

Seasonal succession of four *Acartia* copepods (Copepoda, Calanoida) in Okkirai Bay, Sanriku, northern Japan

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Abstract: Seasonal changes in abundance of four neritic *Acartia* species (*A. hudsonica*, *A. omorii*, *A. longiremis* and *A. steueri*), including identifiable copepodid stages, were investigated in the inner reaches of Okkirai Bay, Sanriku, northern Japan, to elucidate their seasonal succession patterns. Samples were collected monthly at intervals from August 2007 to July 2009 by vertical hauls of a NORPAC net of 100 μm mesh aperture. For identification of morphologically allied *A. omorii* and *A. hudsonica*, the dimensional differences between them were statistically analyzed for the stages of C4 to C6. The dominant species were *A. longiremis* in the colder season and *A. steueri* in the warmer season. *A. longiremis* and *A. omorii* appeared from early spring (February or March) to summer with numerical peaks in April. These April peaks were considered to result from immigration from outside the bay with intrusions of Oyashio Current water. *A. steueri* increased during the summer with a peak in September, then decreased until December or January, and disappeared for two or three months from April, when they were probably only present as diapausing eggs. *A. hudsonica* occurred from early spring to mid-summer as in *A. omorii* but with higher abundances in summer than in spring, though the seasonal abundances varied somewhat between years. These results suggest that temperature, determining reproductive activity (and production of diapausing eggs in *A. steueri*), and intrusions of Oyashio water are important environmental factors determining seasonal succession of acartiid copepods in the bay.

Key words: *Acartia*, copepods, Oyashio water, Sanriku, seasonal succession

Introduction

Acartia spp. are typical calanoid copepods that occur in coastal and inlet waters across the world from boreal to tropical regions (Bradford 1976, Mauchline 1998). They are major copepods in these waters and their numbers sometimes reach more than 20,000 ind. m^{-3} (e.g. Onoue et al. 2006). They are important not only as consumers of phytoplankton and microzooplankton (Putland & Iverson 2007) but also as prey for fish larvae (Seki & Shimizu 1997). Thus, acartiid copepods are key organisms to link the primary producers and the secondary consumers in coastal and inlet waters (Putland & Iverson 2007). In temperate waters of Japan, seasonal changes in the geographical distribution and community structure of *Acartia* species are well documented (Ueda 1987, Uye et al. 2000). In the coastal areas of Tohoku and Hokkaido in northern Japan, *A. hudsonica* Pinhey, 1926, *A. omorii* Bradford,

1976, *A. longiremis* (Lilljeborg, 1853) and *A. steueri* Smirnov, 1936 commonly inhabit the inlet waters (Terazaki 1980, Uye 1982, Ueda 1986b, Saito & Taguchi 1996, Seki & Shimizu 1997). However, information on their seasonal succession is still not enough in northern Japan. In the present study, we investigated the seasonal changes in abundances of acartiid copepods, including immature copepodids, for two years in Okkirai Bay, a small inlet on the Rias coast of the Sanriku area, northern Japan, and discussed the relationship between their seasonal occurrence and the environmental factors.

Materials and Methods

Field sampling

Field sampling was carried out almost every month for two years from August 2007 to July 2009 at an inner station of Okkirai Bay, which faces the northwestern Pacific Ocean (Fig. 1). The water depth at the sampling site ranged

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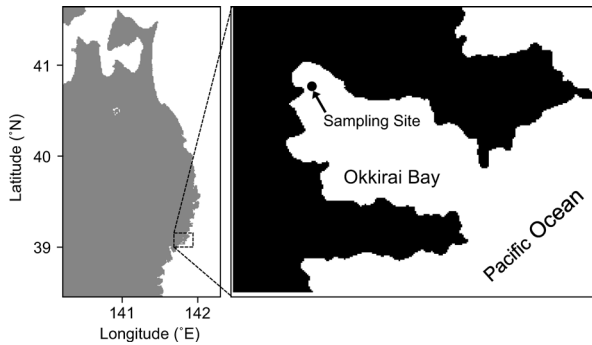


Fig. 1. Sampling site in Okkirai Bay, Sanriku, northern Japan.

from 17 to 19 m depending on the tide. Zooplankton samples were collected by vertical hauls of a NORPAC net (mouth opening 45 cm, mesh size 100 μ m) from the near-bottom to the surface, and were preserved in 5% buffered formalin seawater immediately after sampling. The amount of water filtered was measured with a flow meter (5571-A, Rigosha Co., Ltd., Japan) set at the mouth of the net; the filtered volumes are presented in Table 1. Vertical profiles of temperature, salinity, and chlorophyll *a* concentration were determined for each 0.1 m using a CTD system equipped with a chlorophyll fluorescence sensor (ACL200-PDK, JFE Alec Co., Ltd., Japan).

Developmental stage analysis and species identification

All copepodids and adults of *Acartia* spp. were sorted, under a dissecting microscope from the entire samples, or 1/2 or 1/4 aliquots (Table 1) when too many acartiid copepods were collected. The sorted copepods were then separated into nine groups according to the ontogenetic stages (C1–C6) and sexes (female and male of C4–C6) following Sabatini (1990). Since no morphological characteristics enabling the species to be differentiated could be found in C1, they were not classified into species. In C2 and higher stages, *A. steueri* could be distinguished from other acartiid copepods by the presence of rostral filaments, which were absent in the other three species. As for the other three species, no species-specific morphologies enabling us to distinguish the species from each other were observed in either C2 or C3, and they were counted without species discrimination. *Acartia longiremis* could be identified by having spinules along the posterodorsal margins of the urosomites in C4 and higher stages.

Since acartiid copepods identifiable to species other than the present four species did not occur in our samples, C4 and higher stages without rostral filaments and/or urosomal spinules could be identified as either *A. omorii* or *A. hudsonica*. The two species can be distinguished by the length/width ratio of the genital double somite of adult females (<1.1 for *A. omorii* and \geq 1.1 for *A. hudsonica*) and by the number of convex surfaces in the inner lobe of the third segment of the fifth right leg of adult males (2 for *A. omorii* and 1 for *A. hudsonica*) (Bradford 1976, Ueda

Table 1. List of sampling date, volume of the water filtered, and aliquot of sample examined.

Year	Date	Volume of the water filtered (m ³)	Aliquot examined
2007	30 Aug	0.82	1/1
	19 Sep	2.49	1/4
	17 Oct	2.03	1/4
	16 Nov	2.10	1/1
	20 Dec	2.42	1/1
2008	15 Jan	2.10	1/1
	19 Feb	2.03	1/1
	25 Mar	2.23	1/1
	17 Apr	1.37	1/2
	15 May	1.82	1/1
	20 Jun	1.16	1/2
	22 Jul	1.44	1/1
	18 Aug	4.44	1/2
	16 Sep	2.30	1/4
	17 Oct	2.51	1/1
	18 Nov	2.61	1/2
15 Dec	2.30	1/1	
2009	28 Jan	1.84	1/1
	12 Feb	2.09	1/2
	13 Mar	2.34	1/1
	17 Apr	0.81	1/4
	23 May	1.87	1/1
	13 Jun	0.96	1/1
	16 Jul	1.85	1/1

1986b). However, these diagnostic characters cannot be used for identification of immature copepods and are sometimes difficult to observe without dissection, even in adult copepods. Accordingly we classified them into the two species by prosome length, which is known to be larger in *A. omorii* than in *A. hudsonica* (Ueda 1986b). To test the criteria of length for separating the species, all of these C4–C6 individuals were photographed using a digital camera equipped on a microscope, and their prosome lengths were measured to the nearest 0.01 mm using ImageJ[®] software (NIH, USA). The results showed that the prosome length distribution was apparently bimodal in every stage and sex (Fig. 2) with boundaries at 0.85 mm for C6 females and 0.79 mm for C6 males. Three hundred and twenty seven individuals of C6 females (150 for the larger mode and 177 for the smaller mode) and 129 individuals of C6 males (76 for the larger mode and 53 for the smaller mode) were examined for the diagnostic characters used in the identification of each species. The individual numbers of *A. omorii* and *A. hudsonica* were 145 and 5 for the larger mode, and 8 and 169 for the smaller mode in C6 females. For C6 males, larger and small modes were determined as *A. omorii* and *A. hudsonica* without exception. To determine the boundary between the species in both sexes, a linear discriminant (Goebel et al. 2007) calculated with the Mulcel[®] software program (OMS Publishing Inc.) re-

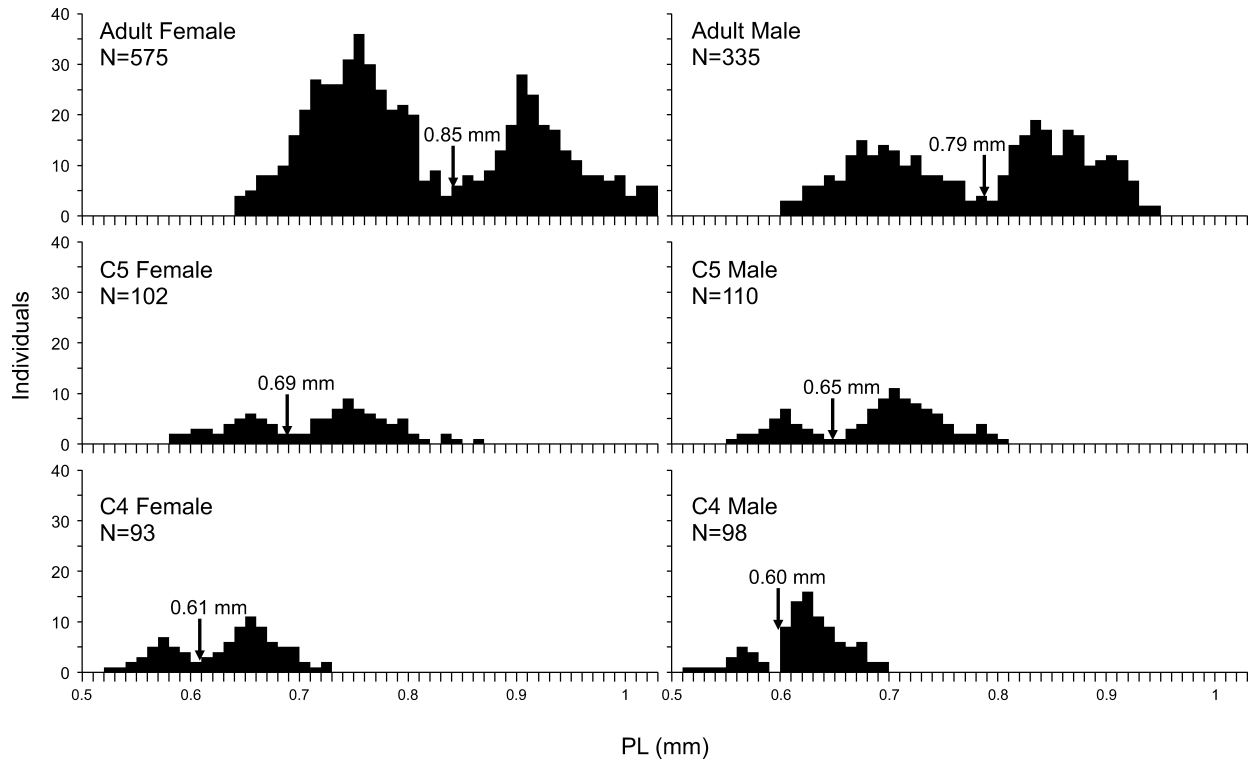


Fig. 2. Prosome length distribution of all C4–C6 (adult) copepods of *Acartia omorii* and *A. hudsonica* collected from Okkirai Bay from April 2007 to July 2009. Arrows indicate the boundary lengths calculated by the linear discriminant function analysis.

vealed that *A. omorii* and *A. hudsonica* could be classified with 96.7 and 99.4% probability, respectively, with a boundary at 0.85 mm for C6 females, and both at 100% probability at 0.79 mm for C6 males. Although the size distributions of the two species overlapped each other in some cases, the number of individuals beyond the boundary between the modes was considered negligible compared with the total number individuals in each mode.

Results

Water temperature increased from March to September with the minimum temperature of 4.4°C in March 2008 and the maximum of 20.3°C in September 2007 (Fig. 3). The annual minimum temperature was recorded in March in both 2008 and 2009, but was much lower in 2008 (4.4°C) than in 2009 (6.2°C). Salinity varied between 33.2 in March and April 2008 to 34.2 in December 2007. High salinities (>33.7) were observed from October 2007 to February 2008 and from October 2008 to March 2009, and low salinities (<33.5) occurred from March 2008 to May 2008 and in September 2008 and June 2009. Chlorophyll *a* concentration exhibited annual peaks in March 2008 (2.13 $\mu\text{g L}^{-1}$) and April 2009 (1.81 $\mu\text{g L}^{-1}$). In 2008, the concentration decreased to the season's lowest (0.63 $\mu\text{g L}^{-1}$) in January 2009, partially recovering in June and October.

Seasonal variations in the abundance of the four *Acartia*

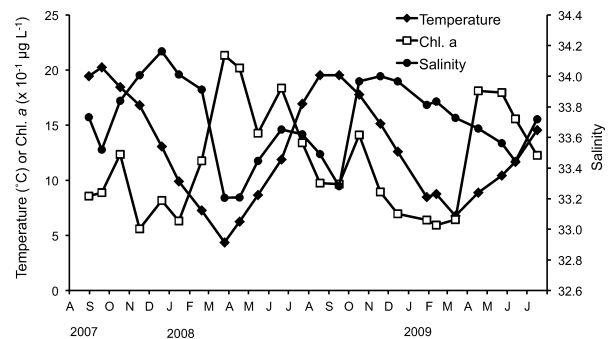


Fig. 3. Seasonal changes in temperature, salinity, and chlorophyll *a* concentration in Okkirai Bay. The values are vertical means from 0 to 17 m depth.

species are shown in Fig. 4, in which the species-specific data are presented by compiling the stages for which the species were distinguished, i.e. C2–C6 for *A. steueri* and C4–C6 for the other three species. Seasonal abundances of unidentified C1 and C2–C3 of the species other than *A. steueri* are also presented.

Acartia steueri C2–C6 was abundant (>200 ind. m^{-3}) from August to November 2007 and from September to October 2008 with prominent annual peaks in September 2007 and 2008 (6,055 and 1,491 ind. m^{-3} , respectively), while it was less abundant (<100 ind. m^{-3}) from December

to June or July and was not detected from April to June 2008 or from April to May 2009 (Fig. 4a). Since the first month (August 2007) of this study, this species was extremely abundant ($>1,000$ ind. m^{-3}) until October 2007 and was the only species in the *Acartia* community for six months until *A. omorii* appeared in February 2008.

Acartia longiremis C4–C6 was absent from August 2007 to February 2008, but suddenly appeared in March 2008 with a relatively high abundance (204 ind. m^{-3}) and soon reached the peak abundance (1,317 ind. m^{-3}) in April (Fig. 4b). Then it greatly decreased in number to 12 ind. m^{-3} in June, and completely disappeared from August 2008 to January 2009 with the exception of a low abundance (16 ind. m^{-3}) in September 2008. In 2009, the species began its seasonal occurrence in February and exhibited a peak (2,602 ind. m^{-3}) in April after it decreased once in March. The peaks in both years were coincident with the annual maxima of chlorophyll *a* concentrations and were one month later than the annual lowest temperatures.

The seasonal pattern of *A. omorii* C4–C6 was similar to that of *A. longiremis* with high abundances during the springs and low abundances during the summers and falls (Fig. 4c). However, the annual peak abundances of both years (283 ind. m^{-3} in April 2008 and 229 ind. m^{-3} in February 2009) were much less than those of *A. longiremis*, and the period when the species was completely absent in 2008 was shorter (two months from October to November) than in *A. longiremis* (four months from October to January).

Acartia hudsonica C4–C6 occurred from March to September 2008 and from February 2009 to the end of the study period in July 2009 with the occurrence of a small number in December 2008 (Fig. 4d). This seasonal occurrence pattern was similar to those of *A. longiremis* and *A. omorii*, but the annual maximum abundances (104 ind. m^{-3} in September 2008 and 140 ind. m^{-3} in June 2009) were not in sharp peaks and occurred during the warmer months (September 2008 and June 2009) in contrast to the colder months in *A. longiremis* and *A. omorii*. The abundances during mid-summer (August and September) differed greatly between 2007 and 2008; the species was absent in 2007 while it reached its annual maximum in 2008.

Unidentified C1 copepods showed prominent peaks twice a year, i.e. one in spring (April) and the other in late summer (September 2007 and October 2008) (Fig. 4e). Unidentified C2 and C3 consisting of *A. longiremis*, *A. omorii*, and/or *A. hudsonica* exhibited clear seasonality with sudden peaks in April in both 2008 and 2009 (780 and 1,072 ind. m^{-3} , respectively) and a secondary peak in June 2008 (280 ind. m^{-3}). They were completely or nearly absent from August 2007 to March 2008, and exhibited a small increase in December 2008. This seasonal pattern of C2–C3 was most similar to that of *A. longiremis*.

Discussion

The present study showed clear seasonal succession of *Acartia* species in Okkirai Bay. *Acartia longiremis* and *A. omorii* were abundant during the three to six colder months from February or March with the highest annual abundance in February to April. In contrast, *A. steueri* was more abundant during warmer months than in colder months, and exhibited extremely high abundances from August to October. The abundance of *A. hudsonica* was also higher during warmer months than in colder months.

Occurrences of *A. longiremis* have been reported from cold waters in the northern Pacific and northern Atlantic Oceans and at their margins, e.g. western Greenland (Madsen et al. 2008), the Chukchi Sea (Hopcroft et al. 2010), Faroe Islands (Debes et al. 2008), southwestern Alaska (Park et al. 2004), an estuary in Maine, USA (Lee & McAlice 1979), and the Oregon coast (Keister & Peterson 2003). Lee & McAlice (1979) reported that *A. longiremis* disappeared in August, when water temperature reached the annual maximum ($>15^{\circ}\text{C}$), and reappeared soon in September. In Okkirai Bay, the C4–C6 stages of *A. longiremis* began their seasonal occurrence by a sudden increase in February or March with subsequent prominent peaks in April, and disappeared from the mid or late summer until the following spring. If they were reproducing within the bay, abundance peaks of the unidentifiable C2–C3 copepodids should have appeared before the first increase of the C4–C6 stages. However, the present study did not show such a peak for C2–C3 in 2008, that is, the C4–C6 stages began to increase in March, whereas the C2–C3 stages were completely or almost absent until March. In 2009, the C2–C3 population exhibited a similar change from January to April to that of C4–C6 but a small increase in December 2008, two months before the first increase of C4–C6. The C2–C3 population in December 2008 is highly unlikely to have grown into C4–C6 by February 2009, because two months is too long a period for development from C2–C3 to C4–C6. Considering that the 2008 population of *A. longiremis* C4–C6 suddenly appeared at high abundances in March without a preceding peak in abundances for the younger stages, it is likely that they were not reproducing in the bay but were introduced through lateral advection from outside the bay. The most plausible explanation for the immigration is with intrusion of Oyashio Current water. Takasugi & Yasuda (1994) demonstrated that Oyashio Current water appeared along the Sanriku coast most frequently from March to April and least from November to December. These months coincide precisely with those of the annual highest abundances and absence of *A. longiremis* C4–C6 in Okkirai Bay, respectively. Despite the location of the sampling station in the innermost part of the bay, where the land runoff and air temperature generally have strong effects on *in situ* conditions, the low temperature (4.4°C) and low salinity (33.2) observed at the station in March 2008, when *A. longiremis*

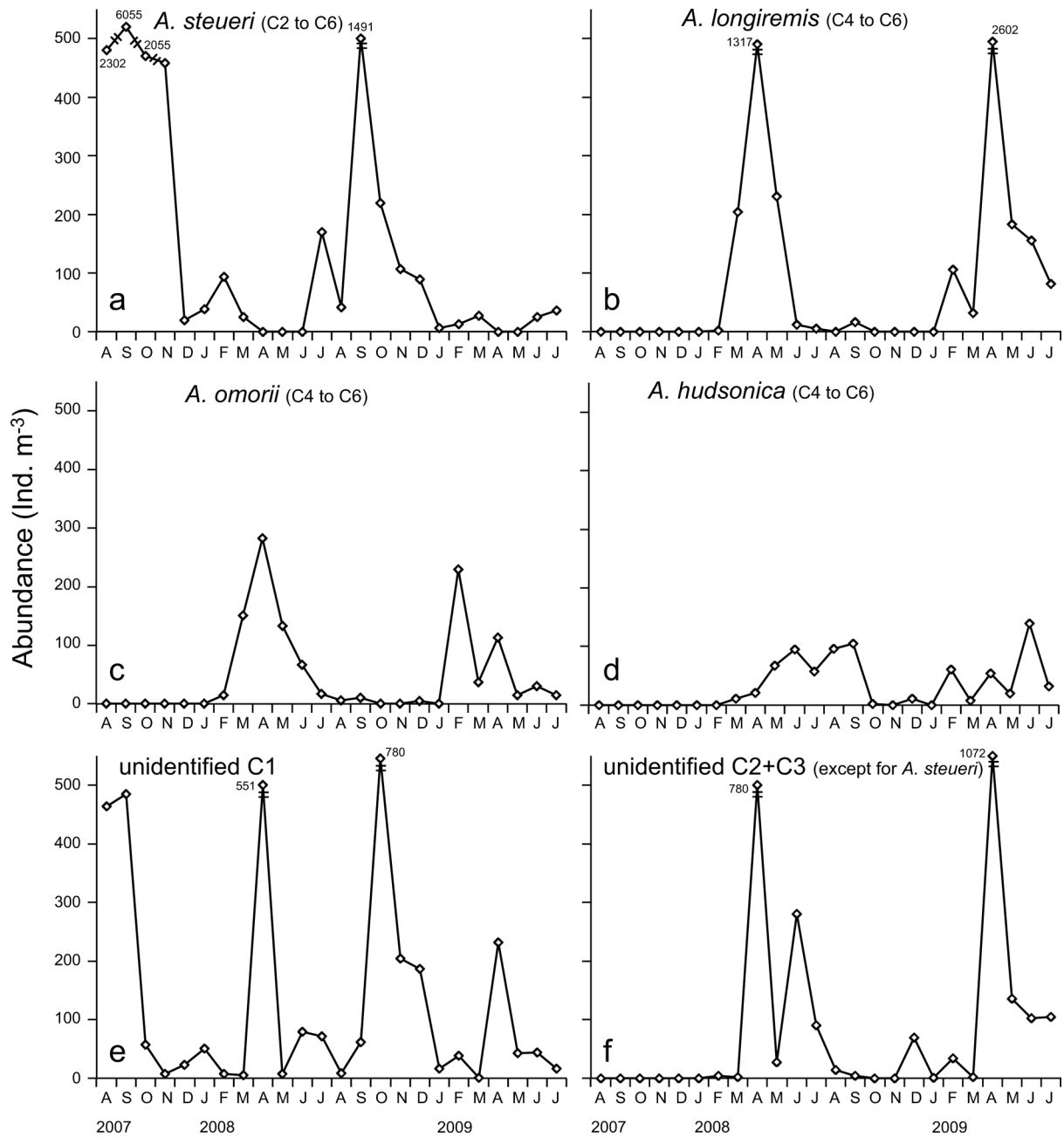


Fig. 4. Seasonal changes in abundance of *Acartia steueri* (a), *A. longiremis* (b), *A. omorii* (c), and *A. hudsonica* (d), with those of unidentified C1 (e) and C2–C3 (f), in Okkirai Bay.

C4–C6 suddenly increased, were very similar to those of surface waters of the Oyashio Current reported in the same month (Japan Oceanographic Data Center 2008). These observations suggest that in March and April Oyashio Current water had extensively intruded into the bay, bringing with it the *A. longiremis* population. Lee & McAlice (1979) also suggested that immigration from coastal waters was necessary for the maintenance of the *A. longiremis* population in an estuary in Maine.

In Okkirai Bay, the cold-water copepod *Pseudocalanus* spp. appears with intrusions of Oyashio water, and disap-

pears when the water temperature rises above 15°C (Yamada, unpublished data). Because the highest tolerable temperature for *Pseudocalanus* spp. has been estimated to be 12–15°C (Yamaguchi & Shiga 1997), these copepods probably cannot reproduce in Okkirai Bay when the water temperature rises beyond 15°C in July (see Fig. 3). In contrast to *Pseudocalanus* spp., *A. longiremis* occurred even in September 2008 when the water temperature was 19.9°C, indicating that this copepod is tolerable of higher temperatures than *Pseudocalanus* spp. although it cannot reproduce for year-round maintenance of populations in

the bay.

The abundance of *A. steueri* C2–C6 peaked in September when the water temperature reached its maximum (around 20°C), and was low from December or January to June or July. Kang & Kang (2005) and Onoue et al. (2006) reported that *A. steueri* was most abundant at around 20°C from July to August in Ilkwang Bay on the southeastern coast of Korea and from May to June in Sagami Bay, central Japan, respectively. This suggests that 20°C is the optimum temperature for their growth and reproduction. The abundances of *A. steueri* in these bays were very low when the water temperatures reached the maxima (26.8 and 25.4°C, respectively). Onoue et al. (2006) revealed that adult copepods of *A. steueri* in Sagami Bay increased in numbers with water temperature from February to June and produced diapausing eggs from February to August. Since most diapausing eggs were produced in the early summer with the maximum rate in June, they considered that *A. steueri* produced diapausing eggs to survive the high temperature season. In contrast, the *A. steueri* C2–C6 population in Okkirai Bay completely disappeared from April to May or June, when the water temperature was below 11°C. Our preliminary laboratory rearing of *A. steueri* collected from Okkirai Bay indicated that they produced diapausing eggs at the low temperatures prevalent in December (below 13°C). These results suggest that low temperatures are not favorable for this copepod for growth and reproduction and that they spend low-temperature periods as diapausing eggs.

Compared to *Acartia longiremis* and *A. steueri*, the peak abundances of *A. omorii* and *A. hudsonica* were low in Okkirai Bay. According to Ueda (1987), *A. omorii* and *A. hudsonica* in Maizuru Bay, western Japan, exhibited almost synchronous seasonal changes, but were more or less segregated in their regional distributions; *A. omorii* was located relatively more seaward than *A. hudsonica*. The seasonal occurrences of these species in Okkirai Bay were also similar to each other, but differed in the timing of their peak abundances, i.e. in the colder months (April 2008 and February 2009) for *A. omorii* and the warmer months (September 2008 and June 2009) for *A. hudsonica* (Fig 4c,d). A possible reason for this difference is species-specific seasonal variation in their regional distributions, which may result in different seasonal variations at a single sampling station.

The temporal differences in their peak abundances may be explained by the differences in their modes of recruitment. Ueda (1991) classified planktonic copepods in embayments into four ecological categories based on their distributions within a bay. In his classification, *A. hudsonica* is referred to as an “eutrophic neritic” species, which is more abundant in strongly enclosed bays or in the inner half of bays, while *A. omorii* is a “mesotrophic neritic”, species which is more abundant in open inlets or in the outer half of bays. Ueda (1986a) noted that *A. omorii* was widely distributed around Japan, being reported from

strongly enclosed bays to open oceanic waters such as 300 km off the Pacific coast of Honshu, and was the exclusively dominant copepod in samples collected from oceanic waters off Hokkaido and Honshu. Such distributional characteristics of *A. omorii* suggest that immigration from outside Okkirai Bay with intrusion of Oyashio Current water may have resulted in its high abundance in April, as suggested for the changes in seasonal abundance of *A. longiremis*. As for the “eutrophic neritic” copepod *A. hudsonica*, recruitment from outside the bay is unlikely. Instead, the seasonal abundance of this species at the sampling site is considered to result from recruitment, mortality, and regional distribution of the population within the bay. The seasonal abundance of this species differed greatly between 2007 and 2009, i.e. absent in August and September 2007 whereas it was abundant in the corresponding months of 2008. This may be due to differences in the regional distribution of their populations in the bay between the two years.

The seasonal succession of *Acartia* copepods in Okkirai Bay can be summarized as follows. The dominant *Acartia* species were *A. longiremis* in the colder season and *A. steueri* in the warmer season, followed by *A. omorii* or *A. hudsonica*. *Acartia longiremis* and *A. omorii* increased in numbers sharply during the colder months (February to April), probably by lateral advection of immigrants due to intrusion of the Oyashio water, and then decreased with increasing water temperature. *Acartia steueri* occurred almost throughout the year except for the coldest season (March to May) when the copepod is considered to spend a phase as a diapausing egg. *Acartia hudsonica* exhibited a similar seasonal occurrence to *A. omorii*, but it was more abundant during the warmer months. Water temperature and intrusion of the Oyashio Current water are thus major environmental factors determining the seasonal successions of *Acartia* species in Okkirai Bay.

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