

Reproductive success of Pacific copepods in the Arctic Ocean and the possibility of changes in the Arctic ecosystem

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Abstract The species composition of Arctic zooplankton differs greatly from that of the zooplankton of the North Pacific and Bering Sea. Particularly with greater warming from sea-ice retreat, the reproduction of North Pacific species transported into the Chukchi Sea and beyond may lead to changes in the Arctic pelagic ecosystem. We report the egg production and hatching of the Pacific copepod *Neocalanus flemingeri* in the Chukchi Sea based on shipboard experiments performed in September 2013. The reproductive capability of *N. flemingeri* observed in the Chukchi Sea resembled that reported in the Pacific, with the exception of a lower hatching success. Only 7.5 % of *N. flemingeri* eggs hatched compared with 93 % in Pacific experiments. Low hatching success is considered to be caused by failures of fertilization. The potential recruitment number for *N. flemingeri* suggests that it is unlikely to establish expatriate Arctic populations in the near future.

Keywords Arctic Ocean · Pacific copepods · *Neocalanus flemingeri* · Reproduction

Introduction

The drastic reduction in the extent of Arctic Ocean sea ice is thought to be severely affecting marine ecosystem structures (Grebmeier et al. 2006; Hunt and Drinkwater 2007). The Pacific sector of the Arctic Ocean, which is seasonally ice covered, receives a substantial inflow of Pacific water through the Bering Strait (Coachman and Aagaard 1966). This current transports nutrients and plankton from the Bering Sea into the Arctic Ocean (Springer et al. 1989; Springer and McRoy 1993). Since the 1930s, a few endemic North Pacific copepods (*Eucalanus bungii*, *Metridia pacifica*, *Neocalanus cristatus* and *N. plumchrus/flemingeri*) have been observed among the zooplankton transported to the Arctic Ocean (Nelson et al. 2014). Although these transfers have been thought to be abortive and not establishing permanent populations, an increase in species entering the Arctic has been recently reported (Matsuno et al. 2011). Because the planktonic copepod fauna is vastly different between the Arctic and Pacific Oceans (Conover 1988; Longhurst 2006), successful reproduction of Pacific copepods in the Arctic would change the Arctic's pelagic ecosystem structure. To date, our knowledge of Pacific copepods in the Arctic Ocean has been limited to their distributions, and no information has been available regarding their reproduction in the Arctic Ocean.

In the present study, we report observations of the egg production and hatching of the Pacific copepod *N. flemingeri* in the Chukchi Sea based on shipboard experiments performed in September 2013. The reproductive parameters measured in this study were compared with values reported for this species in the Pacific Ocean (Saito and Tsuda 2000). Combining the abundance data for Pacific copepods (Matsuno et al. 2012) with the observed

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reproductive parameters allowed for the calculation of their recruitment potential in the Arctic Ocean.

Materials and methods

From 10–25 September 2013, adult females of *N. flemingeri* were collected by the vertical towing of a ring net (mesh size: 0.335 mm, mouth diameter: 80 cm) at a fixed station (72°45'N, 168°15'W, bottom depth 56 m) in the Chukchi Sea. The net was towed from 49 m depth to the surface at 0.5 m s⁻¹ once a day. The collected females ($n = 19$) were gently placed in a 10-ml microplate filled with GF/F filtered seawater (because the females do not have functional mouthparts and do not feed) and were incubated at 0 °C in the dark. This temperature was determined by range of in situ temperature (−1.4 to 3.1 °C) and an integrated mean temperature (0.3 °C). The presence of eggs was checked every day. Experiments were continued until the death of all adult females. In total, we performed the incubation experiments for 216 days (40 days in a shipboard and 176 days in a land laboratory). After death, the prosome lengths of the adult females were measured to a precision of 0.05 mm using an eyepiece micrometer. The eggs were counted (clutch size) and gently placed in a 50-ml glass bottle filled with filtered seawater. Egg diameter was measured to a precision of 0.01 mm using an eyepiece micrometer. The eggs were incubated at 0 °C and checked daily for hatching; hatched nauplii were counted. Observations of hatching continued for a maximum of 10 days after the spawning of a clutch. Hatching time (-days) and the proportion of the hatched eggs (%) were estimated for each clutch.

Results

During the study period (10–25 September 2013), five Pacific copepods (*E. bungii*, *M. pacifica*, *N. cristatus*, *N. flemingeri* and *N. plumchrus*) occurred at a fixed station (72°45'N, 168°15'W, bottom depth 56 m) in the Chukchi Sea (Table 1). Among those species, adult females were collected only for *N. flemingeri*. The abundance of adult females in the different samples ranged from 0 to 1.40 ind. m⁻³ (mean: 0.16 ind. m⁻³). It is notable that no adult males were detected throughout the study period.

The prosome lengths of the adult females ranged from 4.10 to 4.75 mm (mean ±1 SD: 4.42 ± 0.16 mm, Table 2). Spawning was observed for all of the specimens (Fig. 1), and nearly half (10/19) produced four or more clutches during the experiments. Spawning intervals were 11.5 ± 5.6 days. The maximum clutch size was 1,005 eggs clutch⁻¹ (mean ±1 SD: 377 ± 79 eggs clutch⁻¹, Table 2),

Table 1 Abundance of Pacific copepods at a fixed station in the Chukchi Sea during 10–25 September 2013

Species	Stage	Abundance (ind. m ⁻²)
<i>Eucalanus bungii</i>	C3	1.46 ± 10.03
	C5F	1.51 ± 10.36
	C5M	1.36 ± 9.35
<i>Metridia pacifica</i>	C1	2.76 ± 13.27
	C2	32.21 ± 65.83
	C3	139.51 ± 128.28
	C4F	8.41 ± 26.46
	C4M	15.49 ± 37.20
	C5F	1.30 ± 8.88
<i>Neocalanus cristatus</i>	C5	5.62 ± 18.71
<i>Neocalanus flemingeri</i>	C5	47.88 ± 61.46
	C6F	8.03 ± 21.34
<i>Neocalanus plumchrus</i>	C4	1.61 ± 11.05
	C5	11.61 ± 27.34

Values are the means ± 1 SD. Stages with zero abundance are not shown in the table

and the clutch size decreased after 20 days of incubation. The maximum number of clutches for a single specimen was ten. The maximum total fecundity was 1,488 eggs female⁻¹ (mean ±1 SD: 960 ± 316 total eggs female⁻¹). The longevity of the adult females during the experiments ranged from 15 to 205 days (mean ±1 SD: 69 ± 47 days). The mean egg diameter was 152 ± 2 µm. The hatching time was 5.1 ± 1.2 days, and the hatching success for the clutches ranged from 0.2 to 31.5 % (mean ±1 SD: 7.5 ± 8.7 %, Table 2).

Discussion

The reproduction of *N. flemingeri* from September to October was reported in the western Bering Sea, which is adjacent to the Chukchi Sea (Geinrikh 2002). Most of the reproductive parameters of *N. flemingeri* in the Arctic Ocean (this study) were within the range of those observed previously in the Pacific Ocean (Saito and Tsuda 2000; Table 2). Spawning interval and hatching time, two indices of physiological rates, were longer in the Arctic Ocean. This was likely due to the 0 °C incubation temperature in the Arctic Ocean compared with 2 and 4 °C in the Pacific Ocean. After combining the results obtained from the Arctic and Pacific Oceans, the relationships of the spawning interval and hatching time with temperature (T : °C) are well described by the Bělehrádek equation (Fig. 2):

$$\begin{aligned} \text{Spawning interval (days)} \\ = 6240.2 (T + 21.7)^{-2.05} (r^2 = 0.99, p < 0.0001) \end{aligned}$$

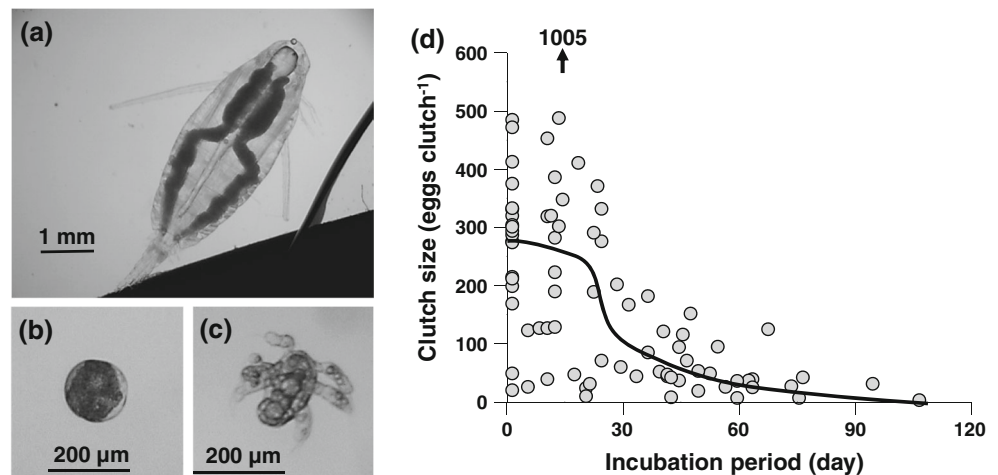
Table 2 Reproductive parameters of the Pacific copepod *Neocalanus flemingeri* in the Chukchi Sea and NW Pacific Ocean. Values are the mean \pm 1 SD

Reproductive parameters	Chukchi Sea (This study)	NW Pacific Ocean (Saito and Tsuda 2000)
Adult female		
Prosome length (mm)	4.42 \pm 0.16 (4.10–4.75)	3.94 \pm 0.44 (2.91–5.14)
Spawning intervals (days)	11.5 \pm 5.6 (0 °C)	9.3 \pm 1.8 (2 °C)
		8.2 \pm 2.1 (4 °C)
Mean maximum clutch size (eggs clutch ⁻¹) ^a	377 \pm 79	443 \pm 133
Maximum individual clutch size (eggs clutch ⁻¹)	1,005	687
Maximum number of clutches (female ⁻¹)	10	6
Mean fecundity (total eggs female ⁻¹) ^a	960 \pm 316	924 \pm 346
Maximum fecundity (total eggs female ⁻¹)	1,488	1,398
Egg		
Diameter (μ m)	152 \pm 2.0	154 \pm 3.0
Hatching time (days)	5.1 \pm 1.2 (0 °C)	4.6 \pm 0.5 (2 °C)
		3.8 \pm 0.5 (4 °C)
Proportion hatching (%)	7.5 \pm 8.7 (0.2–31.5)	93

Parentheses indicate range (prosome length and hatching proportion) or experimental temperature (spawning interval and hatching time)

^a Calculated based on the females that produced four or more clutches

Fig. 1 Adult female (a), reproduced egg (b) and nauplius (c) of *Neocalanus flemingeri* in the Chukchi Sea. Temporal changes in the clutch size of *N. flemingeri* during the incubation period (d). Solid lines indicate eye-fitted line



Hatching time (days)

$$= 4628.0 (T + 27.6)^{-2.05} (r^2 = 0.96, p < 0.0001)$$

Apart from these expected effects of temperature, only hatching success varied greatly between the two oceans. For the Arctic Ocean, the maximum hatching success was 31.5 %, with a mean of 7.5 %, while the hatching success in the Pacific Ocean has been reported to be as high as 93 % (Saito and Tsuda 2000). This large discrepancy may be the result of differences in the fraction of eggs successfully fertilized. Adult males of *N. flemingeri* were not observed in this study (Table 1). For various large-sized planktonic copepods, failure to fertilize large fractions of spawned eggs has been reported (Ershova and Kosobokova 2012). The extremely low hatching success in the Arctic Ocean (7.5 %) suggests that a majority of the eggs could have been unfertilized. The effect of the low habitat

temperature (0 °C) in the Arctic Ocean on low hatching success should also be considered. However, because *N. flemingeri* can maintain their population at near-zero temperatures in the Sea of Japan (Miller and Terazaki 1989), it is unlikely that the low temperature was the cause of the observed low egg hatching success.

In the typical life cycle of *N. flemingeri* in the North Pacific and Bering Sea, mating and spawning both occur below a 250-m depth (Miller and Clemons 1988; Kobari and Ikeda 2001; Geinrikh 2002). Because the spawning adult females in the Chukchi Sea were collected at 0–49 m (Fig. 1a), they presumably had either matured prior to being transported by Pacific waters into the Chukchi Sea or they could not descend to a deeper layer because of the shallowness (ca. 50 m) of the Chukchi Sea in comparison to the Pacific Ocean. These abnormal conditions may affect the mating and reproduction of *N. flemingeri*, resulting in

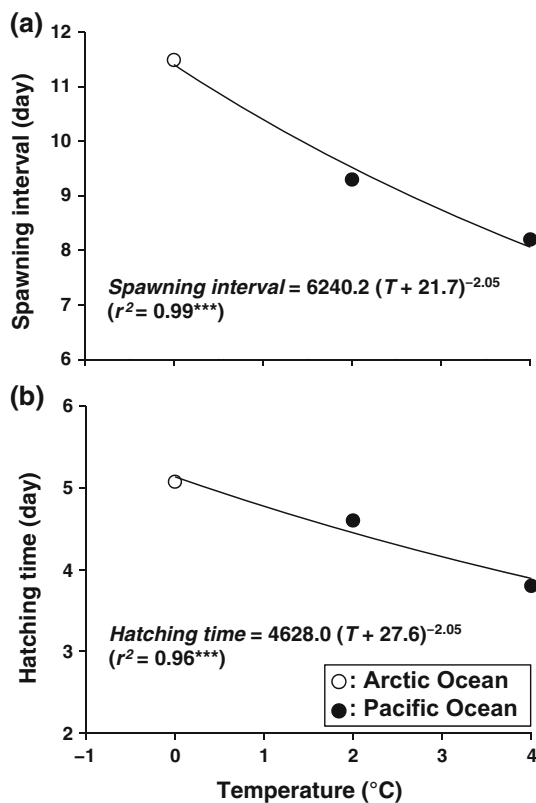


Fig. 2 Relationship between spawning interval and temperature (a) and egg hatching time and temperature (b) for *Neocalanus flemingeri*. Data at 0 °C were collected in the Arctic Ocean (open circle, this study), and data at 2 and 4 °C were collected in the western North Pacific (solid circle, Saito and Tsuda 2000). The relationships were expressed by Bělehrádek equations. *** $p < 0.0001$

low hatching success. While their hatching success in the Arctic Ocean was extremely low, eggs were capable of hatching, suggesting that there is potential for a change in the zooplankton fauna in the Arctic Ocean as conditions continue to warm.

To evaluate the quantities of Pacific copepods transported into the Arctic Ocean, we re-analyzed the copepod

abundance data reported for the entire area of the western sector (Matsuno et al. 2012). In the Arctic Ocean, from August–October 2008, the Pacific copepods *N. cristatus*, *N. flemingeri* and *E. bungii* occurred maximally at 523 ind. m^{-2} , with mean values of 5.8, 26.6 and 6.1 ind. m^{-2} , respectively. Their northernmost occurrence was at 76°00'N, 176°00'W, approximately 1,100 km from the Bering Strait (Fig. 3). Assuming the reported current velocity at the Bering Strait (22.4–29.1 $cm s^{-1}$, Woodgate et al. 2005), the transport of the Pacific copepods from the Bering Strait to their northernmost occurrence was estimated to take 44–57 days. The observed occurrences of Pacific copepods were limited; the three species were found at only 4–8 of 54 stations. The historical analysis of copepod abundance beginning in the 1930s also confirmed that the distribution of Pacific copepods is restricted to the continental shelf in the Arctic Ocean (Nelson et al. 2014).

Combining abundance data and reproductive parameters, we simulated the potential recruitment numbers of *N. flemingeri* in the Arctic Ocean. If *N. flemingeri* transported into the Arctic Ocean have an observed mean abundance (26.6 ind. m^{-2}) (Matsuno et al. 2012) and observed mean fecundity (960 total eggs $female^{-1}$) with 7.5 % of eggs hatching to nauplii (as observed in our shipboard experiments), the recruitment of the September generation would be 1,916 nauplii m^{-2} ($=26.6 \times 960 \times 0.075$). For *N. flemingeri* in the Pacific Ocean, the annual mean abundance = 1,852 ind. m^{-2} (Kobari and Ikeda 2001), laboratory-based fecundity = 924 total eggs $female^{-1}$ and hatching success = 93 % of eggs hatch to nauplii (Saito and Tsuda 2000). Those values yield a recruitment of 1,591,841 nauplii m^{-2} ($=1,852 \times 924 \times 0.93$), approximately 800 times the estimated value in the Arctic Ocean.

This large discrepancy in recruitment numbers suggests that the Pacific copepods are unlikely to establish an expatriate population in the Arctic Ocean at its present state. While the poleward transport of Pacific copepod species has been observed since the 1930s (Nelson et al. 2014), the low abundance of adults (especially females, cf. Table 1)

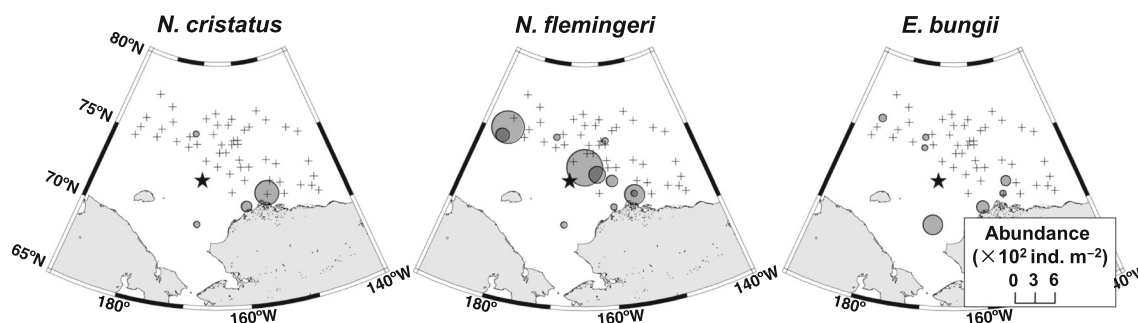


Fig. 3 Horizontal distribution of the Pacific copepods (*Neocalanus cristatus*, *N. flemingeri* and *Eucalanus bungii*) in the western Arctic Ocean from 29 August to 4 October 2008. The solid star indicates the

sampling station that collected *N. flemingeri* females in this study. Crosses indicate no occurrence of each species

and low egg survival to hatching have prevented populations from becoming permanently established. However, recent increases in the transport of individuals (Matsuno et al. 2011) may increase the chance that populations of copepods endemic to the North Pacific will become established in the Arctic Ocean. Permanent Arctic populations of endemic North Pacific and Bering Sea copepod species could eventually be introduced to the North Atlantic (Reid et al. 2007). Their very different life history patterns (phenology) could generate a substantial change in all Northern Hemisphere pelagic ecosystems (Conover 1988). Continuous monitoring is needed in the future to see what is happening and perhaps help us to project the effects on higher trophic levels (e.g., fish, marine mammals, etc.).

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