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Horizontal and vertical distribution of the appendicularian community and population structure in the Bering and Chukchi Seas during the summer of 2007

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Abstract

The horizontal and vertical distributions of the appendicularian community and the population structure of dominant species in the southeastern and northern Bering Sea shelf and the Chukchi Sea were studied during the summer of 2007. The feeding impact was also calculated and the results were compared with those found in 1983–1996. *Oikopleura vanhoeffeni* was the dominant species in this region and stage I specimens with small tail lengths ($TL < 2$ mm) dominated the population. The mean daily clearance rate was $16.4 \text{ ml ind.}^{-1} \text{ day}^{-1}$, which corresponded to a population daily clearance rate in the water column of $0.003\text{--}25.5\% \text{ day}^{-1}$. The dominance of stage I and specimens with a small TL suggest that the main spawning of *O. vanhoeffeni* occurred before summer in 2007. Large-sized individuals ($TL > 14$ mm) dominated in 1983–1996 and, considering the generation length of *O. vanhoeffeni* (ca. one year), the main spawning of *O. vanhoeffeni* would not have occurred before summer from 1983–1996. In 2007, *O. vanhoeffeni* are considered to have spawned earlier because newly recruited small individuals are more abundant. Recently, the timing of the sea ice retreat is becoming earlier in this region, and the fastest ice-free timing was reported in 2007. Earlier sea ice retreat may induce an altered timing of primary production and other biological phenology. Thus, the early spawning of *O. vanhoeffeni* in 2007 may result in the dominance of smaller specimens observed in that year.

Key words : Appendicularia, Arctic, Larvacea, *Oikopleura vanhoeffeni*, population structure

Introduction

Appendicularia are holozooplankton that are distributed widely through the world's oceans. Appendicularia form an elaborate “house” of mucus to collect small food particles (pico- and nano-sized plankton and colloids) effectively (Flood et al., 1992 ; Urban et al., 1992 ; Acuña and Deibel, 1996). Houses are abandoned frequently when clogging occurs. Along the coast of Newfoundland, *Oikopleura vanhoeffeni* create 1–6 houses per day when thermal conditions are between -1.6 to 4.5°C (Gorsky and Fenaux, 1998). Discarded houses provide a habitat for copepods, krill, and polychaete larvae, which feed on house trapped-flagellates, coccoliths, silicoflagellates and diatoms (Alldredge, 1972 ; Alldredge, 1976a). The discarded houses and fecal pellets also contribute substantially to vertical material transport (Alldredge, 1976b).

In the western Arctic Ocean, Appendicularia are abundant and form a biological hot spot. They are frequently observed in the gut contents of Arctic cod (Nakano et al., 2016). The reduction of sea ice coverage during the summer

is an increasingly common occurrence in the Arctic Ocean (cf. Perovich, 2011). This reduction of sea ice coverage is known to affect copepod communities (Matsuno et al., 2011) and the horizontal distribution of sea birds (Gall et al., 2017). However, little information is available on the effects of sea-ice reduction on Appendicularia in this area.

In this study, we assessed the horizontal and vertical distribution of the appendicularian community and measured the population structure and body size of the dominant species, *O. vanhoeffeni*, in the southeastern and northern Bering Sea shelf and Chukchi Sea from July to August 2007. Appendicularian data were compared with those obtained from the same region during the same period in the previous nine years (1983, 1986 and 1990–1996) (Shiga, 1993a, 1993b ; Shiga et al., 1998) and yearly changes were discussed. To evaluate the impacts of appendicularians in marine ecosystems, the feeding clearance rate of *O. vanhoeffeni* was also calculated by applying a reported algorithm.

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Materials and methods

Field sampling

Vertically stratified hauls from the sea surface to the thermocline and from the thermocline to the sea bottom were made by closing nets (mouth diameter 60 cm, mesh size 100 μm) at three stations in the southeastern Bering Sea shelf (B01, B09 and B25), two stations in the northern Bering Sea shelf (B28 and B40) and three stations in the Chukchi Sea (C14, C24 and C28) from 24 July to 11 August 2007 (Fig. 1). Bottom and thermocline depths were 26–135 m and 18–20 m, respectively. The volume of water filtered through the net was measured by reading a flow-meter mounted on a mouth ring. After recovery, zooplankton samples were immediately preserved in 5% buffered formalin seawater. At each station, temperature, salinity and σ_t were measured by CTD (Sea-Bird Electronics). Water samples (300 ml) were collected from five to eight depths at each station, then filtered through a GF/F filter. Chlorophyll *a* (Chl. *a*) was measured by fluorometer (Turner Designs) after extraction with DMF (Suzuki and Ishimaru, 1990).

Sample analysis

In the land laboratory, zooplankton samples were split to between 1/10 and 1/160 with a large bore pipette, depending upon the appendicularian abundance within the subsamples. Appendicularians (ca. 200 individuals) were sorted and enumerated from these subsamples. The identification of Appendicularia followed Shiga (1993a) and Choe and Deibel (2008). For the dominant species, *Oikopleura vanhoeffeni*, six maturation stages were identified based on the external characteristics of the gonad (Shiga, 1976).

Stage I : Gonad is absent.

Stage II : A small and thin gonad appears as a testis.

Stage III : The ovary is distinguished from the testis, and the width of the gonad is always less than the width of the trunk.

Stage IV : The width of the gonad is nearly equal to the width of the trunk.

Stage V : The width of the developed gonad is greater than the width of the trunk. This stage is regarded as an adult.

Spent : The body wall at the posterior trunk is ruptured after the release of eggs and sperm.

The tail length (TL : mm) of *O. vanhoeffeni* was measured with a precision of 12.5–125 μm using an ocular micrometer under a stereomicroscope. The total clearance rate (TCR : $\text{ml ind.}^{-1} \text{ day}^{-1}$) of *O. vanhoeffeni* was calculated by using the following equation (Knoechel and Steel-Flynn, 1989) :

$$\text{TCR} = 22.608 \text{ TL}^{1.578}$$

By multiplying the TCR data with the population density (ind. m^{-3}), the population clearance rate (PCR : $\text{L m}^{-3} \text{ day}^{-1}$) was calculated. From this PCR, the percentage daily water column clearance rate (% day^{-1}) was also calculated.

Results

Hydrography

In the southeastern Bering Sea shelf (stations B01, B09 and B25), temperature and salinity ranged from 2.1 to 9.3°C and from 31.1 to 32.9, respectively (Fig. 2). The thermocline was weak for these stations. Particularly for the shallowest station (B25), density was uniform throughout the water column. Peak Chl. *a* concentration was 1.25 to 3.99 mg m^{-3} . Peaks were observed at 0 m at B01, 30 m at B09 and 20 m at B25.

In the northern Bering Sea shelf (stations B28 and B40), temperature and salinity ranged between -1.7 and 10.9°C and 30.6 and 32.8, respectively. A clear thermocline and halo-

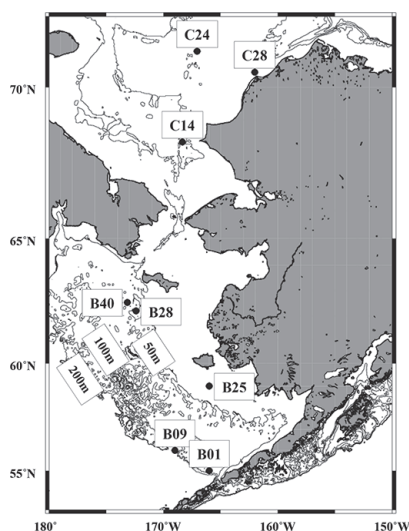


Fig. 1. Location of sampling stations in the southeastern Bering Sea shelf, northern Bering Sea shelf, and the Chukchi Sea during 24 July–11 August 2007.

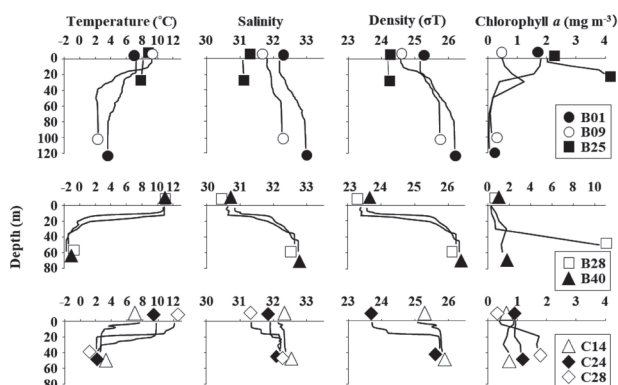


Fig. 2. Vertical profiles of temperature, salinity, density, and chlorophyll *a* in the southeastern Bering Sea (upper), northern Bering Sea (middle), and Chukchi Sea (lower) during 24 July–11 August 2007.

cline were observed at approximately 18 m for both stations. For the upper pycnocline, temperature, salinity and σ_T were 10°C, <31 and 23.5, respectively, while cold saline-dense water (−1.5°C, 32.5 and >26) was observed for the lower layer. Peak Chl. *a* (1.7–10.5 mg m^{−3}) was observed below the pycnocline for both stations. An extremely high Chl. *a* concentration value (10.5 mg m^{−3}) was observed for the near bottom (50 m) at station B28.

In the Chukchi Sea (stations C14, C24 and C28), temperature and salinity ranged from 2.1 to 12.2°C and from 31.3 to 32.4, respectively. Compared to the other region, the salinity range was small (Fig. 2). For the northern C24 and C28, the thermocline was observed approximately 20 m. Peak Chl. *a* value was 0.9 to 1.8 mg m^{−3}. A near-bottom peak was seen for station C28, while few vertical changes were observed for Chl. *a* in the remaining stations.

Community structure

Through this study, three appendicularian species belonging to two genera (*Oikopleura vanhoeffeni*, *Oikopleura labradoriensis* and *Fritillaria borealis*) were observed. Appendicularian abundance ranged from 0 to 1,707.05 ind. m^{−3} and was low in the southeastern Bering Sea shelf and high in the south of St. Lawrence Island and the Chukchi Sea (Fig. 3). At the lower layer of the shallowest station (B25), no appendicularians were observed. Population density was high in the upper layer for most of the stations, but a high density at the lower layer was observed at station C14. The species composition showed a clear regional pattern; only *F. borealis* occurred at station B01 in the southeastern Bering Sea shelf (Fig. 3), while in the northern Bering Sea shelf, *O. vanhoeffeni* predominated. In the Chukchi Sea, *O. vanhoeffeni* dominated while *F. borealis* accounted for approximately 20% of the appendicularian population. It was noted that *O. labradoriensis* only occurred at the lower layer of station B09, the deepest offshore station in the southeastern Bering Sea shelf.

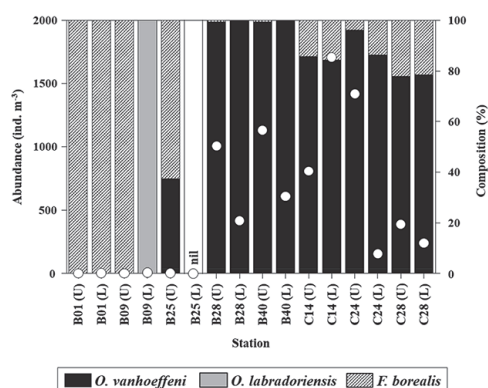


Fig. 3. Geographical and vertical changes in abundance and species composition of appendicularians in the southeastern-northern Bering Sea and the Chukchi Sea during 24 July–11 August 2007. (U) : upper layer, (L) : lower layer.

Population structure

The population structure of the dominant appendicularian, *Oikopleura vanhoeffeni*, was dominated by stage I at all stations (Fig. 4A). Mature individuals (stage V) were only observed in both the upper and lower layer of station C14. Though no developmental stage identification was

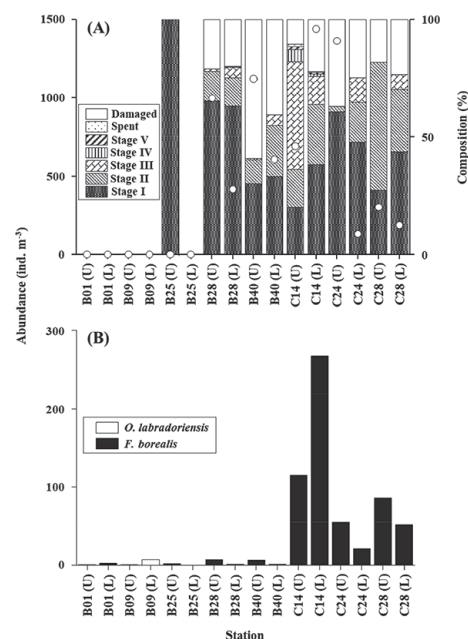


Fig. 4. Geographical and vertical changes in abundance and developmental stage composition of *O. vanhoeffeni* (A) and abundance of *O. labradoriensis* and *F. borealis* (B) in the southeastern-northern Bering Sea and the Chukchi Sea during 24 July–11 August 2007. Note that stage identification was only made for *O. vanhoeffeni*. (U) : upper layer, (L) : lower layer.

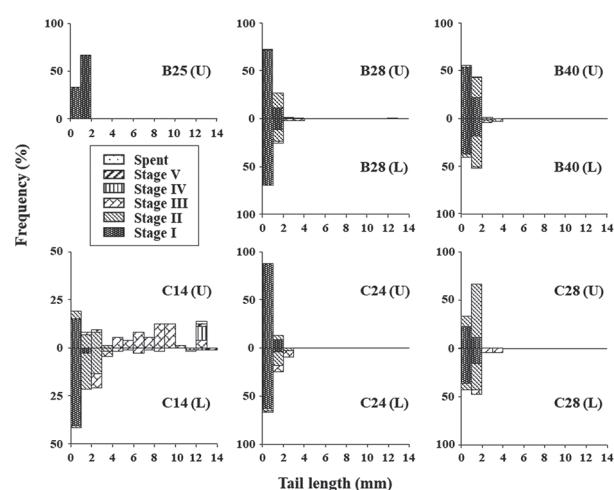


Fig. 5. Geographical and vertical changes in tail length and developmental stage of *O. vanhoeffeni* in the southeastern-northern Bering Sea and the Chukchi Sea during 24 July–11 August 2007. (U) : upper layer, (L) : lower layer.

Table 1. Density, individual clearance rates, population clearance rates, and percentage of daily water column clearance of *Oikopleura vanhoeffeni* at each station in the Bering and Chukchi Seas during July–August 2007. The clearance rate was calculated from tail length with an equation by Knoechel and Steel-Flynn (1989).

Station	Density (ind. m ⁻³)	Individual clearance rate (ml ind. ⁻¹ day ⁻¹)	Population clearance rate (L m ⁻³ day ⁻¹)	Water column (% day ⁻¹)
B25 (U)	1.0	28.5	0.029	0.003
B25 (L)	0	0	0	0
B28 (U)	997.8	20.2	20.1	2.01
B28 (L)	415.4	24.7	10.2	1.02
B40 (U)	1,122.2	23.0	25.8	2.58
B40 (L)	606.6	31.3	19.0	1.90
C14 (U)	691.2	368.5	254.7	25.5
C14 (L)	1,439.6	82.0	118.1	11.8
C24 (U)	1,363.0	16.4	22.4	2.23
C24 (L)	132.6	22.5	3.00	0.30
C28 (U)	302.4	26.2	7.93	0.79
C28 (L)	187.7	31.3	5.88	0.59
Mean	604.9	41.6	25.2	2.52

made for the other species, clear regional distribution patterns were detected. Thus, *Oikopleura labradoriensis* only occurred in the lower layer of B09 in the southeastern Bering Sea shelf, and *Fritillaria borealis* was abundant in the Chukchi Sea (Fig. 4B).

Body size

The body size (TL) of *Oikopleura vanhoeffeni* increased with developmental stage. Thus, the TL of stage I, II, III, IV and V were 0.33–2.75 mm, 0.69–3.76 mm, 0.94–12.6 mm, 11.8–14.5 mm and 12.6–13.3 mm, respectively (Fig. 5). For most of the stations, stages I and II (TL < 2 mm) were more prevalent, while large-sized individuals in stages III, IV and V (TL > 14 mm) occurred at station C14. Though no differences in TL were detected between the upper and lower layers for most of the stations, significantly larger specimens occurred in the upper layer of station C14 ($p < 0.01$, U -test).

Feeding impact

The TCR, estimated from the TL of *Oikopleura vanhoeffeni*, was 16.4–368.5 ml ind.⁻¹ day⁻¹ (Table 1). The PCR, calculated by multiplying the TCR by population densities, was 0.03–254 L m⁻³ day⁻¹. This PCR corresponds to daily water column clearance rates of 0.003–25.5% day⁻¹ (mean : 2.52% day⁻¹).

Discussion

Community structure

In the present study, appendicularian abundance was low in the southeastern Bering Sea shelf but high in the northern Bering Sea shelf and the Chukchi Sea (Fig. 3). *Oikopleura*

vanhoeffeni, the dominant species in this study, is reported to be a neritic species and their occurrence around St. Lawrence Island was reported in the northern shelf of the Bering Sea (Shiga, 1993a). On the other hand, *Oikopleura labradoriensis* is known to be abundant offshore of the Bering Sea, and with a mean density of 11.1 ind. m⁻³, it is known to be the most common appendicularian in that region (Shiga, 1982). Two dominant species in this study, *O. vanhoeffeni* and *Fritillaria borealis*, are reported to be indicator species in the Arctic region (Fenaux et al., 1998). These two species occurred in the Canada Basin (Hopcroft et al., 2005). *Oikopleura vanhoeffeni* is known to be abundant in Jones Sound and Kane Basin, which connect the Arctic Ocean and Baffin Bay (Longhurst et al., 1984).

Appendicularian density observed in this study was between 0.32 and 1,707.05 ind. m⁻³. In the Bering Sea shelf, the occurrence frequency of *Oikopleura* spp. is reported to be 30% with a mean density of 0.3 ind. m⁻³ (Shiga, 1982). A low reported abundance of appendicularians in the southeastern Bering Sea shelf is confirmed by this study. Based on a 150 µm mesh net, the abundances of *O. vanhoeffeni* and *F. borealis* in the northeastern Chukchi Sea are reported to be 2–139 ind. m⁻³ and 898–3,809 ind. m⁻³, respectively (Questel et al., 2013). The abundances along lines between Alaska and Russia in the Chukchi Sea and Herald Valley are reported to be 256 ind. m⁻³ (*O. vanhoeffeni*) and 85 ind. m⁻³ (*F. borealis*) (Hopcroft et al., 2010). The abundance of *O. vanhoeffeni* south of St. Lawrence Island during the summer of 1986 is reported to be 61–82 ind. m⁻³ (Shiga, 1993a), and the abundances from 1990–1996 are reported to be 1–143 ind. m⁻³ (Shiga et al., 1998). In the present study, appendicularian abundances at stations around St. Lawrence Island (B28 and

B40) and the Chukchi Sea (C14) in 2007 were 153–1,707 ind. m^{-3} (Fig. 3). These facts suggest that the appendicularian abundance in 2007 is high relative to the reported values.

For most of the stations, appendicularian abundance was higher in the upper layer than the lower layer. In this study, the development of the pycnocline was most pronounced south of St. Lawrence Island; both thermoclines and haloclines developed approximately 18 m and Chl. *a* peaked below the pycnocline (Fig. 2). Thus, in terms of food availability, the upper layer, where a high appendicularian density occurred, seems to be lacking. Shiga (1993b) also reported a 3.2–93.2 times higher density of appendicularians in the upper layer than in the lower layer where a strong pycnocline formed at a 20 m depth, south of St. Lawrence Island. A high appendicularian abundance at the upper layer where a strong pycnocline developed is also reported in this study. The one exception to this pattern, where a higher density occurred in the lower layer at station C14 (Fig. 4A), could be related to the weak pycnocline at this station (Fig. 2).

Population structure

For most of the stations, the population structure of *Oikopleura vanhoeffeni* was dominated by stage I. Adults (stage V) of *O. vanhoeffeni* only occurred at station C14 in the Chukchi Sea (Fig. 4A). In the appendicularian population, the dominance of young juveniles (stage I and II) without adults is typical because spawning finished just before the sampling period (Shiga, 1982). Since the egg spawning of appendicularians occurs via rupturing of the body wall at the posterior trunk, spent individuals die off within a day (Paffenhöfer, 1976). Thus, within the field samples, adult individuals would occur for only a short period. In the present study, the dominance of *O. vanhoeffeni* in stages I and II for most of the stations (Fig. 4A) indicates that a large spawning of this species likely occurred before the sampling period. The spawning season of *O. vanhoeffeni* is reported to be late spring to summer in the Bering Sea (Shiga, 1993b), and starting from mid-February to mid-April and ending mid-April to mid-June in Conception Bay, Newfoundland in the western North Atlantic (Choe and Deibel, 2011).

Shiga (1993b) reported that the juveniles distributed in the upper pycnocline were shallower than the adults distributed at the lower pycnocline in the south of St. Lawrence Island. Since appendicularian eggs have less buoyancy, spawning of *O. vanhoeffeni* may occur near the surface layer, and pre-spawning adults may inhabit a deeper layer below the pycnocline in this region with an optimum temperature and sufficient phytoplankton food (Shiga 1993b). In the present study, adult *O. vanhoeffeni* did not even occur in the lower pycnocline layer for most of the stations (Fig. 5). These facts suggest that adults at lower layers also died off before the samplings in 2007. Adults only occurred at station C14 in the Chukchi Sea, and spent individuals were also observed

in both upper and lower layers at this station (Fig. 5). As mentioned before, spawned appendicularians may die off within a day, thus the occurrence of spent individuals is expected to be limited. The data suggest that spawning and reproduction of *O. vanhoeffeni* may have occurred during the study period in 2007 only at station C14. The main spawning events might have already finished before samplings were conducted at the other stations in 2007.

It is notable that *Oikopleura labradoriensis* only occurred in the lower layer of station B09 (Figs. 3, 4B). *O. labradoriensis* is known to be adapted to cold water, and their vertical distribution becomes deeper as surface warming occurs during spring and summer in Funka Bay, the coast of Hokkaido (Shiga, 1985). Within the stations in the southeastern Bering Sea, the water temperature of the lower layer of station B09 was the lowest (Fig. 2). This is a possible explanation for why the occurrence of *O. labradoriensis* was limited to the lower layer at this station.

Body size

Concerning body size (TL) and gonad maturation stage interaction for *Oikopleura vanhoeffeni*, TL of stages I, II, and V are reported to be 0.67–2.87 mm, 1.73–4.03 mm and 12.96–19.98 mm, respectively (Shiga, 1993a). In our study, the smallest (<1 mm TL) stage I specimens were the most abundant for most of the stations (Fig. 5). In the Arctic area, the generation length of *O. vanhoeffeni* is reported to be one year (Choe and Deibel, 2011). After spawning, appendicularians die off within a day because of the rupture of their body wall by spawning (Paffenhöfer, 1976). In this study, the abundances of *O. vanhoeffeni* south of St. Lawrence Island and the Chukchi Sea were 133–1,440 ind. m^{-3} (Fig. 4A). This value is much higher than the reported values for the same area during 1983–1986 (61–82 ind. m^{-3} ; Shiga, 1993a) and 1990–1996 (1–143 ind. m^{-3} ; Shiga et al., 1998). There are also great inter-annual differences in body size observed between 1983–1996 and 2007. Thus, the mean TL of *O. vanhoeffeni* in the lower layer during 1983 and 1986 was 13.6 mm and the maximum TL reached 20 mm (Shiga, 1993a). In the present study, such large-sized TL only occurred at station C14 with only a small number; most of the station's populations were composed of small-sized individuals (TL < 2 mm) (Fig. 5). Body size measurements were made for trunk length in Shiga et al. (1998), so after applying a TL – trunk length equation for this species (Riehl, 1993), the converted maximum TL was 26 mm during 1990–1996, which was also much larger than the TL measured in 2007 for this study (Fig. 5). Thus, while sampling locations, seasons (Julian day) and methods (mesh sizes) were similar, great differences in abundance and body size were observed for *O. vanhoeffeni* between the previous studies (Shiga, 1993a and Shiga et al., 1998) and this study.

Considering the generation length of *O. vanhoeffeni* in the

Arctic region (one year ; Choe and Deibel, 2011), the results during 1983, 1986, and 1990–1996 (low abundance of large-sized adults) suggest that the samplings of those years were made before the onset of reproduction in *O. vanhoeffeni* (Shiga, 1993b and Shiga et al., 1998). On the other hand, the results from this study in 2007 (high abundance of small-sized early juveniles) suggest that the samplings were made after the main reproduction event of *O. vanhoeffeni*. The sampling periods of Shiga (1993a, 1993b) and Shiga et al. (1998) have similar Julian dates in 1983, 1986, and 1990–1996 (17 July to 4 August) that are comparable to those in 2007 (24 July to 11 August). In recent years, the timing of the retreat of sea ice during the summer has become faster, with the earliest timing of the sea ice retreat and the largest open ocean area reported for 2007 (Perovich, 2011). These environmental changes (early biological phenology) in 2007 may result in greater differences than in 1983–1996 when the previous studies conducted (Shiga, 1993a, 1993b ; Shiga et al., 1998).

Feeding impact

The daily water column clearance rates of *Oikopleura vanhoeffeni* were estimated to be 0.003–25.5% day⁻¹ (mean : 2.52% day⁻¹) (Table 1). Similar estimates were made for *O. vanhoeffeni* at 0.1–12.8% day⁻¹ (Deibel, 1988) and 0.03–2.16% day⁻¹ (Knoechel and Steel-Flynn, 1989) in Newfoundland, in the western North Atlantic. Compared to those values, the clearance rates of this study were slightly higher. These differences are partly attributable to the differences in abundance densities ; 4–110 ind. m⁻³ (Deibel, 1988) and 1.1–92.9 ind. m⁻³ for Newfoundland (mean : 23.6 ind. m⁻³ ; Knoechel and Steel-Flynn, 1989), while mean abundance was as high as 1–1,439 ind. m⁻³ (mean : 604 ind. m⁻³) in the Bering and Chukchi Seas in this study. Since appendicularians form high densities within biological hot spots (Nakano et al., 2016), their functional roles and quantitative fluctuations need to be understood in more detail in the future.

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