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Distribution and species-specific egg production of *Pseudocalanus* in the Gulf of Alaska

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Pseudocalanus species are important contributors to the secondary production of the northern hemisphere mid- to high-latitude oceans. In the coastal Gulf of Alaska, Pseudocalanus are present year round and are represented by three species. In 2001, Pseudocalanus mimus was the dominant Pseudocalanus species on the shelf during spring and summer, comprising 30–100% of the total, while Pseudocalanus newmani dominated in Prince William Sound (10–90%). Pseudocalanus minutus were only abundant in Prince William Sound during early spring. Egg production (by number and volume) was a function of female prosome length and decreased from spring to summer; however, significant variability was attributable to regional influences that were independent of size. For the same sized female, P. newmani produced more eggs per clutch than P. mimus. Pseudocalanus mimus, however, tended to have a larger mean egg size than P. newmani. Consequently, clutch volumes of the two species were indistinguishable. Pseudocalanus egg production rates (EPRs) (eggs female^{-1} day^{-1}) were lower in July and August (ca. 2–4) than April and May (ca. 1–9), but total egg production by the population (eggs day^{-1}) was nearly equivalent for the two time periods due to higher female concentrations in summer.

INTRODUCTION

The copepod genus *Pseudocalanus* is common in temperate and boreal pelagic ecosystems and is thought to play an important role in the trophic ecology of these systems due to its high rate of production relative to larger crustacean zooplankton (Corkett and McLaren, 1978). Researchers once published results for a complex of copepods (often called *Pseudocalanus* spp. or *Pseudocalanus elongatus*); a relatively recent revision of the genus now recognizes seven species (Frost, 1989). This has facilitated species-specific studies of the genus that examine differences in life history of sympatric species (McLaren *et al.*, 1989a; Bucklin *et al.*, 2001).

The coastal Gulf of Alaska (northern North Pacific Ocean) is a biologically productive ecosystem that appears to be driven by downwelling (Weingartner *et al.*, 2002; Stabeno *et al.*, 2004). It contains many harvested and protected living resources. In this region, *Pseudocalanus* is generally the second most numerically abundant genus (behind *Oithona*) among the crustacean zooplankton (Cooney, 1986; Incze *et al.*, 1997; Coyle and Pinchuk, 2003), yet only a single report has documented species proportions (Siefert, 1994). Within this system and the adjacent Bering Sea, *Pseudocalanus* spp. are estimated to be among the top secondary producers (Coyle and Pinchuk, 2002) and are important prey items for both larval and juvenile fish (Kendall and Nakatani, 1991; Hilgruber *et al.*, 1995; Napp *et al.*, 1996; Schabetsberger *et al.*, 2003).

Female *Pseudocalanus* spp. are clutch spawners, laying their eggs into a single egg sac that is carried by the female until hatching. Egg production rates (EPRs) are a function of the clutch size, the embryonic duration and the interclutch period (Corkett and McLaren, 1978). Egg production is thought to be independent of food concentration above ca. 100 μg C L^{-1} (Corkett and McLaren, 1978) or ~2 mg Chl m^{-3} (Bunker and Hirst, 2004). Temperature has a strong influence on EPR by modulating clutch size (through female size) and embryonic duration (Lee *et al.*, 2003). Species-specific

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EPRs are only now appearing in the literature (Ban *et al.*, 2000; Lee *et al.*, 2003), but there are few comparisons among sympatric species.

The present study combines initial results of two research groups' efforts to understand secondary production in the coastal Gulf of Alaska as part of the **N**orth **E**ast **P**acific **GLOB**al Ocean **EC**osystems Dynamics Program (NEP GLOBEC; Weingartner *et al.*, 2002). We ask here, what are the temporal and spatial patterns of female *Pseudocalanus* species distribution in the Gulf of Alaska, and how does female length, clutch size and egg production vary between the species during a year?

METHOD

Samples were collected, and experiments conducted aboard the R/V *Alpha Helix* during the GLOBEC Process and Long-Term Observation Program (LTOP) cruises in 2001. Process cruises were in April, May and late July/early August, while LTOP cruises occurred in April, May, July, August and October. Investigations were generally conducted in three regions of the shelf (inner, middle and outer) and in Prince William Sound, a large, deep fjord (Fig. 1). The geographic location of stations varied among Process cruises, but not LTOP cruises (GAK Stations 1, 4, 9, 13 on the Seward Line and PWS2). The inner shelf station was typically within the Alaska Coastal Current during both types of cruises. Concurrent environmental sampling was accomplished with a SeaBird 911*Plus* CTD. Preserved samples from the first year of LTOP cruises (1998) were also used to examine cross shelf patterns in species distributions. Their method of collection was identical to the protocol given below.

Zooplankton collections

Samples for the temporal and spatial distribution of small zooplankton were collected with a 25-cm diameter mouth

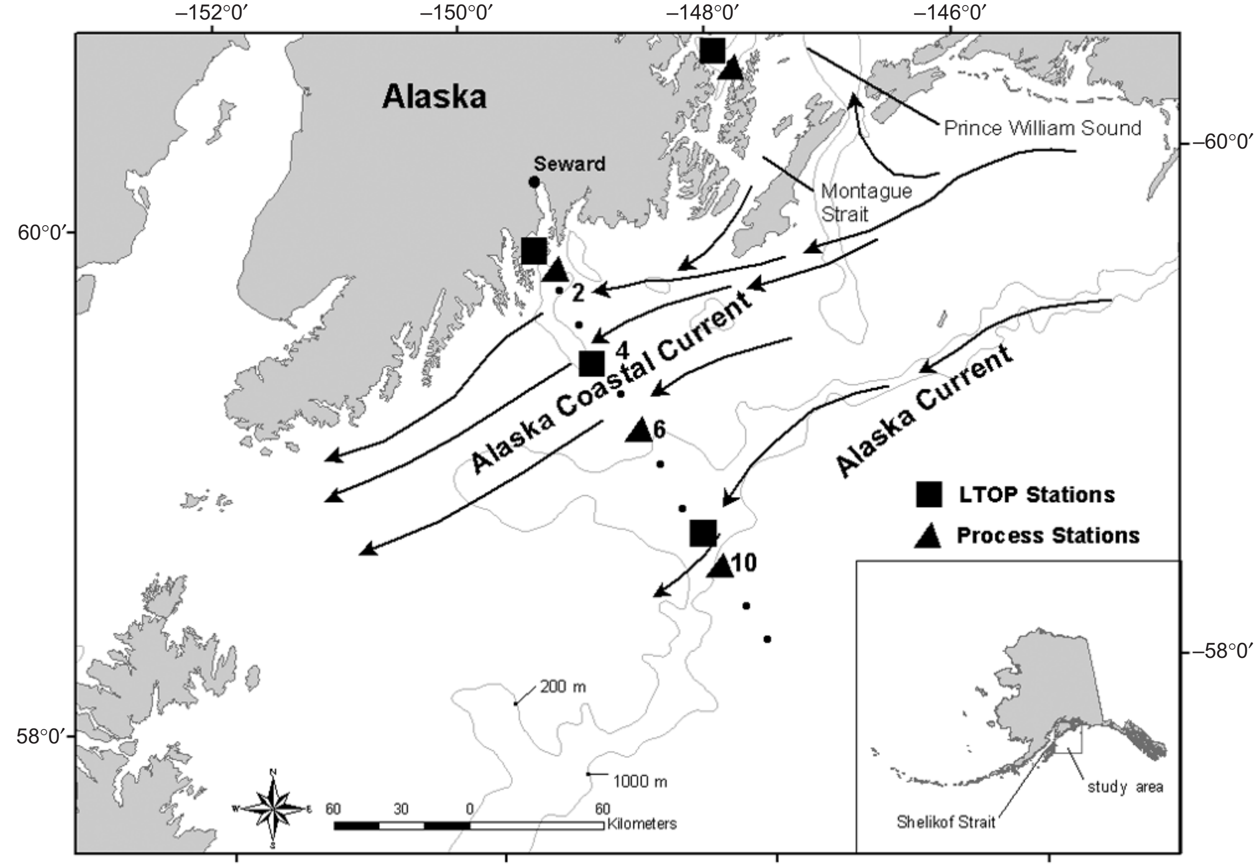

Fig. 1. **GLOB**al Ocean **EC**osystems (GLOBEC) study area. The Northeast Pacific GLOBEC study area was in the northern Gulf of Alaska between 145° and 152° W. Measurements were taken along the Seward Line (GAK Stations) and in Prince William Sound. The Alaska Coastal Current was always over the inner shelf (between GAK 1 and 3). The term 'middle shelf' refers to the area between GAK 4 and GAK 6, and the 'outer shelf' was seaward of GAK 9. Station in Prince William Sound was PWS2.

CalCOFI vertical egg tow (CalVET) frame (Smith *et al.*, 1985) or a QuadNet (four, 25-cm rings welded together in a square frame). Both CalVET nets had 150-μm mesh and the catch from the two nets was combined. The QuadNet had two 150- and two 53-μm mesh nets (on opposing corners), and the catches from identical mesh sizes were combined (only the 150-μm data are presented here, samples from the 53-μm mesh nets were used to capture copepodite stages of smaller copepods such as *Oithona* and copepod nauplii). Tows of both frames were vertical, from 100 m to the surface. Flow meters in each net mouth were used to estimate filtered volume. All samples were preserved in 5% buffered formalin seawater. Samples from the LTOP cruises were enumerated in Fairbanks, Alaska. Samples from the Process cruises were sorted and enumerated at the Polish Plankton Sorting and Identification Center, Szczecin, Poland. In both cases, *Pseudocalanus* copepodites were only identified to the generic level. Species identifications for *Pseudocalanus* females were accomplished in Seattle and Fairbanks by the authors (C. Baier and C. Clarke).

Egg production studies

Females for egg production studies were captured using comparable techniques: Process cruises used a 0.8-m diameter ring net (150- or 200-μm mesh) while the LTOP cruises used a 0.5-m diameter net with 200-μm mesh net. In both cases, nets were equipped with large volume cod ends and slowly hauled vertically through the upper water column. Sorting was usually completed within 1, or at most, 2 h of capture for the Process cruises and within 2–3 h for LTOP. Non-egg sac bearing *Pseudocalanus* females were transferred with a wide bore pipette to the incubation chambers (20-ml plastic vials, Process; 70-ml polystyrene tissue culture flask, LTOP) filled with prescreened water from the mixed layer (35-μm screened surface water, Process; 100-μm screened subsurface water, LTOP). All incubations were accomplished within 1–2°C of the mixed layer temperature.

Process cruises incubated 30–50 females per experiment in the dark for 24 h at the mixed layer temperature; a new experiment was initiated each day for three successive days while at the same station. The first two Process cruises incubated up to four females per container; however, species-specific EPRs were only calculated when each and every clutch from an experiment could be attributed to a species. Clutch size–length relationships were only recorded for females with attached egg sacs. The third Process cruise used one female per container. All females were preserved at the end of the experiment by adding formalin to the vial. LTOP cruises incubated 60–80 females under natural lighting cycles at mixed layer temperatures for 3 days. LTOP experiments incubated a single female per flask. Females were checked every 24 h; females producing egg sacs before the conclusion of the experiment were removed and individually preserved. All non-producing females were preserved together at the conclusion of each LTOP experiment.

In the laboratory, females were identified to species (Frost, 1989) and measured for prosome length. The number and size of eggs in a clutch were also determined, with either an ocular micrometer (Process) or a computer-assisted measuring system (LTOP; Roff and Hopcroft, 1986). The operational measurement resolution was 6 μm for the ocular micrometer measurements of eggs, 36 μm for female prosome length and ≤ 5 μm (eggs and prosome length) for the computer-assisted method. EPR was calculated as (mean observed clutch size) × (fraction of females extruding a clutch)/the incubation time in days (1 day for Process and 2 or 3 days for LTOP; Runge and Roff, 2000).

Statistical analyses

Analysis of covariance (ANCOVA) was used to detect significant differences among sources of variation (e.g. laboratories, regions or months) in the relationship between prosome length and clutch size. A natural logarithm transformation of prosome lengths was necessary to stabilize the variance. Linear regressions were accomplished with Systat v. 10.2. Descriptive statistics for the concentration of *Pseudocalanus* females were calculated after applying the 4th root transformation to the raw data.

RESULTS

Distribution of species

Initial investigation of species distribution on the northern Gulf of Alaska shelf in 1998 demonstrated that *P. mimus* females dominated the catches during late winter to early autumn (Fig. 2). *Pseudocalanus newmani* was present on almost all occasions and was most prevalent in the spring samples (March–May). *Pseudocalanus minutus* was rarely observed. There did not appear to be a cross-shelf trend in the relative occurrence of the three species (Fig. 2); females were most abundant in the summer and autumn samples (not shown).

In 2001, when both the GLOBEC Process and LTOP program components were in the field, we observed a similar pattern to that observed in 1998 using the species composition of females obtained for egg production experiments (Fig. 3). In April, May, July and August, *P. mimus* dominated the shelf stations, with the exception

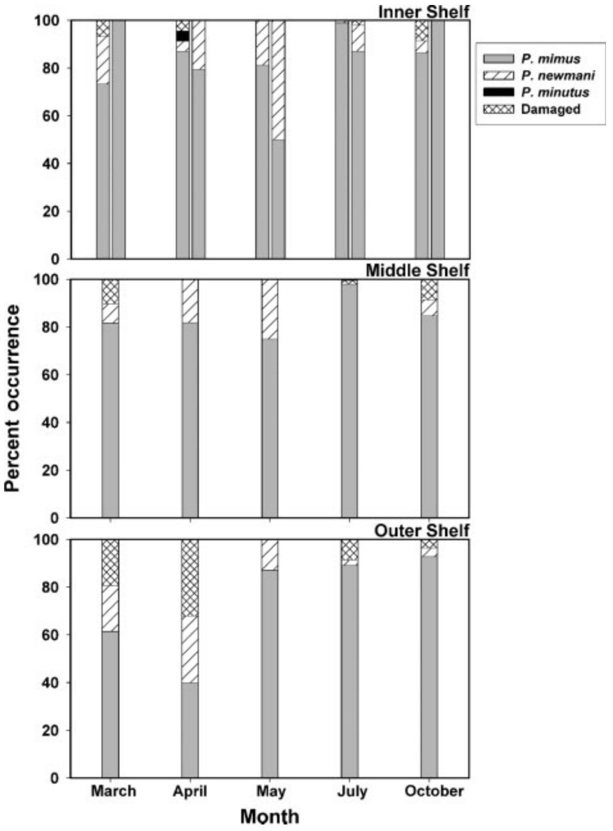

Fig. 2. Seasonal distribution of *Pseudocalanus* adult females by species in the northern Gulf of Alaska, 1998. Percent occurrence was determined from CalCOFI vertical egg tow (CalVET) or Quadnet samples collected by the **GLOB**al Ocean **EC**osystems (GLOBEC) Long-Term Observation Program (LTOP) (K. Coyle, University of Alaska, Fairbanks, unpublished). Samples were obtained at GAK Stations 1 and 2 (inner shelf), 6 (middle shelf) and 9 (outer shelf).

of the LTOP collections in the inner shelf (May and August). *Pseudocalanus newmani* females dominated collections in Prince William Sound and were sometimes a significant fraction of the total number of females in the coastal region. *Pseudocalanus minutus* occurred more frequently in our 2001 collections than in 1998 and was most prevalent during spring in Prince William Sound, which was not sampled in 1998.

Seasonal trends in female length

Female prosome lengths exhibited a distinct seasonal signal (Fig. 4) with the largest individuals of both species being found from late April through May. There was an increase in the median prosome length of animals collected on the Seward Line between the April LTOP and Process cruises, and a subsequent decrease in length between the July LTOP and Process cruises. The mean (lower 95%CI/upper 95%CI) prosome length for *P. newmani* decreased from 0.975 (0.965/0.985) to 0.794 (0.788/0.801) mm, while the mean length of *P. mimus* decreased from 1.127 (1.119/1.134) to 1.001 (0.993/1.009) mm. The prosome length of female *P. mimus* in April was the most variable with both very small and very large individuals present.

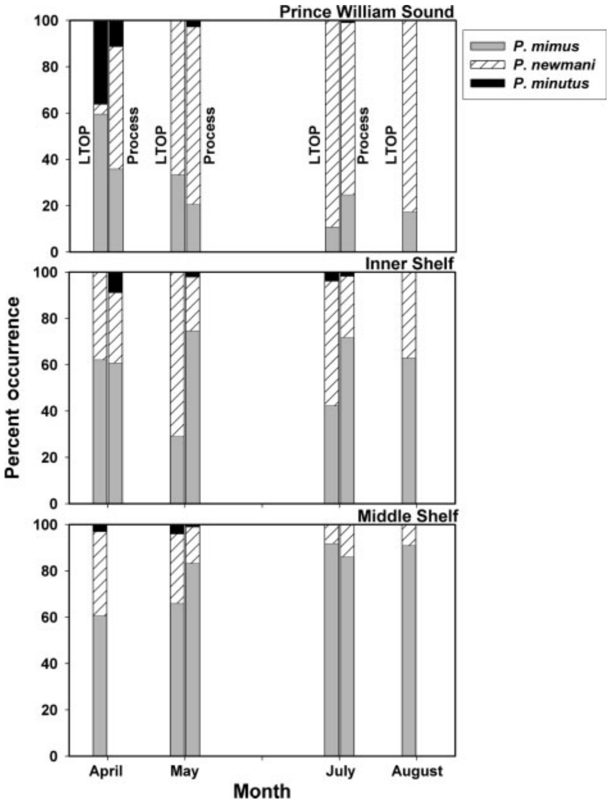

Fig. 3. *Pseudocalanus* species composition in the Northern Gulf of Alaska. Percent occurrence of females for the three species found in this region during spring and summer of 2001 in three of the four areas sampled. Percent occurrence was determined from live collections used for the egg production experiments.

Species-specific egg production

The number of eggs per clutch increased as a function of female prosome length (Fig. 5A and B), and for the same sized female, *P. newmani* tended to lay more eggs per clutch than *P. mimus*. There were no significant differences between the Process and LTOP data sets for clutch size as a function of female length for the two species (ANCOVA; *P. newmani*, $P > 0.68$; *P. mimus*, $P > 0.64$). There was a difference in the mean egg diameter for the two species. *Pseudocalanus mimus* tended to have slightly larger eggs (mean diameter ± SE; 121.0 ± 1.0 μm) than *P. newmani* (112.0 ± 0.7 μm) for the same size female (Fig. 5C). Egg diameter was not a function of clutch size

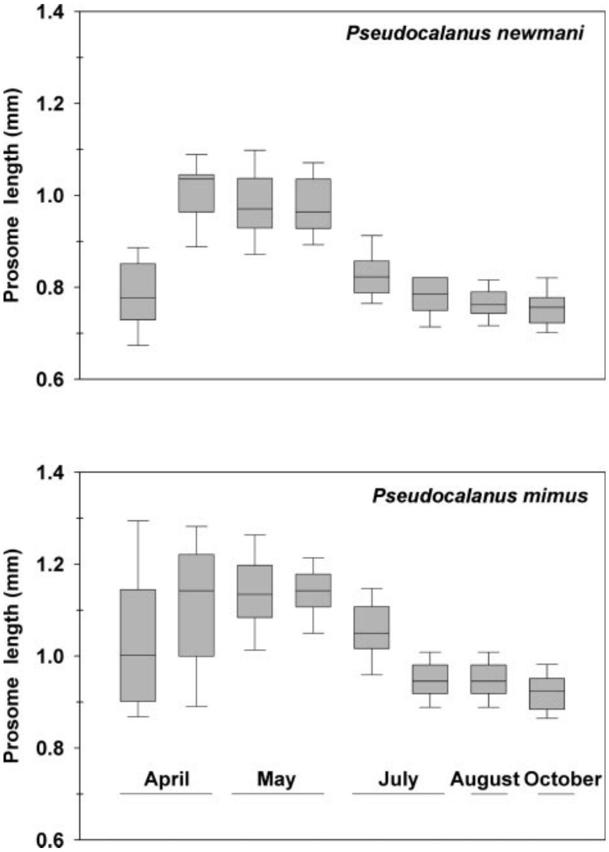

Fig. 4. Variations in *Pseudocalanus* female prosome length. Box plots of the data from both projects showing prosome length as a function of month. The line through the box is the sample median; limits of the box are the 25th and 75th percentile and whiskers are the 10th and 90th percentiles. In April and May, the Long-Term Observation Program (LTOP) data (first set of each pair) were collected in the first half of the month and the Process data were collected in the second half. In July, the LTOP data were collected in early to mid-July and the Process data were collected late July/early August.

(Fig. 5D). Clutch volume (number of eggs × average egg volume) for the two species was nearly equivalent and a function of female length (not shown).

Predicting clutch size from female length

The statistics of predicting clutch size from female length were complicated for our data. The ANCOVA model included terms for female prosome length, month, region, data source (LTOP or Process), duration (LTOP data only), their interaction terms and the residual variance. The duration term (LTOP data only; see Methods) was not significant for *P. newmani* ($P = 0.724$), but *P. mimus* had a significant duration × month interaction term ($P = 0.048$). Further use of the LTOP data for *P. mimus* combined data from the first and third durations as they could not be distinguished from one another (*a posteriori* test).

For both species, prediction of clutch size from female length was complicated by several significant interactions between variables [*P. newmani*, month × region ($P = 0.001$) and length × month ($P = 0.002$); *P. mimus*, month × source ($P = 0.006$) and month × region ($P = 0.015$)]. To take into account each and every complicating factor would have resulted in a large number of regression equations with very low sample sizes for each. We chose instead to pool the data and examine predictions based on month (the strongest effect; Table I). When we did this, 8 of 10 linear relationships by month (4 for each species) had slopes that were significantly greater than zero. For *P. newmani*, clutch size increased with prosome length for all months except July. The increase was greatest in April when the mean prosome length of females increased between the first and second cruises (Fig. 4). Clutch size as a function of prosome length for *P. mimus* also increased for all months except July. The greatest increase was in May, not April as observed for *P. newmani*. (Table I).

Overall, when the data from all months were combined, there was a strong trend in clutch size as a function of female prosome length for each species ($P < 0.001$). There was also a high degree of variability (Fig. 6) associated with each regression, and this produced low amounts of explained variance for each relationship (*P. newmani*, $R^2 = 0.595$; *P. mimus*, $R^2 = 0.347$).

Temporal trends in egg production and egg production rate

During 2001, *Pseudocalanus* spp. females were most abundant in Prince William Sound and on the inner shelf (Alaska Coastal Current), and their concentration increased during the year until August when the highest concentration of females was observed over the inner shelf (Fig. 7). Mean individual EPRs varied over the course of our sampling (Fig. 8). Initial rates (April) were quite variable among regions. EPR was high in May for both species (>8 eggs female^{-1} day^{-1}) in one or more regions. *Pseudocalanus newmani* had high rates of egg production in Prince William Sound (late April through late May) and *P. mimus* had its highest rate over the middle shelf (GAK 4) in early May. By July, the EPR had dropped for both species; both species had their lowest rates in Prince William Sound and their highest rates on the middle shelf. In August and October, the EPR for both species was moderate (2–4 eggs female^{-1} day^{-1}) and less variable among habitats than in July.

Patterns of population egg production were different for the two species (Fig. 8). *Pseudocalanus newmani* had more or less constant production in Prince William Sound from late April to August, except for the large increase in early May. Total production over the inner

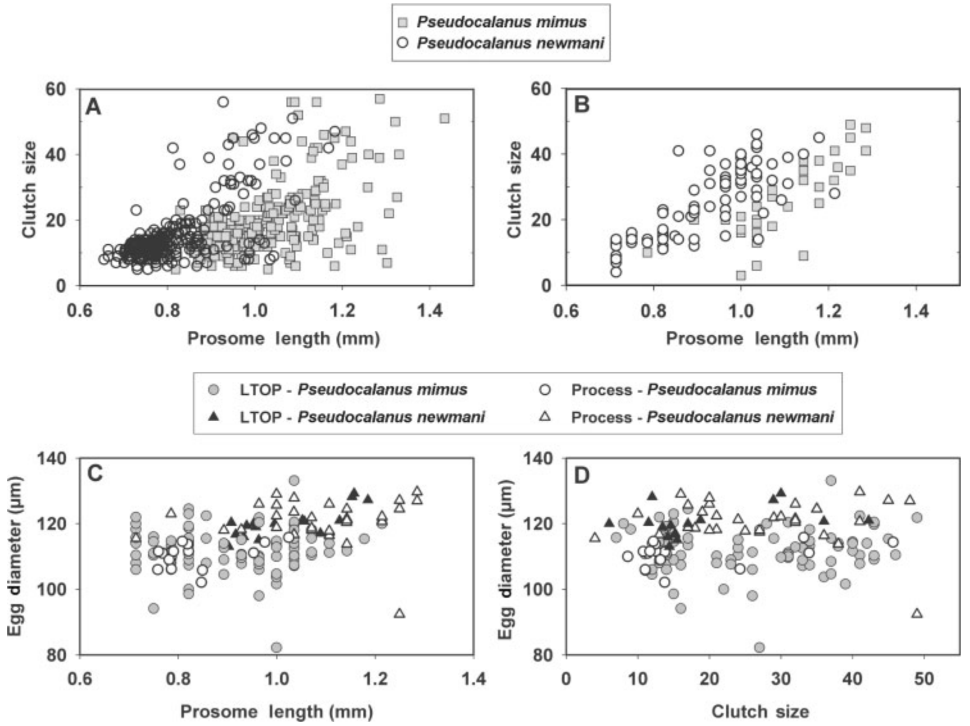

Fig. 5. Species-specific clutch size, prosome length and egg diameter. Data are species and laboratory-specific; clutch size is the number of eggs per female. (**A**) Long-Term Observation Program (LTOP)-clutch size versus female prosome length; (**B**) Process-clutch size versus female prosome length; (**C**) Combined egg diameter versus female prosome length; (**D**) Combined egg diameter versus clutch size.

Table I: Pseudocalanus species-specific predictive equations for clutch size (CS, number of eggs) as a function of prosome length (PL, mm)

Month	Equation	*N*	*P*	R^2
Pseudocalanus newmani				
April	$CS = 29.32 + 65.59 \ln (PL)$	44	<0.001	0.570
May	$CS = 33.84 + 27.21 \ln (PL)$	70	0.047	0.043
July	$CS = 14.26 + 3.808 \ln (PL)$	49	0.577	0.000
August	$CS = 18.60 + 25.69 \ln (PL)$	88	<0.001	0.240
October	$CS = 17.40 + 19.14 \ln (PL)$	73	<0.001	0.183
All Months	$CS = 29.81 + 63.62 \ln (PL)$	324	<0.001	0.595
Pseudocalanus mimus				
April	$CS = 18.65 + 48.06 \ln (PL)$	26	0.002	0.318
May	$CS = 19.61 + 95.20 \ln (PL)$	29	0.003	0.254
July	$CS = 18.74 - 21.39 \ln (PL)$	25	0.311	0.003
August	$CS = 15.17 + 14.51 \ln (PL)$	53	0.016	0.092
October	$CS = 18.459 + 41.35 \ln (PL)$	27	0.002	0.282
All Months	$CS = 18.17 + 50.56 \ln (PL)$	160	<0.001	0.346

Equations use the combined data of the Long-Term Observation Program (LTOP) and Process cruise, and are presented for each month when experiments were conducted.

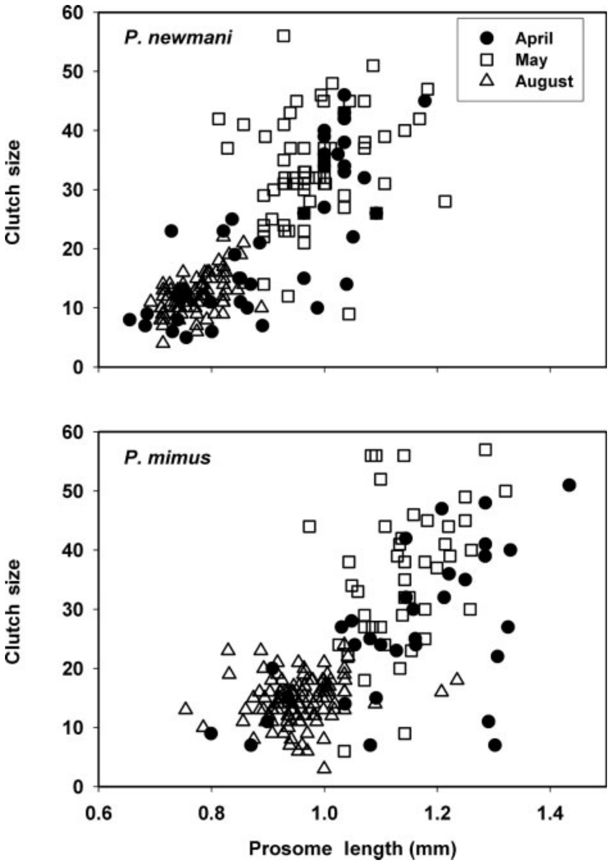

Fig. 6. Combined Long-Term Observation Program (LTOP) and Process species-specific clutch size and female length by month. Clutch size is the average number of eggs per female.

shelf was without the large spike seen in Prince William Sound. *Pseudocalanus mimus* on the other hand appeared to have increasing production over the inner and middle shelf from early May through August. Both species had low production in October, although the values were higher in October than in early April.

DISCUSSION

Pseudocalanus spp. play a key role in the trophic ecology of northern temperate and subarctic waters (Corkett and McLaren, 1978). Their estimated production in other coastal ecosystems, for example Georges Bank, is often much greater than that of larger copepods such as *Calanus* (Davis, 1984a). In the Gulf of Alaska, average annual production of *Pseudocalanus* spp. was estimated to be >700 μg C m^{-2} $year^{-1}$ (or >70 μg C m^{-3} $year^{-1}$ over the upper 100 m). This was more than seven times greater than *Calanus* spp., but comparable to the combined production of *Neocalanus plumchrus* and *Neocalanus flemingeri* (Coyle and Pinchuk, 2003).

Secondary production by *Pseudocalanus* spp. is thought to be controlled more by temperature than by food (McLaren, 1978; Davis, 1984b; Frost, 1985; Klein Breteler *et al.*, 1995; Hirst and Lampitt, 1998; Hirst and Bunker, 2003), thus their populations may respond directly to interannual and decadal variability in water temperature making them a good species for study of the direct consequences of global climate change (Coyle and Pinchuk, 2002; Möllmann *et al.*, 2003). In late winter and spring, their egg production is important for

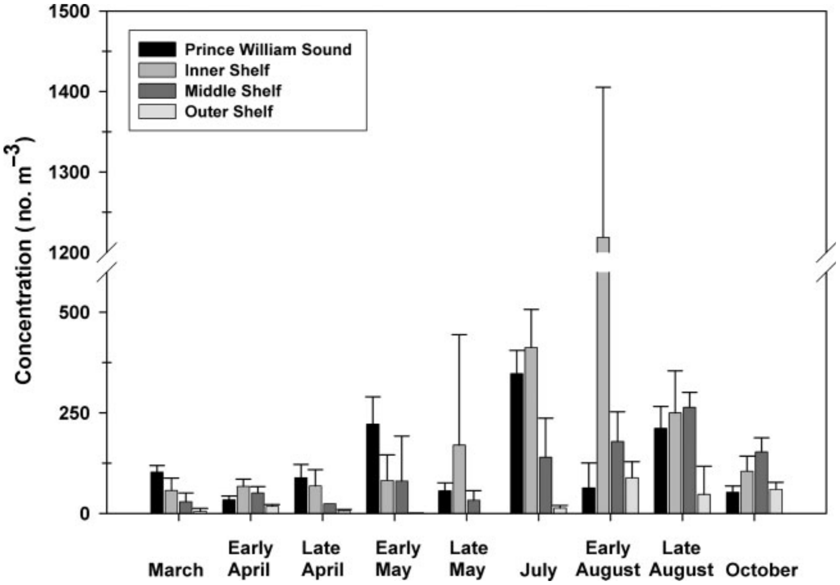

Fig. 7. Seasonal variation of *Pseudocalanus* spp. females. Concentration of females (no. m^{-3}) in the four regions sampled by the two programs from March to October.

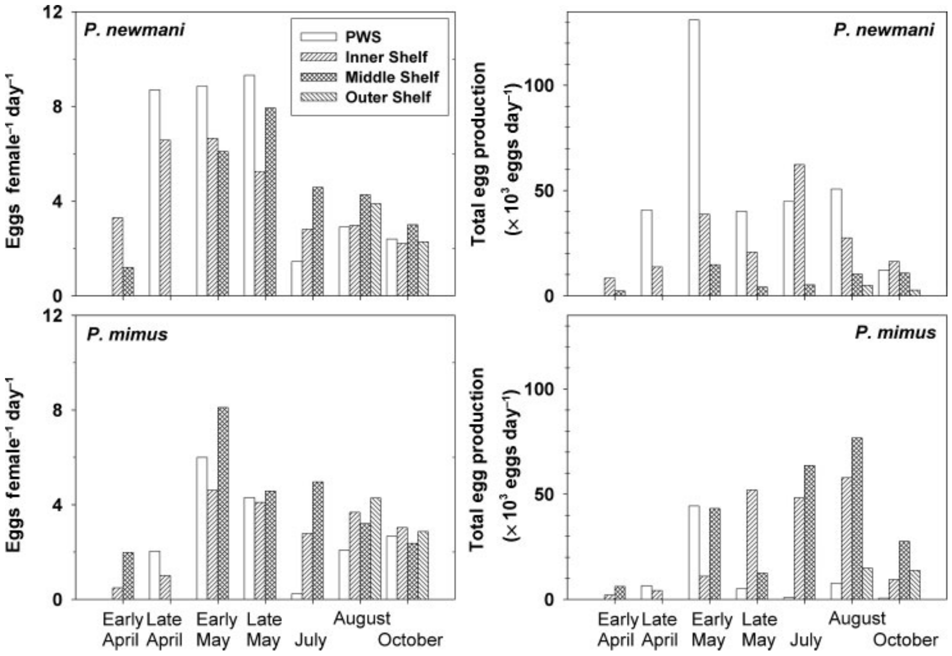

Fig. 8. Seasonal variation in species-specific *Pseudocalanus* egg production rates (EPRs) and total egg production. Left Panels: mean EPR (egg female^{-1} day^{-1}) by *Pseudocalanus* as a function of month and region. Right Panels: estimated total egg production (eggs m^{-3}day^{-1}) is the product of the mean EPR and mean adult female abundance of each species (no. m^{-3}).

establishing prey levels of recently spawned fish larvae such as walleye pollock (Kendall and Nakatani, 1991; Napp *et al.*, 1996) and Atlantic cod (Lynch *et al.*, 2001; Hinrichsen *et al.*, 2002). Due to improvements in the taxonomy of the genus (Frost, 1989), as well as the introduction of molecular techniques (Sévigny *et al.*, 1989; Bucklin *et al.*, 2001), scientists are now able to address species-specific ecological and life history problems of this genus (McLaren *et al.*, 1989a,b; Yamaguchi *et al.*, 1998; Lee *et al.*, 2003).

In the Northeast Pacific, Gulf of Alaska GLOBEC program, rate measurement of processes, including *Pseudocalanus* egg production, were conducted on both LTOP and Process cruises. Due to limited availability of ships, both programs used the same vessel, but at different times. This provided better temporal coverage during spring and summer than would have been achieved if the programs had simultaneously sampled. Our combined studies used similar, but slightly different techniques, coming to the same conclusions. For example, although species distributions were described from animals sorted for experimental work rather than direct net tows, the results were very similar. This is remarkable given that the live sorting as well as final identifications were accomplished by different persons. Similarly, female size distributions and EPRs were very similar, despite the different experimental protocols (e.g. duration of the incubations).

Distribution of species

Frost (Frost, 1989) describes the coastal northern Gulf of Alaska as having three *Pseudocalanus* species present: *P. mimus* (temperate), *P. minutus* (arctic) and *P. newmani* (temperate). In 2001, we found the distribution of species to be similar to other regions of the Pacific coast of North America (off Oregon and Washington) where *P. mimus* tends to dominate the coastal current (Landry *et al.*, 1991; Keister and Peterson, 2003; Morgan *et al.*, 2003). Similarly, *P. newmani* was found in Prince William Sound year round, similar to its occurrence in Puget Sound (Jonasdottir, 1989). *Pseudocalanus newmani* is also important in Funka Bay, Japan (Ban *et al.*, 2000; Lee *et al.*, 2003), another walleye pollock nursery area (Kendall and Nakatani, 1991). Individual species of *Pseudocalanus* may show geographical differences in life history traits (McLaren *et al.*, 1989a). For example, numbers of *P. newmani* diminish in Bedford Basin during the warm water season (>10°C), while those in Prince William Sound appear to increase and maintain their dominance during the warm water season (maximum ca. 15°C). In Toyama Bay, Japan, the period of active growth and reproduction by *P. newmani* is restricted to February, March and April when the surface waters are 10–12°C. They begin to disappear from the Bay after the surface waters become >14°C (Yamaguchi *et al.*, 1998).

Pseudocalanus moultani, a temperate species, was present in one offshore Gulf of Alaska sample (Frost, 1989), but was not observed in this study. In Washington state, *P. moultani* occurs during winter and early spring in Puget Sound. Its absence from Prince William Sound is noteworthy.

In 2001, *P. minutus* was abundant in early spring, but soon disappeared from the samples. We suspect that the timing of its disappearance varies among years, as a subsequent year (2003) shows higher abundances into late April/early May (Hopcroft and Clarke, unpublished data; Napp and Baier, unpublished data). It may sink from the surface waters of Prince William Sound as a CV copepodite to overwinter in the deep holes (Cooney *et al.*, 2001; Hopcroft, unpublished data) as in Toyama Bay, Japan (Yamaguchi *et al.*, 1998), and Bedford Basin (McLaren *et al.*, 1989a). *Pseudocalanus minutus* represents one of several relict arctic species found within Prince William Sound (Coyle and Pinchuk, in press).

Seasonal trends in female length

A seasonal decrease in adult *Pseudocalanus* spp. size concomitant with increasing temperatures and decreasing food concentrations is commonly observed [Yamaguchi *et al.*, 1998 (and references therein); Ban *et al.*, 2000; Halsband and Hirche, 2001; Lee *et al.*, 2003]. In our study, female size peaked in spring and then decreased with increasing temperature. Gulf of Alaska surface water temperature increased from about 5°C to nearly 15°C during the course of our investigations. Animals at the end of summer were approximately 15–23% shorter in length compared to those in the spring. In the laboratory, growth of *P. newmani* incubated at different temperatures began to diverge at the second copepodite stage (C2; Lee *et al.*, 2003). In that study, the reduction of mean female total length between 6 and 15°C was 15% (from 1.3 to 1.1 mm), consistent with our observations.

April length frequency distributions for *P. mimus* had long tails or a second mode at the smaller sizes. This was also observed for *P. newmani* from Shelikof Strait, Alaska (Siefert, 1994). It is not clear whether the smaller individuals represent a different generation or animals from a different source. Application of cohort analysis in these regions may thus be difficult given the complicated hydrography of the Gulf of Alaska.

Species-specific egg production

Despite the colder temperatures observed in the Gulf of Alaska, the EPRs for *P. newmani* and *P. mimus* were similar and comparable to the mean (ca. 4 eggs $\text{female}^{-1}\text{day}^{-1}$) reported for these species in other locales (Table II). Our maxima for *P. newmani* and *P. mimus* (9.3 and 8.1 eggs female^{-1} day^{-1}, respectively), however, tended to be slightly higher than that observed in other regions of the North Pacific Ocean. A recent compilation of EPRs (Bunker and Hirst, 2004) suggested that saturated EPR for *Pseudocalanus*, standardized to 15°C is 7.8 eggs female^{-1} day^{-1}. Scaling this published statistical result to 5°C (using a Q_{10} of 2) predicts an EPR of ~4 eggs female^{-1} day^{-1} which is similar to the mean from other locations (Table II), but seriously underestimates the maximum rates observed in this

Table II: Comparison of Pseudocalanus species-specific egg production rates (EPRs, eggs female^{-1} day^{-1}) from the North Pacific Ocean

Location	EPR	Temperature (°C)	Clutch size predictability	Source
Pseudocalanus newmani				
Dabob Bay, USA	1–4	12	0.03	Jonasdottir (1989)
SW Hokkaido, Japan	5–8	3–15	0.71	Lee *et al.* (2003)
Funka Bay/SW Hokkaido	NA	2–17	0.90	Ban *et al.* (2000)
Coastal Gulf of Alaska	1.4–9.3	5–15	0.60	This Study
Pseudocalanus mimus				
California Current	3.9	<10–14		Peterson, Gómez-Gutiérrez and Morgan (2002)
California Current	1.7–6.6	8–18		Gómez-Gutiérrez and Peterson (1999)
Coastal Gulf of Alaska	1.0–8.1	5–15	0.35	This Study
Pseudocalanus spp.				
Auke Bay, Alaska	0.5–5.3	4.5–7.3		Paul *et al.* (1990)
SE Bering Sea	5.1	3–5		Dagg *et al.* (1984)
Dabob Bay	0.3–3.3	8–18	0.47	Frost cited in Ohman (Ohman, 1985)

NA, not available. Clutch size predictability is the amount of explained variance (R^2) for the relationship between clutch size (number of eggs) and female size (prosome or total length).

study at that temperature. We hypothesize that the cool temperatures and sustained production of large phytoplankton cells (in the Alaska Coastal Current and Prince William Sound) create favorable conditions for high reproductive output by *Pseudocalanus* (i.e. large females and food-replete waters).

The two species, *P. newmani* and *P. mimus,* have different reproductive strategies. For the same sized individuals, *P. newmani* has larger clutches than *P. mimus*, but *P. mimus* has larger eggs. Our egg diameter measurements were almost identical to those reported by Frost (Frost, 1989). The relative advantages of these strategies warrant future study particularly when the species co-occur. Recent studies demonstrate variable hatching success and a high proportion of births with presumably debilitating deformities associated with some diatom blooms (Ban *et al.*, 2000; Halsband-Lenk *et al.*, personal communication). Molecular markers will be useful to determine the relative survival/reproductive success of each of these species that co-occur in open coastal and fjord environments.

Predicting clutch size from female length

Within the Calanoida there exist relationships between brood volume and body volume, and egg diameter and prosome length for egg sac spawners (Mauchline, 1998). As in other studies of the genus *Pseudocalanus*, clutch size was a function of female size (prosome length, Corkett and McLaren, 1978). We did not, however, observe a relationship between egg diameter and prosome length over the short length interval measured during this study. Our statistical analyses suggest that length was not the only variable that contributed to clutch size. ANCOVA detected significant effects of the underlying seasonal cycle (i.e. month) and the location of the experimental animals (i.e. region) that were independent of variations in size. While general univariate regression equations can be used to predict clutch size over all regions, the most accurate equations for the coastal Gulf of Alaska would be ones uniquely developed for each region. Ideally one would construct a predictive equation for each combination species, month and region. Unfortunately, in this current study, sample size was insufficient to derive useful predictive equations for each region and month. Thus, for pragmatic reasons we chose to construct simple, univariate predictive equations by species and month and ignored the other sources of variability identified by the ANCOVA.

In other areas of the North Pacific Ocean, predictions of *Pseudocalanus* clutch size from length have been accomplished (Table II). Examples of studies of *P. newmani* outnumber those of *P. mimus* at this point in time. There is a large range in the amount of explained variance (R^2) for the various predictive relationships (0.03–0.90). The study with the highest amount of explained variance (Ban *et al.*, 2000) used averages from seven different experiments where both clutch size and female prosome length were allowed to vary. The lower explained variance in the present study is due, in part, to inclusion of data from the summer months when the population was dominated by small females with low individual reproductive output.

Temporal trends in egg production and egg production rate

Pseudocalanus species in the Gulf of Alaska increase in relative abundance as the summer progresses and *Neocalanus* species enter diapause (Incze *et al.*, 1997; Cooney *et al.*, 2001; Coyle and Pinchuk, 2003; Coyle and Pinchuk, in press). Due to their relatively high production rates compared with other late summer members of the mesozooplankton community, *Pseudocalanus* spp. are likely an important conduit of primary and secondary production to upper trophic levels. Large seasonal increases in the number of females in some areas of our study more than compensated for the smaller clutch sizes produced by the smaller summer females (mean clutch size was reduced by about 50–75%). Thus, total population of EPRs were approximately comparable between the early spring and late summer for *P. newmani* and increased from late April to August for *P. mimus*.

Increasing population size, in our study, suggests that rates of mortality did not keep pace with increases in reproduction as the season progressed. In addition to our increasing knowledge regarding the importance of predation (Ohman, 1985; Bollens, 1988; Eiane and Ohman, 2004), egg viability, hatching success and naupliar survival rates as a function of diet are just now being recognized as potentially important variables modifying recruitment in *Pseudocalanus* (Ban *et al.*, 2000; Halsband-Lenk *et al.*, personal communication). It would be interesting to explore whether species-specific differences are manifested in these variables, and whether they bear any relationship to the differences in the reproductive strategies (clutch size and EPR) observed between *P. mimus* and *P. newmani* in this study and in other regions.

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