DISTRIBUTION OF MARINE CLADOCERANS IN THE NORTHERN BERING SEA AND THE CHUKCHI SEA

Takashi ONBÉ^{1, *}, Atsushi TANIMURA², Mitsuo FUKUCHI², Hiroshi HATTORI³, Hiroshi Sasaki⁴ and Osamu MATSUDA¹

¹Faculty of Applied Biological Science, Hiroshima University, 4–4, Kagamiyama 1-chome, Higashi-Hiroshima 739 ²National Institute of Polar Research, 9–10, Kaga 1-chome, Itabashi-ku, Tokyo 173

³Department of Marine Sciences and Technology, School of Engineering, Hokkaido Tokai

University, Minamizawa 5-1-1-1, Minami-ku, Sapporo 005

⁴Department of Biotechnology, Senshu University of Ishinomaki, Shin-mito 1, Minamizaki, Ishinomaki 986

Abstract: Distribution and abundance of marine cladocerans were studied in the northern Bering Sea and the Chukchi Sea during the period from July to October in 1988–1990. Two species of marine onychopod cladocerans belonging to Podonidae, Evadne nordmanni LOVÉN and Podon leuckarti G. O. SARS, were detected in both seas at varying densities during this period. In particular, at stations located in eastern Bering Strait, maximum densities of 912 indiv · m⁻³ for E. nordmanni and 1725 indiv · m^{-3} for P. leuckarti were recorded in July 1989. In addition, a few specimens of the marine ctenopod species belonging to Sididae, Penilia avirostris DANA, and a single specimen of the freshwater anomopod species belonging to Moinidae, Moina sp., were collected at the easternmost nearshore station in Bering Strait only once, in July 1989. This appears to be the northernmost record for P. avirostris. Abundances of cladocerans were higher in July-August than in September-October, all species preferring less saline, chlorophyll-rich, warmer waters than colder waters of higher salinity. In both podonid species, gamogenetic individuals were found together with more prevalent parthenogenetic females. Proportions of gamogenetic individuals were less pronounced in July-August, but increased in September and October, sometimes surpassing 86% of the whole population, beyond the proportion recorded in mid-latitudinal populations in the Atlantic and the Pacific waters. The resting egg production is considered as an effective life-history strategy for the maintenance and survival of populations of E. nordmanni and P. leuckarti in these boreal and polar seas.

1. Introduction

Out of more than 600 species of cladocerans (SCHRAM, 1986), only eight species have been known to be distributed in the world oceans (Dolgopolskaya, 1958; Della CROCE, 1974; ONBÉ, 1974). Most works on marine cladocerans have been carried out in temperate and subtropical seas, and our knowledge of these animals in boreal and polar regions is meager.

In temperate, subtropical and tropical seas, they comprise significant portions of the local zooplankton community, usually represented by *Penilia avirostris* DANA and *Evadne tergestina* CLAUS. However, other species such as *Evadne nordmanni* Lovén

^{*}Present address: 2-60-406, Saijo Nishi-Honmachi, Higashi-Hiroshima 739.

and *Podon leuckarti* G.O. SARS, if present, appear at low densities only in low-temperature months, and are regarded as cold-water species.

As part of the U.S. Program "ISHTAR" (Inner Shelf Transfer and Recycling in the Bering-Chukchi Seas) and the NIPR Arctic Program "PREFLA" (Temporal Variability of Primary Production and Energy Flow in the Arctic Sea Area) to make explicit the general feature of the ecosystem and its energy flow in the polar seas, international, interdisciplinary cooperative investigations were undertaken by several cruises in 1988– 1990 in the northern Bering and Chukchi Seas.

Zooplankton samples collected during the cruises were analyzed for cladocerans. This work deals with their distribution and abundance in these cold seas with special reference to gamogenetic individuals.

2. Materials and Methods

Plankton samples were collected by a vertical tow of a twin NORPAC net from near the bottom up to the surface at a speed of approximately 1 m per s. The twin net consists of two conical nets, with nylon nettings of 0.35 mm (NGG 54) and 0.11 mm (NXX 13) mesh, respectively, having a mouth diameter of 45 cm and a side length of 180 cm.

Cladocerans were sorted from split subsamples, and counted by species and by reproductive type, *i.e.*, parthenogenetic females and gamogenetic individuals (restingegg bearing females, and males). Only samples collected with the 0.11 mm-mesh net were used in the present study, because some cladocerans might have escaped through the 0.35 mm-mesh net.

3. Results

3.1. Hydrography

According to COACHMAN et al. (1975), three principal water masses can be identified in the northern Bering Sea, based on salinity: Anadyr Water, Bering Shelf Water and Alaskan Coastal Water. The most saline and coldest Anadyr Water lies in the western part of the northern Bering Sea, whereas the least saline and the warmest Alaskan Coastal Water occupies the eastern part of the sea, deriving its origin from the Yukon River estuary in the southeastern part (Fig. 1). Between these two water masses lies the Bering Shelf Water of intermediate temperature-salinity characteristics, originating from the southern part of the Bering Sea. The flow regime is generally northward, and these water masses, maintaining their own positions from west to east with little lateral mixing, pass through Bering Strait into the Chukchi Sea. Immediately north of the strait the three water masses are reduced to two: Bering Sea Water, which is formed through mixing of Anadyr Water and Bering Shelf Water, and Alaskan Coastal Water. These two water masses flow north as far as Point Hope. At this point, the flow bifurcates. Most of the Bering Sea Water goes northwest toward Herald Island and thence into the Arctic Ocean, whereas most of the Alaskan Coastal Water turns northeast off Point Hope toward Point Barrow, and enters the Beaufort Sea of the Arctic Ocean. Along the Siberian coast, cold bottom water derived from the East



Fig. 1. The northern Bering Sea and the Chukchi Sea including Bering Strait (modified from COACHMAN et al., 1975). Depth in meters.

Siberian Sea flows southeast.

3.2. Species present

Two species of marine onychopod cladocerans belonging to the Family Podonidae occurred in the area investigated, *i.e., Evadne nordmanni* Lovén and *Podon leuckarti* G. O. SARS. Each of these is considered to be a cold-water species occurring in temperate, boreal and polar parts of the world oceans (Della Croce, 1974; MORDUKHAI-BOLTOVSKOI and RIVIER, 1987). Both parthenogenetic females and gamogenetic individuals (males, and females bearing one, or rarely two, resting eggs) were represented in most of the samples.

In addition, only once in July 1989 a few specimens of a marine ctenopod species belonging to the Family Sididae, *Penilia avirostris* DANA, and a single specimen of a freshwater anomopod species belonging to the Family Moinidae, *Moina* sp. (species name not identified) were collected at the easternmost nearshore station in Bering Strait.

3.3. Distribution and abundance

3.3.1. Cruise A: R/V THOMAS WASHINGTON, ISHTAR "Leg V," 3-18 October 1988

An extensive survey was conducted widely over the whole northern Bering and Chukchi Seas. Zooplankton samples were collected at 16 stations, of which 5 were T. ONBÉ et al.



Fig. 2. Distribution and abundance of Evadne nordmanni and Podon leuckarti during Cruise A (R/V THOMAS WASHINGTON "Leg V," 3–18 October 1988) in the northern Bering Sea and the Chukchi Sea. Each circle is proportional to the abundance scale shown in Fig. 3. For symbols, see Fig. 3.

located in the northern Bering Sea, 4 in the Chukchi Sea south of Cape Lisburne and 7 in Bering Strait (Fig. 2). Cladocerans were found at only 3 stations.

At Stn. 46 in the southern part of the Chukchi Sea, only *Podon leuckarti* occurred at a very low density of 0.29 indiv \cdot m⁻³. At Stn. 116 in Bering Strait, *Evadne nordmanni* appeared at a low density of 0.61 indiv \cdot m⁻³. At Stn. 115 close to the Alaskan coast of the strait, *E. nordmanni* and *P. leuckarti* were found at much higher densities, 16 and 30 indiv \cdot m⁻³, respectively, and gamogenetic individuals represented 30% of the whole population for *E. nordmanni* and 46% for *P. leuckarti*.

3.3.2. Cruise B: R/V Alpha Helix "Hx-128," 12-23 July 1989

Collections were taken at the same stations as in Cruise A (Fig. 3). The distribution of cladocerans was concentrated exclusively in, or near, Bering Strait; none occurred at 4 stations around St. Lawrence Island in the northern Bering Sea and all 4



Fig. 3. Distribution and abundance of Evadne nordmanni, Podon leuckarti, Penilia avirostris and Moina sp. during Cruise B (R/V ALPHA HELIX "Hx-128," 12-23 July 1989) in the northern Bering Sea and the Chukchi Sea. Olique-shaded, open, crossed and vertical-shaded parts indicate parthenogenetic females, respectively, of the species listed above. Solid parts: gamogenetic females with resting eggs; dotted parts: males.

stations in the Chukchi Sea.

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Samplings were taken twice on 15 and 23 July in Bering Strait. On the first date, a high abundance of slightly less than 1000 indiv \cdot m⁻³ was recorded for both *E. nordmanni* and *P. leuckarti* at the most nearshore station (Stn. 63), *i.e.*, 912 indiv \cdot m⁻³ for the former, and 756 indiv \cdot m⁻³ for the latter. In addition, a few specimens of *P. avirostris* were collected at the same station, which fell within a low density of 93 indiv \cdot m⁻³. On the next visit, a similar high abundance of the two podonid species was noted; in particular, at a station next to the former (Stn. 159) *P. leuckarti* attained the highest density of 1725 indiv \cdot m⁻³. At the most nearshore station (Stn. 158), which is located at almost the same position as Stn. 63, a freshwater moinid, *Moina* sp., appeared at a density of 7.1 indiv \cdot m⁻³.

On 15 July, gamogenetic individuals were composed mostly of males, representing 7-30% for *E. nordmanni*, but for *P. leuckarti* the population consisted completely of parthenogenetic females at all stations. On 23 July, on the contrary, both species contained gamogenetic individuals at 7-30% of their populations, of which resting-egg bearing females comprised 2-6%.

3.3.3. Cruise C: R/V ALPHA HELIX "Hx-131," 13-17 September 1989

Zooplankton samples were collected at 14 stations: 8 located in the northern Bering Sea and 6 along the Bering Strait Section (Fig. 4). Cladocerans were distributed at 10



Fig. 4. Distribution and abundance of Evadne nordmanni and Podon leuckarti during Cruise C (R/V ALPHA HELIX "Hx-131," 13-17 September 1989) in the northern Bering Sea and Bering Strait. For symbols, see Fig. 3.

stations except for 4 stations lying north of St. Lawrence Island. As in Cruise B in July, nearshore stations in eastern Bering Strait had a high density of cladocerans; in particular, the density of *P. leuckarti* attained 796 indiv m^{-3} at Stn. 7. Only *E. nordmanni* occurred at 3 stations around St. Lawrence Island at densities of 0.68–10 indiv m^{-3} .

The decrease in population density and the increase in the intensity of gamogenesis are characteristic features of this month, in contrast to the situation in July. The frequency of gamogenetic individuals was 4–60% for *E. nordmanni* and from 36% to as high as 86% for *P. leuckarti*.

3.3.4. Cruise D: T/S Oshoro MARU "Cruise 33," 24 July-1 August 1990

This time zooplankton were collected at 25 stations over the entire area of the present investigation (Fig. 5). Cladocerans were distributed at 7 out of 12 stations in the Chukchi Sea and Bering Strait, and none were found at 13 stations in the northern Bering Sea.

In the Chukchi Sea, the highest densities of cladocerans occurred at the northernmost nearshore station (Stn. 149) off Cape Lisburne, with 319 indiv $\cdot m^{-3}$ for *E. nordmanni*, and at the southernmost station (Stn. 160), with 413 indiv $\cdot m^{-3}$ for *E. nordmanni* and 433 indiv $\cdot m^{-3}$ for *P. leuckarti*. At other positive stations, both species showed much lower densities of 5.4–45 indiv $\cdot m^{-3}$.

Gamogenetic individuals represented a maximum of 20% at two northernmost stations and 5% at others for *E. nordmanni*, whereas for *P. leuckarti* they comprised only 2-12% of the whole population. These low values are similar to those obtained during the second cruise (Cruise B) in July.



Fig. 5. Distribution and abundance of Evadne nordmanni and Podon leuckarti during Cruise D (T/S OSHORO MARU "Cruise 33," 24 July-1 August 1990) in the northern Bering Sea and the Chukchi Sea. For symbols, see Fig. 3.

3.4. Relationship between abundance of cladocerans and characteristics of surface water In order to characterize, if any, the environmental conditions in which marine cladocerans occurred in these cold seas, abundances of two dominant species (E. nordmanni and P. leuckarti combined) were plotted on a T-S diagram based on the surface data (Fig. 6), because they are known to be distributed mainly in surface layers (THIRIOT, 1968; ONBÉ, 1974; ONBÉ and IKEDA, 1995). It is clear that marine cladocerans occur abundantly at stations having low salinities and warmer temperatures.

The abundances of the two species were then plotted against chlorophyll-*a* concentrations of surface water (Fig. 7). Apparently, both *E. nordmanni* and *P. leuckarti* have a tendency to increase their own population density with increasing chlorophyll-*a* concentrations ranging from $1 \mu g l^{-1}$ to $2.5 \mu g l^{-1}$, although there were a few exceptionally low cases at higher concentrations.



Fig. 6. Relationship between abundance of Evadne nordmanni and Podon leuckarti (two species combined) and temperature-salinity characteristics of surface water in the northern Bering Sea and the Chukchi Sea. Stations where Penilia avirostris and Moina sp. occurred are indicated by P. a. and M. s., respectively.

4. Discussion

The present study revealed that two species of podonid cladocerans, *Evadne* nordmanni and Podon leuckarti, were distributed in the northern Bering Sea and the Chukchi Sea at least from July through October, and that the abundance was higher in July-August than in September-October, indicating the existence of a possible seasonal fluctuation. Both species were shown to prefer less saline (>32 ppt), chlorophyll-rich, warmer waters, which can be attributed to Alaskan Coastal Water defined by COACHMAN et al. (1975), than colder waters of high salinity, defined also as Anadyr and Bering Shelf Waters (COACHMAN et al., 1975). A characteristic absence of cladocerans in the northern Bering Sea during Cruise D in July 1990 (Fig. 5) is due to the high salinity of water which prevailed there at that time. In a recent monograph, MORDUKHAI-BOLTOVSKOI and RIVIER (1987) also indicated the occurrence of these two species in this



Fig. 7. Abundance of Evadne nordmanni and Podon leuckarti in relation to chlorophyll-a concentrations of surface water in the northern Bering Sea and the Chukchi Sea.

region.

Although E. nordmanni was reported to occur in oceanic waters in the North Atlantic and the North Sea (GIESKES, 1970, 1971a), the Indian Ocean (DELLA CROCE and VENUGOPAL, 1972) and the northwestern Pacific (KIM, 1989; KIM and ONBÉ, unpublished), they usually abound in neritic regions (JORGENSEN, 1933; BAINBRIDGE, 1958; ONBÉ, 1974; KIM, 1989; KIM et al., 1989). P. leuckarti is also known to be distributed in neritic waters (GIESKES, 1970, 1971b; ONBÉ, 1974; KIM, 1989; ONBÉ and IKEDA, 1995).

The most noteworthy from the biogeographical point of view is the fact that *Penilia* avirostris, which has been considered to be a typical warm-water species (DELLA CROCE and VENUGOPAL, 1972; DELLA CROCE, 1974; ONBÉ, 1974; KIM, 1989; KIM and ONBÉ, 1995), was collected at the easternmost nearshore station in Bering Strait in July 1989 (Cruise B), albeit quite scarce in number (Fig. 3, Stn. 63). The station is located close to the coast of Alaska as far north as Lat. $65^{\circ}40'$ N, which appears to be the northern-most record of distribution of this species (cf. LOCHHEAD, 1954; DELLA CROCE, 1964, 1974). Out of all three females of P. avirostris collected, two contained a few parthenogenetic embryos in the brood pouch, one had no embryos, and all had full gut contents. These animals had most probably been carried there by a northward current from the southern part of the Bering Sea, but, interestingly, were found actively feeding and moderately reproducing at this northernmost habitat (see Fig. 6: surface temperature 8.51° C, surface salinity 28.91 ppt). The temperature was almost the same as the lowest known temperature of 8.7° C at which a surviving adult of this species had been taken (STEUER, 1933).

The presence of a freshwater species, Moina sp., at the same station (Fig. 3, Stn.

158) clearly indicated the direct influence of freshwater runoff over this particular area of Bering Strait at that time (see Fig. 6: surface temperature 9.90°C, surface salinity 27.82 ppt). The freshwater discharge from the Yukon River is known to become most pronounced in June–July (COACHMAN *et al.*, 1975).

In temperate seas, it has been commonly known that the gamogenetic individuals, *i.e.*, resting-egg bearing females and males, become most numerous when the planktonic population is about to disappear from the water column (BAINBRIDGE, 1958; GIESKES, 1971b; ONBÉ, 1974). The proportions of gamogenetic individuals within the whole population is reported to vary with species as well as with season and locality. For *E. nordmanni*, high proportions of 60% and 70% have been recorded, respectively, in the Clyde Sea (BAINBRIDGE, 1958) and the North Sea (GIESKES, 1970, 1971a), whereas only 30% was reported as the highest in the Inland Sea of Japan (ONBÉ, 1974). By contrast, an even higher value of 60–80% has been documented for *P. leuckarti* from the North Sea (GIESKES, 1970, 1971b). The present observations revealed that similar, or much higher, proportions of gamogenetic individuals are prevalent for the populations of both species in the northern Bering Sea and the Chukchi Sea. As for *P. avirostris*, whether or not this warm-water species produces resting eggs in such cold waters is unknown, because gamogenetic individuals have not been obtained.

The gamogenesis ultimately gives rise to the formation of resting eggs, which serve to tide over the populations in adverse conditions, such as prolonged frigidity and darkness of the boreal and arctic winter (e.g., ONBÉ, 1991). Therefore, the observed high intensity of gamogenesis in *E. nordmanni* and *P. leuckarti* apparently reflects the greater dependence of these cladoceran populations on the resting eggs for their maintenance and survival in these waters than in temperate, subtropical and tropical seas.

The resting eggs are deposited onto the bottom of the sea floor where they spend the dark and cold polar winter. The cladoceran populations of the next season will be recruited from the hatching of these eggs. This is no doubt an excellent life-history strategy for their populations. For better understanding of the succession of the cladoceran populations in these seas, we should know more about the distribution and abundance of resting eggs existing in the bottom sediments and the hatching requirements of these eggs under different temperature and photoperiodic conditions.

Marine cladocerans belonging to Podonidae have been reported to catch phytoplankters and microzooplankters by vision in well-lighted surface layers during the daytime (BAINBRIDGE, 1958). Recent examinations in temperate waters have revealed the presence of diatoms, dinoflagellates, and other micro-organisms in the guts of some species of *Podon* and *Evadne* (JAGGER *et al.*, 1988; KLEPPEL *et al.*, 1988; KIM *et al.*, 1989, 1993). However, nothing is known on the feeding habits of podonid cladocerans in the polar seas. To understand the functional role of marine cladocerans in the zooplankton community of the polar regions, we should gain much deeper insight into their trophodynamics under this unique environment, particularly in a low-lighted period of time.

As to other important groups of zooplankton of the present survey, in particular, during Cruise A, the distribution of copepods has been reported preliminarily by HATTORI *et al.* (1991) and the feeding habits of a species of copepod have been examined

by OHTSUKA et al. (1993).

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