually smaller from certain angles (Gliwicz & Boavida 1996) and therefore being less visible to fish larvae. The body height of *O. similis* nauplii is greater than that of other *Oithona* nauplii (results of this study), resulting in a similar body shape to *Paracalanus* nauplii. *Oithona similis* nauplii have also been found to be dominant and an important food source for fish larvae off the coast of Hokkaido (Nakatani et al. 2005). In Toyama Bay, Japanese sardine and anchovy prey mainly on *Oithona* nauplii (Hirakawa & Goto 1996, Hirakawa et al. 1997), which have also recently been found in the gut contents of halfbeak *Hyporhamphus sajori* larvae (Oya et al. 2002). The latter occurred in Toyama Bay from May to early-July (late-Spring) when *O. similis* nauplii were at their maximum density. During this period, larvae and eggs of these fish species were distributed in the upper 50 m. From the results of this study, it is clear that *O. similis* nauplii have a high density population in the upper 50 m depth in late-Spring in Toyama Bay, and have a greater comparative body height morphologically. We suggested that *O. similis* nauplii may be an important food source for fish larvae due to their ecological and morphological characteristics, which ensure high encounter rates with their predators.

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