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# Distribution and egg production of *Pseudocalanus* species in the Chukchi Sea

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ABSTRACT

The distribution and egg production of *Pseudocalanus* species was studied in the Chukchi Sea during August 2004. Three species were identified throughout the study area, *Pseudocalanus minutus*, *Pseudocalanus acuspes* and *Pseudocalanus newmani*. The more subpolar/temperate *P. newmani*-dominated stations where water was warmer and likely influenced by Alaska coastal waters, and it penetrated northward into the south-eastern corner of Herald Valley. The Arctic *P. acuspes* dominated the colder waters. The number of eggs produced by individuals and populations differed among species, primarily because of differences in body size, but mass-specific egg production was similar among species, and was on the order of 15% per day. Future increases in the prevalence of *P. newmani* within the Chukchi Sea might be anticipated, and would result in a decreased average size of the copepod community, with potential implication for higher trophic levels.

## 1. Introduction

Copepods of the genus *Pseudocalanus* are one of the most dominant constituents of the zooplankton community of the Chukchi Sea, both in terms of numbers and biomass (Hopcroft et al., in press). *Pseudocalanus* are common throughout coastal waters from temperate to polar ecosystems, where they are thought to play an important role in the trophic ecology of these systems due to their high rate of production relative to many larger crustacean zooplankton (e.g. Corkett and McLaren, 1978). The genus *Pseudocalanus* is now recognized to contain a complex of seven species (Frost, 1989), each with some differences in size, reproductive output, and phenology (McLaren et al., 1989a; Bucklin et al., 1998; Napp et al., 2005). Five of these species are recorded at present in the Chukchi Sea, *Pseudocalanus minutus*, *Pseudocalanus acuspes*, *Pseudocalanus major*, *Pseudocalanus newmani*, and to a lesser extent *Pseudocalanus mimus* (Frost, 1989). However, their occurrence is seldom reported as more than *Pseudocalanus* spp. due to the difficulty involved in separating adults by species, and the near impossibility of routinely separating juveniles (e.g. Smith and Vidal, 1986; Lane et al., 2008) by other than molecular techniques (e.g. Bucklin et al., 1998, 2003).

The Chukchi Sea represents a complex gateway into the Arctic, due to the interplay of several distinct water masses of Pacific origin (i.e. Alaska Coastal, Bering Shelf, and Anadyr Water) with those of the central Arctic Ocean, and its marginal seas (Weingartner et al., 1998; Pickart et al., 2009). The water masses entering the region through the Bering Strait, tend to each have unique assemblages and quantities of zooplankton (Springer et al., 1989; Coyle et al., 1996; Hopcroft et al., in press) and slowly acquire more Arctic faunal characters as they are transformed/modified moving northward (e.g. Smith and Schnack-Scheil, 1990; Lane et al., 2008). Of the *Pseudocalanus* species reported for this region, *P. newmani* and *P. mimus* are more subpolar to temperate in distribution, with some inshore/offshore preferences (e.g. Napp et al., 2005). They are likely seasonal imports to the region, and this raises the possibility that *Pseudocalanus* species could be tracers of water mass origin as well as the magnitude of advection within this region.

The advection of subpolar/temperate *Pseudocalanus* species into a community of more polar affinity raises interesting questions about their short-term and long-term viability, and their competitive success in the Chukchi ecosystem. Ideally one would explore the somatic growth rates of *Pseudocalanus* in their habitat (e.g. Liu and Hopcroft, 2008), but our inability to separate juveniles of these species precludes such an approach. A more practical approach for exploring species success would be to look at the reproductive output of these egg-carrying species. Differences in clutch size are known to occur between *Pseudocalanus* species (e.g. Napp et al., 2005), as well as differences in egg and body size (Frost, 1989; McLaren et al., 1989a, b; Napp et al., 2005). Furthermore, even when co-occurring, the more polar species tend to produce only one generation per year, while the more subpolar/temperate species have multiple generations per year (McLaren et al., 1989a). The net effect of these reproductive attributes is unknown, but there is clearly potential for differences

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in both numerical and weight-specific egg production rates among the different species. To address these questions, we determined the distribution of *Pseudocalanus* species adults within the Chukchi Sea and explored their species-specific patterns of egg production.

## 2. Methods

The Russian American Long-term Census of the Arctic (RUSALCA) survey consisted of 22 stations along three transects in the southern Chukchi Sea between Alaska and Russia, plus four more northern high-speed transects across the Herald Valley (Fig. 1). Non-quantitative 200 μm mesh ring nets were taken at alternate stations on the three southern transects, and at the ends plus midpoint of the upper transects in Herald Valley, for reproductive experiments at 21 stations. Nets were slowly hauled vertically in the upper 25 m of the water column and catches were diluted. Despite the relative gentleness of collection, egg sacs were dislodged from most *Pseudocalanus* females that may have been carrying eggs, leaving only a few females (usually $<5\%$, always $<10\%$) in the samples with partial remnants of clutches. Sorting of female *Pseudocalanus* (genus level only) was usually completed within 2–3 h of capture; further sorting to species level was not possible on live specimens. Single sac-less *Pseudocalanus* females ($N = 30$–$100$) were transferred with a wide bore pipette into 70 ml polystyrene tissue culture flasks, pre-filled with 100 μm prescreened water from the mixed layer (e.g. Napp et al., 2005). Incubations were performed within 1–2 °C of the mixedlayer temperature on a low-light photocycle comparable to ambient. In the southern domain, temperature was held at 3–6 °C, then lowered to 1–2 °C in the northern, Herald Valley domain. Females were checked every 24 hours over 3 days; females producing egg sacs before the conclusion of the experiment were removed and preserved individually. All non-producing females were preserved together at the conclusion of each experiment.

For calculating egg production rates, females removed and preserved during and at the conclusion of the experiments were identified to species (Frost, 1989), with prosome length, egg diameter and eggs per clutch determined with a computer-assisted measuring system (Roff and Hopcroft, 1986). Mean clutch size was calculated for experiments with at least 4 clutches produced. Egg production rate (EPR) was calculated as (Mean clutch size) × (Fraction of females extruding a clutch)/the incubation time in days (Runge and Roff, 2000) for all cases where more then 10 females of a species were present. In practice, egg production declined precipitously after the second day, so analysis was limited to 48 h. Female dry-mass (DW, in μg) was predicted from prosome length (PL, in μm) using a relationship established for a mixture of *P. newmani* and *P. mimus* in the Gulf of Alaska ($\log_{10} DW = -7.62{+}2.85 \log_{10} PL$: Liu and Hopcroft, 2008). Egg mass was predicted from diameter, assuming a density of 0.14 ng C $\mu m^{-3}$ (Kiørboe and Sabatini, 1994). Egg carbon was converted to ash-free dry-mass assuming carbon as 40% of AFDW. Specific egg production rate (SEP) was calculated for each female using the ratio of her predicted weight to that predicted for her eggs.

Standardization of rates for temperature differences proved problematic due the large differences in temperature across the experimental domain, but restriction to a single incubator placed at an intermediate temperature. If we presume there is physiological "inertia" in egg carriers to the multi-day process of preparing eggs to be laid (i.e. 11 days at 0 °C, 3 days at 12 °C; McLaren et al., 1989b), then correction should be relative to ambient temperature. If metabolic processes respond rapidly to change in temperature, then correction should be relative to the incubation temperature. In all likelihood, the appropriate correction will be somewhere in between these possibilities. SEP was standardized from both possible reference temperatures to 5 °C (the intermediate temperature observed over the study area) using a $Q_{10}$ of 2.7 for food-satiated juvenile broadcast spawners (Hirst and Bunker, 2003). Concurrent estimates of the physical environment and chlorophyll were provided by other investigators (Lee et al., 2007; Pickart et al., 2009).

Finally, if a large percentage of the female *Pseudocalanus* were reproductively inactive, the exclusion of individuals with sac remnant may introduce bias in our egg production rates. Based on the proportion of females that produced clutches in our experiments (see below) and the known hatching rates of *Pseudocalanus* (McLaren et al., 1989b), most females appear to have been reproductively active.

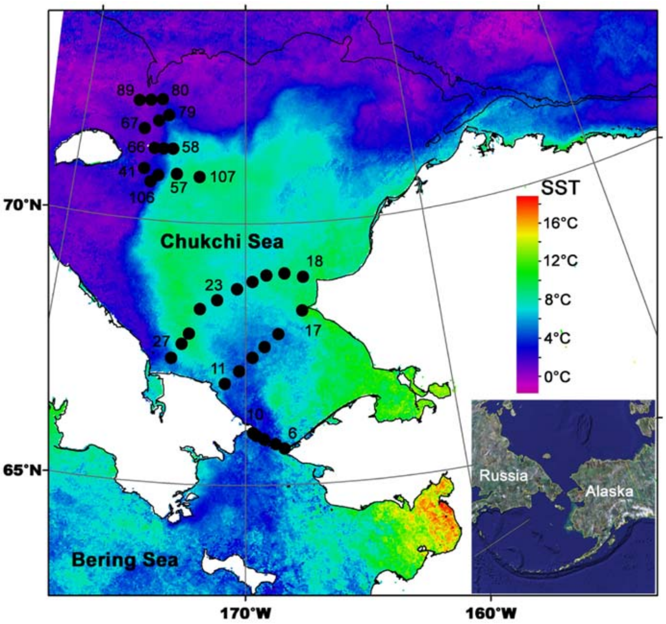

**Fig.1.** Station map overlain on the 7-day composite AVHRR sea-surface temperature during the sampling period (11–17 August 2004). 100 and 500 m contours indicated.

## 3. Results

### 3.1. Distribution

Three species of adult *Pseudocalanus* were identified throughout the study area, *P. minutus*, *P. acuspes*, and *P. newmani* (Fig. 2). The more subpolar/temperate *P. newmani* dominated along the Alaska Coast and the south-eastern corner of Herald Valley. *P. acuspes* dominated the remainder of the valley, as well as those closer to the Siberian Coast. *P. minutus* dominated only at the two central stations in the southern sampling domain, but occurred at virtually all locations except those along the Alaska Coast. Later examination of the concurrent quantitative samples indicated the subpolar/temperate *P. mimus* was present at some stations, and may have been misidentified as the few smaller *P. minutus* in our experiments. Abundances at Station 27 were too low to establish proportions in the live collections, but all three species were observed there in preserved collections. The relative contribution of both *P. acuspes* and *P. newmani* was highly correlated to temperature, either averaged over the collection depth (i.e. upper 25 m) or the entire water column, with *P. acuspes* negatively related to temperature, *P. newmani* positively related to

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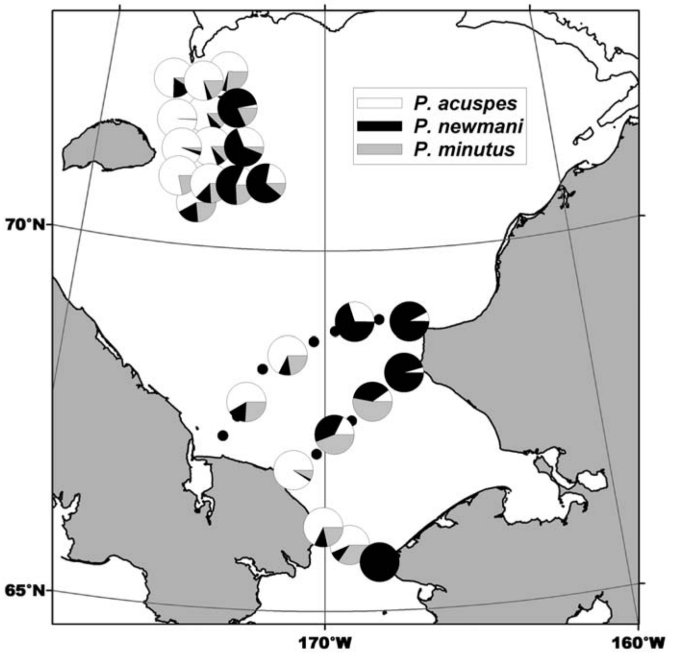

**Fig. 2.** Relative numerical contribution of *Pseudocalanus* species in the Chukchi Sea observed in August 2004.

temperature, and *P. minutus* not significantly related to temperature but notably absent from stations where the upper 25 m exceeded 8 °C (Fig. 3).

### 3.2. Egg production

Egg production experiments were executed at a total of 20 stations, but not all species were present in adequate numbers to provide results at each. In total, egg production rates could be determined in 15 cases for *P. acuspes*, in 8 cases for *P. newmani* and in 5 cases for *P. minutus*, with slightly more experiments yielding estimates of mean clutch size. Within experiments, mean clutch size for each species was similar on each day, and data were therefore pooled across days. Mean clutch size varied between species (Fig. 4), with *P. newmani* producing significantly smaller clutches than the other two species (paired *t*-tests, $P<0.0001$), which were not significantly different from each other (paired *t*-test, $P=0.68$). Most of this difference was driven by an underlying positive relationship between clutch size and body length (Fig. 5; $r^2=0.66$, $P<0.0001$) in the form: Clutch size $=0.040PL-19.1$. The relationship was even stronger ($r^2=0.84$) if only *P. acuspes* and *P. newmani* clutches were considered.

Generally, the number of clutches produced per day declined between the first and second day, and was extremely low on the third day. Thus, EPR was significantly higher if calculated for the first day rather than averaged over the first 2 days for *P. acuspes* ($5.2\pm0.6$ eggs female$^{-1}$ day$^{-1}$, declined to $4.3\pm0.4$; paired *t*-tests $P=0.04$) and *P. newmani* ($3.8\pm0.7$ eggs female$^{-1}$ day$^{-1}$, declined to $2.6\pm0.4$; $P=0.02$), but was not significantly different for *P. minutus* ($5.4\pm2.0$ eggs female$^{-1}$ day$^{-1}$, declined to $4.6\pm0.9$; $P=0.58$) due to high variability. EPR averaged over 2 days had slightly less variability than when estimated from only the first day (Fig. 6), and was weakly related to body length ($r^2=0.22$, $P=0.012$), suggesting other environmental factors also influenced the population egg production rates. After adjusting for body weight by calculating SEP, no relation to body size remained (Fig. 7), and as observed for EPR, SEP values were lower when calculated over 2 days than when only the first day was considered. There were no obvious spatial patterns in the SEP rates, nor clear patterns of between-species differences at individual stations (Fig. 8), although such comparisons were hampered by the relatively low number of cases where adequate numbers of females of each species occurred simultaneously within experiments, and the low rates of egg production (i.e. only 1–6 eggs female$^{-1}$ day$^{-1}$). Attempts to standardize for temperature did not clearly establish any difference in SEP between the species (Table 1). Relationships were not apparent between chlorophyll and SEP as well.

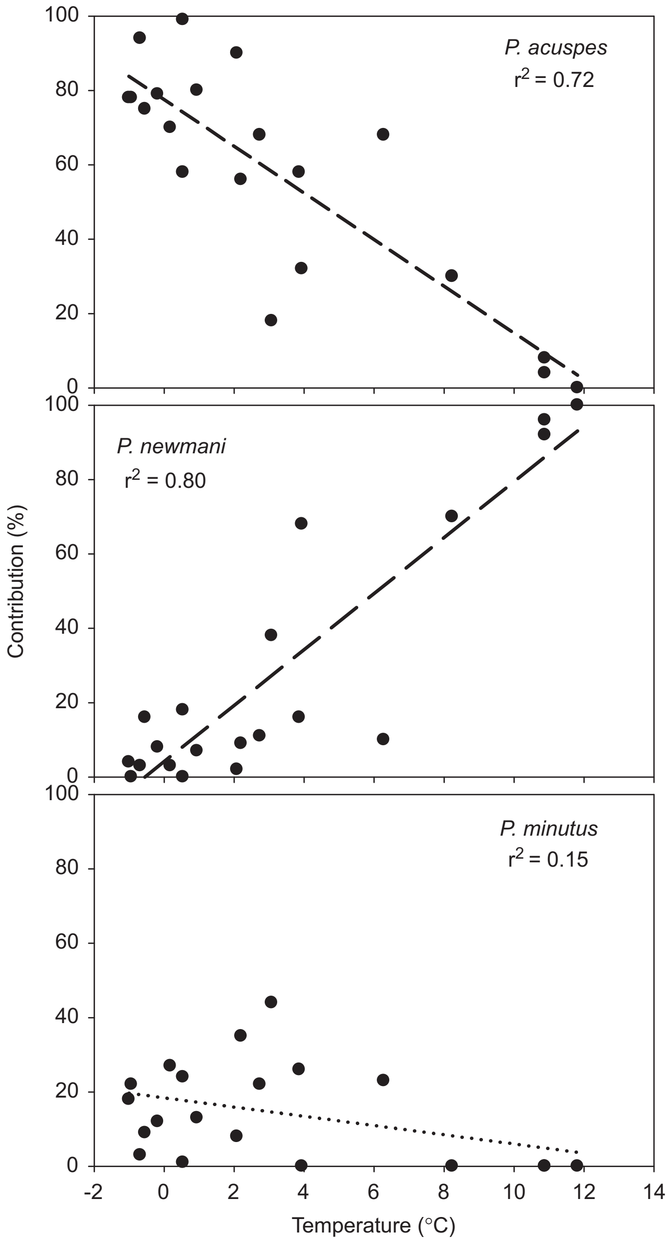

**Fig. 3.** The relationship between the mean temperature of the upper 25 m, and the relative numerical contribution of *Pseudocalanus* species in the Chukchi Sea during August 2004.

## 4. Discussion

Throughout the Arctic's marginal seas, *Pseudocalanus* species are major components of the holozooplankton (e.g. Conover and

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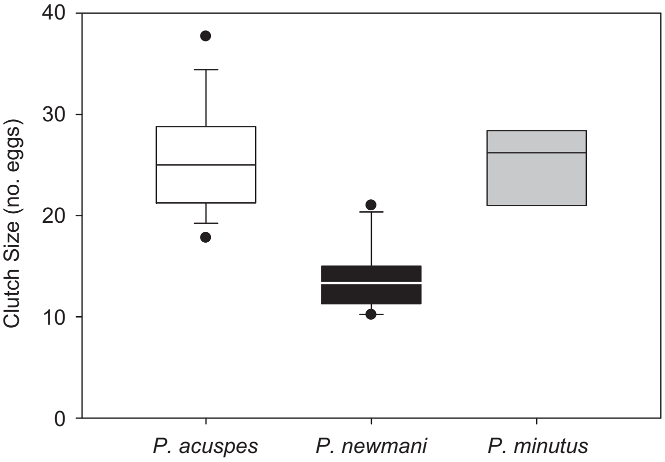

**Fig. 4.** Clutch sizes of *Pseudocalanus* species in Chukchi Sea during August 2004. The line through the box is the sample median; limits of the box are the 25th and 75th percentile. Whiskers are the 10th and 90th percentiles and the single points are the 5th and 95th percentiles, and are absent from *P. minutus* due to limited sample size.

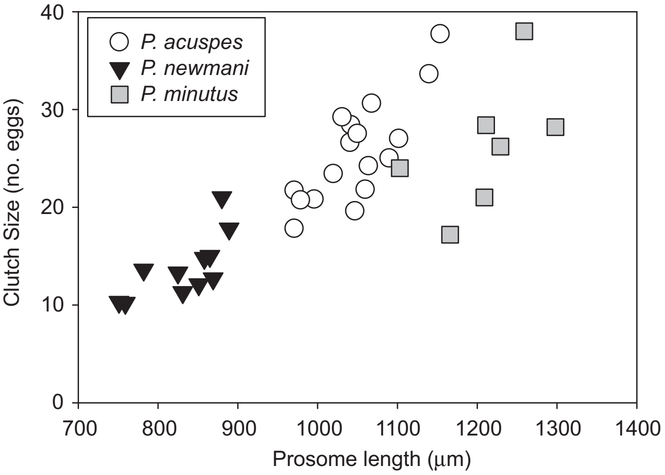

**Fig. 5.** Mean clutch sizes of *Pseudocalanus* species in Chukchi Sea during August 2004. Each point represents the mean for a single experiment for which at least 4 clutches were produced.

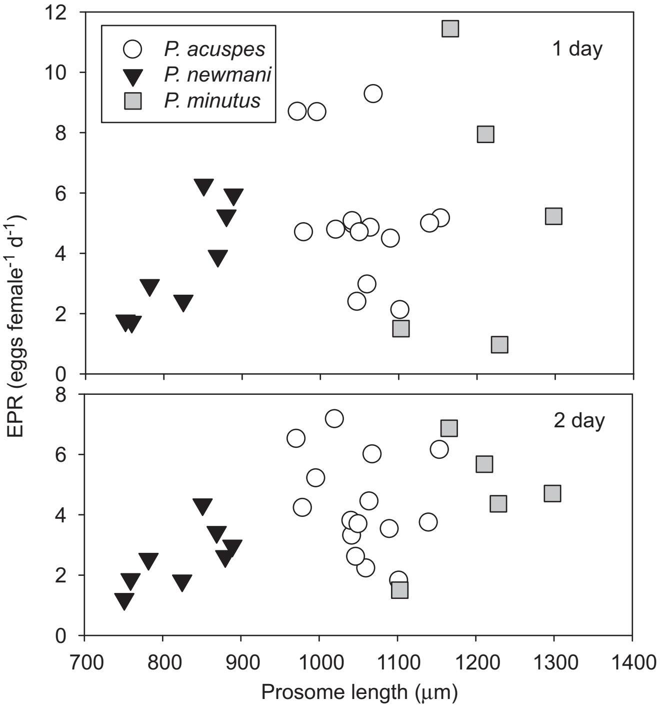

**Fig. 6.** Egg production rate of *Pseudocalanus* species in Chukchi Sea during August 2004, as calculated from 1- and 2-day incubations. Each point represents the mean for a single experiment for which at least 10 females of that species were incubated.

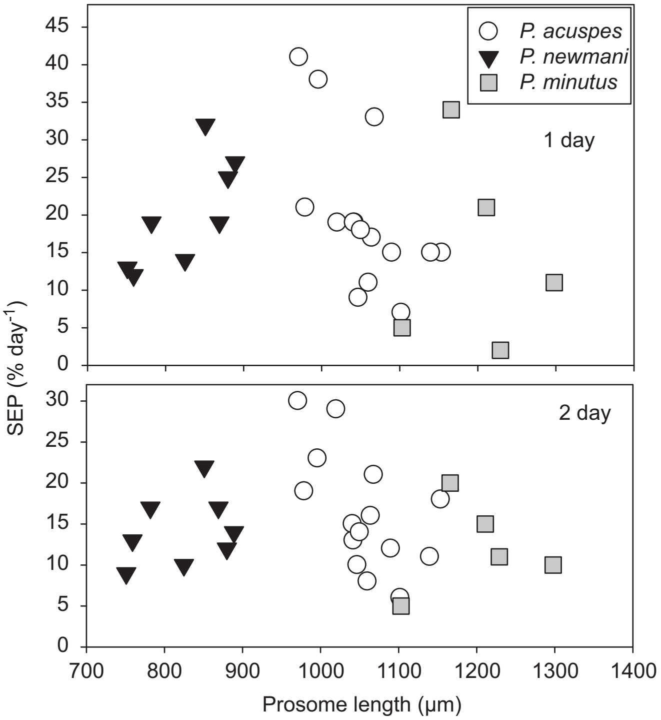

**Fig. 7.** Mass-specific egg production rate of *Pseudocalanus* species in Chukchi Sea during August 2004. Each point represents the mean for a single experiment in which at least 10 females of that species were incubated.

Huntley, 1991; Pertzova and Kosobokova, 2003; Lischka and Hagen, 2005; Hirche et al., 2006; Hop et al., 2006; Michel et al., 2006; Schmid et al., 2006, Wassmann et al., 2006), but are absent from its deep central basins (Kosobokova et al., 1998; Kosobokova and Hirche, 2000; Ashjian et al., 2003; Kosobokova and Hopcroft, 2009). In these marginal seas, *Pseudocalanus* numbers are usually in the thousands per cubic metre, they typically represent one of the top 4–5 species numerically (exceeded only by *Oithona similis*), and at times may represent as much as 50% of the biomass (Lischka et al., 2001; Fahl et al., 2001; Arashkevich et al., 2002; Hopcroft et al., in press).

Sufficient studies have now been conducted since the recognition of the *Pseudocalanus* component species that we can begin to construct distributional patterns for the individual species. In general, *P. minutus* and *P. acuspes* are recognized as the most abundant species in Arctic seas (e.g. Pertzova and Kosobokova, 2003; Lischka and Hagen, 2005; Michel et al., 2006), and there are indications that occurrences of *P. minutus* and *P. acuspes* outside of Arctic waters represent relict populations in places such as deep fjords (e.g. Prince William Sound, Alaska—Napp et al., 2005), deep basins (e.g. Bedford Basin, Nova Scotia—McLaren et al., 1989a) or seasonally ice-covered waters now isolated from the Arctic Ocean (e.g. Baltic Sea—Renz and Hirche, 2006; White Sea—Pertzova and Kosobokova, 2003; Sea of Okhotsk—Pinchuk, Pers. Obs.). The Chukchi Sea and adjoining Beaufort Shelf represent a special case where both *P. newmani*, and to a lesser extent *P. mimus*, have been

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recorded (Frost, 1989). Both these species are characteristic of the temperate/subpolar North Pacific where they dominate the shelf zooplankton communities during summer (Napp et al., 2005; Coyle and Pinchuk, 2005). The high abundance of particularly *P. newmani* in the waters along the Alaskan coast is reflective of its transport into the region with the Alaska Coastal Current's (ACC) flow from the coastal Gulf of Alaska through the Bering Sea and into the Arctic (Weingartner et al., 1998). The high abundance of this species into the south-eastern corner of Herald Valley is consistent with the spreading and bifurcation of water north of the straight that directs water through Herald Valley and Barrow Canyon (Pickart et al., 2006, 2009). In this study *P. newmani* was associated with warmer waters: temperature in the upper 25 m of the Alaska Coastal waters where *P. newmani* dominated exceeded 10 °C, as did the upper 5 m of the water column in the southeast corner of Herald Valley where *P. newmani* continued to dominate. This suggests both physically and biologically that a significant component of the ACC is entrained in the flow toward Herald Valley (also see Hopcroft et al., in press). Oddly, work to the northeast of our southern study area (i.e. Barrow, Alaska region) conducted almost concurrently suggests the *Pseudocalanus* community was dominated by *P. minutus* and *P. mimus* (Llinás, 2007; Lane et al., 2008).

Interestingly, water entering the western and central Bering Strait is already rich in *P. minutus*, *P. acuspes*, and to a lesser extent, *P. newmani*. The presence of these species in "downstream" waters of the southwestern Bering Sea was noted during the original description of these species (Frost, 1989), and has been confirmed in studies in coastal Kamchatka (Samatov, 2001). Both *P. minutus* and *P. acuspes* likely predominate in these waters due to their export from the seasonally ice-covered Sea of Okhotsk where *Pseudocalanus* is abundant (Pinchuk and Paul, 2000) and both of these species occur (Pinchuk, Pers. Obs.). In contrast, the predominance of *P. acuspes* in Herald Valley likely reflects the eastward and north-eastward flow of Siberian Shelf waters (see Pickart et al., 2009). This speculation cannot be fully confirmed because species-specific data from the Siberian shelf are sparse, and when available, have not resolved *P. minutus* from *P. acuspes* (i.e. Pavshitks, 1994; Pinchuk, 1994). Despite the warm surface water in the southeast of Herald Valley, partial ice cover existed along the eastern and northern-most stations. At these and other stations where the entire water column water was colder than 3 °C (see Pickart et al., 2009) the *Pseudocalanus* community was dominated by greater than 75% *P. acuspes*.

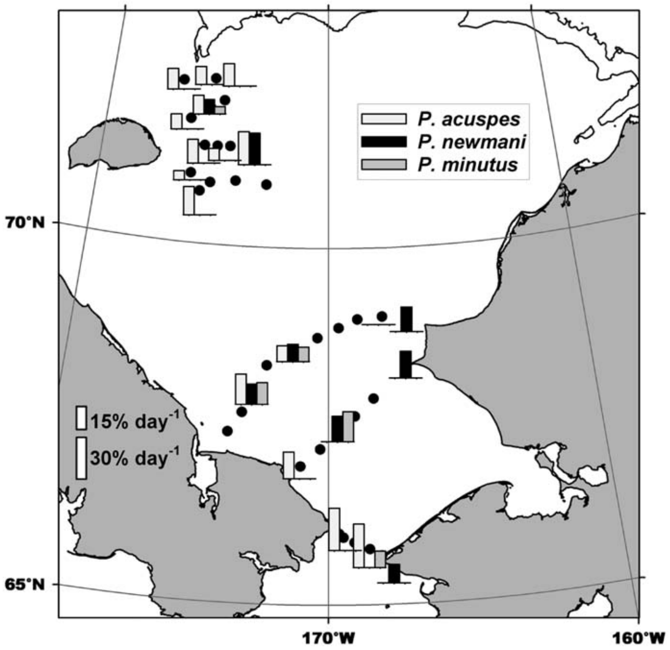

**Fig. 8.** Spatial patterns of *Pseudocalanus* species mass-specific egg production (SEP) in the Chukchi Sea during August 2004.

The truly interesting aspect of this study is the extent to which *P. newmani* penetrates the Arctic Ocean. We can only presume that the observed distributional range of *P. newmani* is ultimately related to their survival as they are diluted into colder Arctic waters. Although the survival of a species is determined by many factors, one would presume that rates of egg production are not only influenced by temperature but reflective of overall metabolic health (e.g. Isla et al., 2008). Studies in the downstream waters of the coastal Gulf of Alaska, show *P. newmani* to be actively growing (Liu and Hopcroft, 2008) as well as reproductively active (Napp et al., 2005) from April to October over a temperature range of 5–15 °C. Work in Japan shows *P. newmani* can remain reproductive at 3 °C (Lee et al., 2003), and we measured egg production at stations were surface waters were $<0$ °C. Not surprisingly, our observed EPR and SEP of *P. newmani* are very similar to summer rates observed by identical techniques in the Gulf of Alaska (Table 2), but our rates also overlap with food-satiated rates at comparable colder temperatures (i.e. Lee et al., 2003). In contrast, in Toyama Bay, Japan, the period of active growth and reproduction by *P. newmani* is restricted to February–April when the surface waters are 10–12 °C, and the species disappears from the Bay after the surface waters become $>14$ °C (Yamaguchi et al., 1998).

While the observed rates of egg production by *P. newmani* at the warmer locations in the study are not surprising, the relatively high rates of egg production measured at the colder stations are somewhat surprising. Initially it appears that EPR by *P. newmani* is lower than the polar species, but because of the relationship between prosome length and clutch size in *Pseudocalanus* (e.g. McLaren, 1963, 1965; Ban et al., 2000; Napp et al., 2005; Renz et al., 2007), when size is taken into account *P. newmani* appears to have similar rates of production as the more polar species. Although egg production data for *P. minutus* and *P. acuspes* are sparse, our observed rates appear consistent with those observations (Table 2), suggesting a surprising consistency of

**Table 1**
Daily specific egg production rates for *Pseudocalanus* species in the Chukchi Sea.

| | Observed | | Ambient environment | | Incubator | |
|---|---|---|---|---|---|---|
| | 1 day | 2 day | 1 day | 2 day | 1 day | 2 day |
| *P. acuspes* | 0.20 ± 0.03 | 0.16 ± 0.02 | 0.28 ± 0.03 | 0.23 ± 0.02 | 0.24 ± 0.03 | 0.19 ± 0.02 |
| *P. newmani* | 0.20 ± 0.03 | 0.14 ± 0.02 | 0.20 ± 0.04 | 0.14 ± 0.02 | 0.24 ± 0.04 | 0.16 ± 0.02 |
| *P. minutus* | 0.15 ± 0.06 | 0.12 ± 0.03 | 0.17 ± 0.07 | 0.15 ± 0.03 | 0.16 ± 0.05 | 0.13 ± 0.02 |

Rates are presented for the first day and averaged over 2 days. Observed rates are presented as well as standardized to 5 °C, from either the mean ambient temperature over the collection depth (i.e. upper 25 m), or the mean measured over the incubation period.

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**Table 2**
Egg production rate (EPR) and daily specific egg production rate (SEP) of *Pseudocalanus* species from cold, Arctic and subarctic waters.

| Location | Mean clutch size | EPR (eggs $d^{-1}$) | SEP ($d^{-1}$) | Temperature (°C) | Source |
|---|---|---|---|---|---|
| *P. acuspes* | | | | | |
| Chukchi Sea | 18–38 | 2–9.5 | 0.16/0.20 | −1–6 | This study |
| Baltic Sea | 4–12 | 0.1–3.6 | 0.01–0.13 | 3–9 | Renz et al. (2007) |
| *P. newmani* | | | | | |
| Chukchi Sea | 10–20 | 1–6 | 0.14/0.20 | 2–12 | This study |
| Dabob Bay, USA | | Max. 2.68 | | 7.5–13 | Frost (1985) |
| Dabob Bay, USA | N/A | 1–4 | 0.4 | 12 | Jonasdottir, (1989) |
| Dabob Bay, USA | 1–34 | 0.5–4 | 0.4 | 7–20 | Halsband-Lenk et al. (2005) |
| SW Hokkaido, Japan | 18–35 | 5–8 | 0.3–1.1 | 3–15 | Lee et al. (2003)[a] |
| Funka Bay/SW Hokkaido | 12–30 | N/A | N/A | 2–17 | Ban et al. (2000) |
| Coastal Gulf of Alaska | 4–60 | 1.4–9.3 | 0.20 | 5–15 | Napp et al. (2005), and unpublished |
| *P. minutes* | | | | | |
| Chukchi Sea | 17–38 | 2–12 | 0.12/0.15 | 0–6 | This study |
| White Sea | 13–19 | N/A | N/A | 0.5–12 | Pertsova and Kosobokova (1996) |
| Barents Sea | 1–8[b] | N/A | N/A | −0.5–0.5 | Hirche and Kosobokova (2003) |
| Barents Sea | 11 (1–39) | N/A | N/A | −0.5–0.5 | Kosobokova and Lischka (1997) |
| *Pseudocalanus* spp. | | | | | |
| Auke Bay, Alaska | N/A | 0.5–5.3 | N/A | 4.5–7.3 | Paul et al. (1990) |
| SE Bering Sea | 33 (14–45) | 5.1 | 0.13[c] | 3–5 | Dagg et al. (1984) |
| Baltic Sea | 13–15 | 0–2.3 | N/A | 2–10 | Isla et al. (2008) |

N/A—not available.

[a] Food-satiated lab rate.

[b] Based on numbers of eggs still attached after collection.

[c] Estimated using mean prosome length of ~1100 μm.

mass-specific egg production across species within the genus *Pseudocalanus*. Although undoubtedly these rates are modified by temperature, food climate and body size, if we standardize for these influences, our observed rates are consistent with recent compilations for this genus (i.e. Hirst and Bunker, 2003; Bunker and Hirst, 2004).

If, for the moment, we consider all three of these species as ecologically equivalent, then what is the future expectation for the role of *Pseudocalanus* in the Chukchi Sea and Arctic in general? Using polynyas as models of the future ice regime on Arctic shelves, it has been suggested that a climate-induced reduction of ice-cover duration on Arctic shelves will favor the population growth of the predominant large calanoid copepods and *Pseudocalanus* (Ringuette et al., 2002). Similarly, under climate warming, the reduction of ice cover on the Mackenzie Shelf is expected to affect zooplankton distribution patterns, to the potential advantage of *Pseudocalanus* spp. (Darnis et al., 2008). Both the Arctic cod (*Boreogadus saida*) and the much larger Atlantic cod (*Gadus morhua*) prey primarily on the naupliar stages of *Pseudocalanus* during the larval stage (e.g. Michaud et al., 1996). Initially a proliferation of *Pseudocalanus* should improve the early survival and population size of the cod (Darnis et al., 2008), thus improving food availability to vertebrate predators (seals, birds, whales), the majority of which feed primarily on this small fish (Welch et al., 1992).

At the same time, the general warming trends are expected to cause changes in the phenology of species (e.g. Edwards and Richardson, 2004; Richardson, 2008) and these in turn will result in the shifts of biogeographic boundaries of individual species (such as within the genus *Pseudocalanus*). One might therefore expect to see an increased prevalence and penetration of *P. newmani* onto the Arctic shelves, at least during summer since it appears to be more prevalent within warmer waters. On the one hand, egg production experiments suggested that this Pacific species is as productive during summer as are its Arctic equivalents on a weight-specific basis. Thus, if total biomass of *Pseudocalanus* remained constant while the proportion of *P. newmani* increased, there might be no actual change in ecosystem productivity, or even a potential increase driven the by the increased temperature. However, because *P. newmani* is smaller, their increased prevalence might influence the efficiency of coupling to higher trophic levels if they are a less suitable prey than the larger-bodied, more lipid-rich polar species (Richardson and Schoeman, 2004).

## 5. Conclusions

The species-specific distribution of *Pseudocalanus* appears closely related to the origin and temperature of the water masses present in this region, and could therefore serve as a biological marker in future surveys. Despite differences in water mass associations, the species co-occurring in the Chukchi Sea appear to have similar mass-specific reproductive rates during at least the summer, suggesting factors other than reproduction must influence their relative distribution. Future surveys, over a wider domain, should help resolve patterns and causes of the different species dominances over the shelves, and the extent of penetrations of Pacific waters and the associated *P. newmani*. Greater attention should be focused on the relative importance of the local *Pseudocalanus* species compared to the expatriates, and the consequences for the flow of energy within this ecosystem.

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