

Egg production and early development of *Thysanoessa inermis* and *Euphausia pacifica* (Crustacea: Euphausiacea) in the northern Gulf of Alaska

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Abstract

Early life history patterns were studied in the dominant euphausiids from the northern Gulf of Alaska (GOA) in 2001–2004. Gravid females of *Thysanoessa inermis* were observed in April and May. Brood size varied from 10 to 1021 eggs with an average of 138 ± 19 (95% CI) eggs female⁻¹. Most gravid females started to release eggs within the first 2 days of incubation. The average number of eggs released per female was similar in incubation Day 1 and 2, but significantly smaller on Day 3 and 4. About 25% of the females were continuously releasing eggs over 3 days rather than producing a single distinctive brood. In contrast, gravid females of *Euphausia pacifica* were observed from early July through October. Most gravid females released eggs on the first day of observation, while only 2% of females produced eggs repeatedly. Brood size varied from 20 to 246 eggs with an average of 102 ± 12 (95% CI) eggs female⁻¹. The relationship between *E. pacifica* brood size and ambient chlorophyll-*a* concentration was sigmoidal ($r^2=0.73$), with food saturated brood size of 144 ± 14 (SE, $P<0.001$) eggs, and half-saturation occurring at 0.46 ± 0.02 (SE, $P<0.001$) mg chlorophyll-*a* m⁻³. The average interbrood interval of *E. pacifica* reared at 12 °C and satiated food conditions in the laboratory was ~8 days, suggesting their potential individual fecundity in the GOA was 1148–1530 eggs per spawning season. Hatching and early development (from egg to furcilia stage) was studied under 5 °C, 8 °C and 12 °C. Hatching was nearly synchronous and lasted 3–6 h, depending on incubation temperature. Development times from egg to the first furcilia stage ranged between 20 and 33 days for *T. inermis*, and 15 and 45 days for *E. pacifica* at 12 °C and 5 °C, respectively. Published by Elsevier B.V.

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1. Introduction

Thysanoessa inermis, *Euphausia pacifica* and *Thysanoessa spinifera* are the dominant euphausiid species found in the Gulf of Alaska (GOA) frequently occur-

ring in high numbers over the broad, deep shelf characteristic of its northern region (Coyle and Pinchuk, 2003, 2005). The oceanic *E. pacifica* are usually abundant over the outer shelf, while *T. inermis* and *T. spinifera* inhabit the inner shelf (Coyle and Pinchuk, 2005). These species are thought to be primarily grazers and predators on variety of phyto- and microzooplankton as well as suspended organic matter (Ponomareva, 1966; Bargu et al., 2003; Nakagawa et al., 2004). They are a major prey for many of the commercially

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harvested fishes in the GOA, including all species of salmon (e.g. Armstrong et al., 2005); pollock (e.g. Brodeur, 1998); herring (e.g. Hart, 1973); and sablefish (e.g. Sigler et al., 2001) as well as seabirds and baleen whales (Mauchline, 1980). Thus, euphausiids represent important elements in the transfer of energy from the lower trophic levels through the planktonic food web upwards to apex predators in the northern GOA marine ecosystem.

Egg production and growth are key parameters characterizing the rates at which euphausiids process material, and are related to euphausiid's potential to supply energy and matter to higher trophic levels. Egg production also determines the potential rate of recruitment to a population, thus representing an important parameter in demographic studies. Egg production is dependent on the resources available to adult females, and consequently may be food-limited, while egg hatching and postembryonic development times show strong temperature dependence in a wide range of animal groups, including zooplankton (Peterson, 2001; Gillooly et al., 2002).

Many euphausiid species are capable of releasing eggs more than once during a single spawning season (Ross and Quetin, 2000). Therefore, the information on brood size as well as frequency of brood releases, and duration of the reproduction season, are prerequisites for estimating individual and population fecundity. A traditional method of counting all stages of eggs in the ovary estimates the fecundity of *E. pacifica* from the Japan Sea to be 1200–1700 eggs female⁻¹ (Ponomareva, 1966). The same technique applied to *T. inermis* suggests a wide range, from 300 to 350 eggs female⁻¹ in the Barents Sea (Zelikman, 1958) to 1700 eggs female⁻¹ in the North Pacific (Ponomareva, 1966). Counting ovarian eggs may, however, lead to an overestimation since not all ovarian eggs are necessarily released (Iguchi and Ikeda, 1994). Broods, obtained during experimental incubations, comprised substantially smaller 12–296 eggs female⁻¹ for *E. pacifica* from the Japan Sea (Iguchi and Ikeda, 1994) and 30–110 eggs female⁻¹ for *T. inermis* from the Barents Sea (Dalpadado and Skjoldal, 1991), however, no multiple spawning events were observed in these studies. Recent work off the Oregon coast has documented repetitive spawning of *E. pacifica* in the laboratory, and estimated potential individual fecundity in excess of 6000 eggs per season (Feinberg et al., 2004). Indirect estimates, derived from observations on proportion of experimental *E. pacifica* females producing eggs over 24 h, and the duration of the spawning season in Puget Sound, imply individual fecundity of 600–4000 eggs female⁻¹ per season (Ross et al., 1982).

Despite their importance as prey for major commercial fisheries in the GOA and the Bering Sea, fundamental information on reproductive and developmental biology of these species is absent from this region, and for the temperature ranges characteristic of it. Nothing is known of fecundity for either *E. pacifica* at the northernmost extreme of its range in the northern GOA or for *T. inermis* in the entire subarctic North Pacific. Similarly, while the general development patterns of *T. inermis* and *E. pacifica* are well documented (Einarsson, 1945; Boden, 1950; Suh et al., 1993), there is little information on development rates of their early larval stages across the broad temperature range characteristic for the North

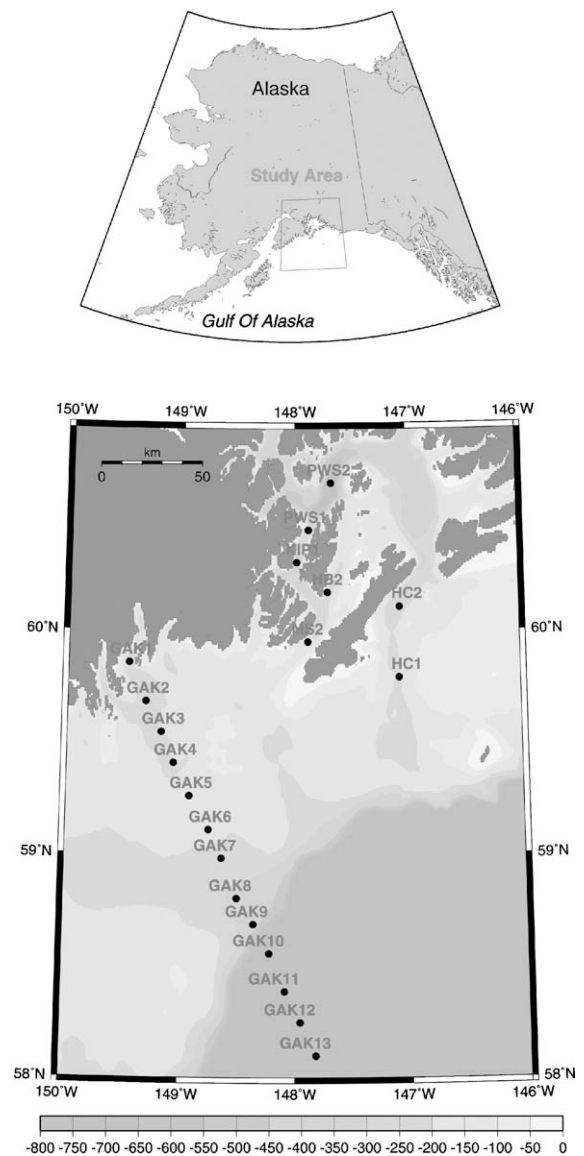


Fig. 1. Map of sampling locations in the Gulf of Alaska.

topis stage, they were individually transferred into single wells and inspected daily. Water and food were changed every 3–5 days. The larvae were fed *ad libitum* a mix of *Thalassiosira* spp., *Isochraxis galbana*, *Pavlova lutheri* and *Chromonas* spp. Feeding was augmented with *in situ* food (10–150 μm) collected in Resurrection Bay to provide a more nutritionally balanced diet. Cyanobacteria, ciliates, flagellates, diatoms, eggs, small nauplii, and small larvaceans were observed in varying concentrations in these *in situ* samples. The experiments were terminated when larvae reached furcilia stages or died, lasting up to 50 days at 5 °C. The euphausiid larvae were staged according to existing descriptions (Lebour, 1926; Einarsson, 1945; Boden, 1950; Suh et al., 1993). The abbreviations used are: N1–N2=nauplius 1 and 2; MN=metanauplius, C1–C3=calyptopis 1–3; F1–2=furcilia 1, 2.

To assess brood size and interbrood interval under food saturated conditions experimentally, a limited number of individual *E. pacifica* larvae hatched during summer 2003 were kept at 12 °C in larger 1000 ml tissue flasks. Water and food were changed every 3–5 days. Chlorophyll-*a* concentrations in the flasks were maintained at $\sim 15 \text{ mg m}^{-3}$. The experiments lasted till the animals died. When the larvae matured during spring 2004, they were inspected daily for eggs. When egg releases occurred, the eggs were counted and preserved. Only if the consecutive egg releases from a female were separated by more than 1 day, they were considered as separate broods.

2.3. Data analysis

All length measurements were made digitally (Roff and Hopcroft, 1986). Carapace length (CL, mm) was measured from the tip of rostrum to the posterior dorsal margin of the carapace. The total length (TL, mm) defined as distance from the tip of rostrum to the end of telson was estimated using linear regressions for euphausiids from GOA collected as outlined in Coyle and Pinchuk (2005):

$$\begin{aligned} \text{TL} &= 2.46\text{CL} + 2.99 \text{ for } T. \textit{inermis} \\ \text{TL} &= 3.75\text{CL} + 0.92 \text{ for } E. \textit{pacifica} \\ \text{TL} &= 2.60\text{CL} + 2.61 \text{ for } T. \textit{spinifera} \end{aligned}$$

All data were uploaded into MS ACCESS database and analyzed using standard STATISTICA routines. Data sets were log-transformed before running statistical tests to satisfy the assumption of normality. The abbreviations used are: CI — confidence interval; SE — standard error, SD — standard deviation.

3. Results

3.1. Egg production

Gravid females of *T. inermis* were observed only during April and May (Table 1). Most females started to release eggs within the first 2 days of incubation (Fig. 2A). The size of spawning females ranged from 16.7 mm to 28.3 mm in total length. The average number of released eggs per female was similar in Day 1 and 2, but significantly smaller on Day 3 and 4 (Fig. 2A). About 25% of females released eggs over 3 days rather than producing a single distinctive brood, while the number of eggs released per day significantly decreased (Fig. 2B). Egg production was arrested during molting. Only a single female produced eggs immediately after molting, and they proved to be non-viable. Brood size varied from 10 to 1021 eggs, and the average brood size was 138 ± 19 (95% CI, $n=195$) eggs female⁻¹. We suspect the smallest broods represented females that had partially released eggs prior to incubation.

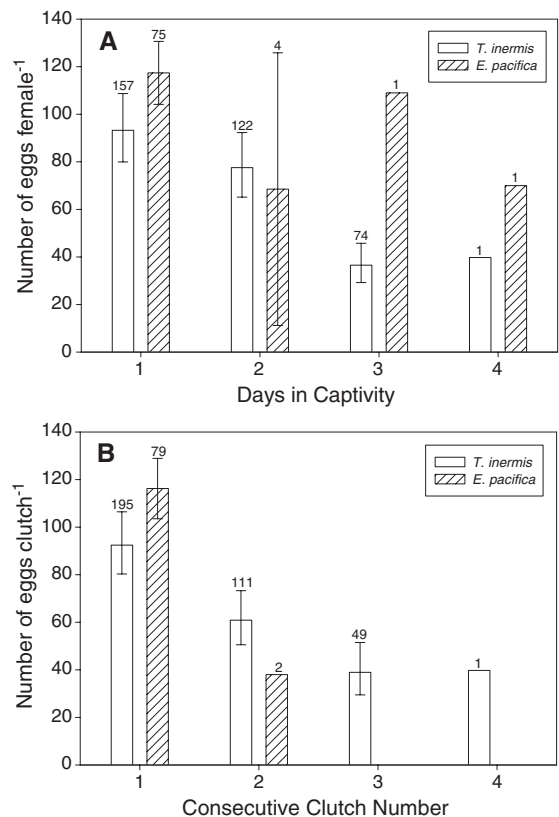


Fig. 2. Egg release of *Thysanoessa inermis* and *Euphausia pacifica* in the northern Gulf of Alaska. Error bars indicate 95% confidence interval. Numbers above the bars are the number of observations.

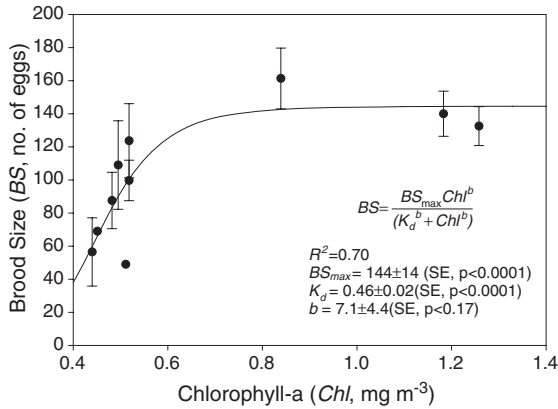


Fig. 3. Functional relationship between mean brood size of *Euphausia pacifica* and chlorophyll-*a* concentration approximated with sigmoidal Hill function (vertical bars — SE).

In contrast, gravid females of *E. pacifica* were observed from early July through October (Table 1). The total length of spawning females ranged from 17.4 mm to 25.6 mm. Most females released eggs on the first day of observation (Fig. 2A) and only 2 females (i.e. 2%) produced eggs repeatedly (Fig. 2B). Brood size varied from 20 to 246 eggs female⁻¹ and the average brood size was 102 ± 12 (95% CI, *n* = 79) eggs female⁻¹. Female body length explained only a small part of brood size variation (*r*² = 0.21 and *r*² = 0.27 for *T. inermis* and *E. pacifica*, respectively). The loss of eggs due to cannibalism in the experimental design was estimated at 11% over 12 h for *E. pacifica* and was considered negligible. There was no attempt to estimate cannibalism of *T. inermis*.

Occasionally we observed gravid females of *T. spinifera* from April through October. The total length of spawning females ranged from 25.2 mm to 31.5 mm, and brood size varied from 46 to 385 eggs and averaged

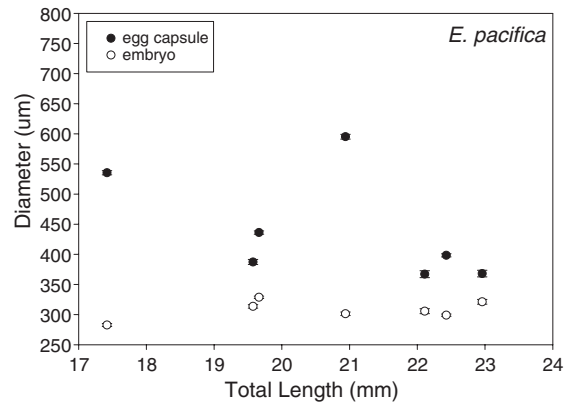
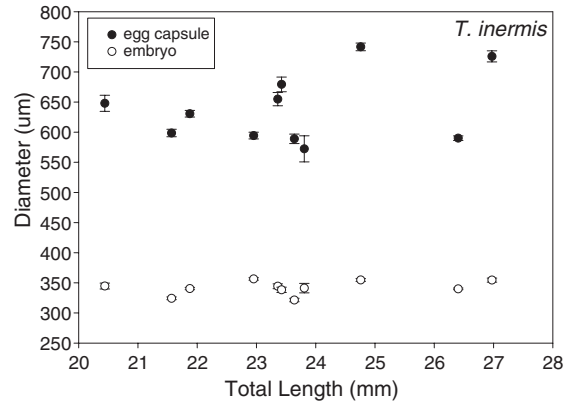


Fig. 5. Size of egg capsules and embryos vs. carapace length of females in *Thysanoessa inermis* and *Euphausia pacifica* from the northern Gulf of Alaska.

153.7 ± 53.8 (95% CI) eggs female⁻¹ (*n* = 13). The extremely adhesive eggs were usually found attached to the bottom of the containers and this made further study of the species problematic.

Much of the observed variation in brood size in *E. pacifica*, but not *T. inermis*, could be attributed to ambient chlorophyll-*a* concentrations. While curves

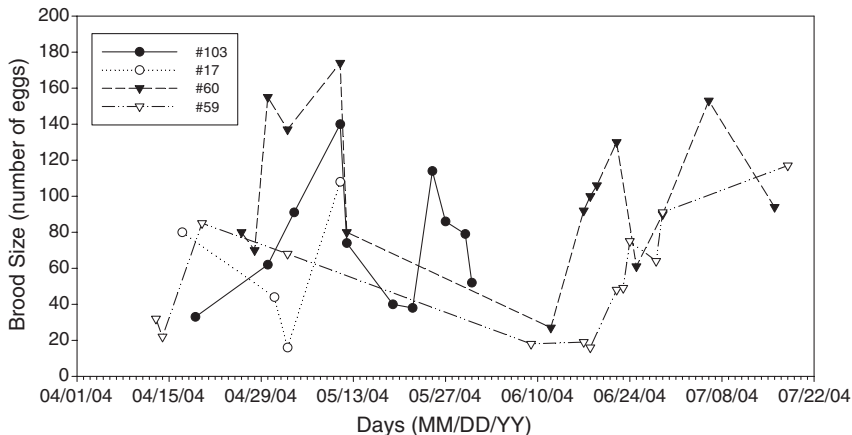


Fig. 4. Spawning of four laboratory-reared *Euphausia pacifica* females (with numbers assigned).

Table 2

Egg capsule, embryo and brood sizes in *T. inermis* and *E. pacifica* (mean values are with 95% CI unless otherwise noted)

Species/Region	Egg capsule (μm)		Embryo (μm)		Brood size (no. eggs)		Reference
	Mean diameter	Range	Mean diameter	Range	Mean	Range	
<i>Euphausia pacifica</i>							
Gulf of Alaska all	439 \pm 6	334–643	309 \pm 2	240–362	102 \pm 12	6–246	Present study
large	561 \pm 6	505–643	290 \pm 3	240–332			
small	404 \pm 3	334–480	314 \pm 2	279–362			
Eastern Pacific	400	360–420	330	300–340	–	–	Brinton et al., 2000
Yellow Sea	580 \pm 30 (SD)	500–680	340 \pm 10(SD)	300–380	–	–	Suh et al., 1993
Northern Japan Sea	550	425–625	300	250–375	–	–	Pogodin, 1982
Southern Japan Sea	460 \pm 20	430–505	–	–	–	12–296	Iguchi and Ikeda, 1994
Puget Sound							
small females	–	–	–	–	60 \pm 21	3–265	Ross et al., 1982
large females	–	–	–	–	132 \pm 79	71–234	
<i>Thysanoessa inermis</i>							
Gulf of Alaska	641 \pm 35	478–792	344 \pm 8	300–409	138 \pm 19	5–1021	Present study
Western Barents Sea	730	620–860	–	380–400	–	32–110	Dalpadado and Ikeda, 1989 Dalpadado and Skjoldal, 1991
Southern Barents Sea	–	575–950	–	325–475	–	350–600	Timofeev, 1996
Japan Sea	–	560–900	–	–	–	–	Ponomareva, 1966
North Atlantic	–	730–760	320	–	–	–	Lebour, 1924

fit to Michaelis–Menten form described a large part of the variation ($r^2=0.56$), the data set was described best by sigmoidal Hill function ($r^2=0.70$) (Fig. 3). The relationship indicates that brood size under food saturated conditions (BS_{max}) reaches 144 ± 14 (SE, $P < 0.001$) eggs female $^{-1}$, with half-saturation (K_d) occurring at 0.46 ± 0.02 (SE, $P < 0.001$) mg chlorophyll-*a* m $^{-3}$.

Four females of *E. pacifica*, reared in the laboratory under food saturated conditions, produced multiple broods (Fig. 4). Since there were no significant differences in brood sizes or interbrood intervals between individual females, the data were pooled. The brood size was ranged from 16 to 298 eggs, averaged 80 ± 23 (95% CI, $n=33$) eggs female $^{-1}$; the interbrood interval ranged from 2 to 36 days, averaging ~ 8 days.

In both species, the variability of egg sizes was generally small within individual broods, but was sub-

stantially larger between broods. Comparison of eggs between individual broods revealed significant morphological differences: while embryos in both species did not differ much, the eggs capsules in some broods were significantly larger than in others (Fig. 5; Table 2) leading to enlarged perivitelline space surrounding the embryos. The difference was especially noticeable in *E. pacifica*. There was no significant relationship between size of females of both species and diameter of the egg capsules they produced.

3.2. Hatching and larval development

Hatching and molting of non-feeding stages (from N1 through MN) was nearly synchronous and occurred within a 3–12 h interval, depending on incubation temperature and stage. Hatching success was generally

Table 3

The Intermolt Periods (IP) in days for early stages of *T. inermis* and *E. pacifica*, measured at different temperatures

Stage	<i>Thysanoessa inermis</i>						<i>Euphausia pacifica</i>							
	5 °C		8 °C		12 °C		5 °C		8 °C		10 °C		12 °C	
	IP \pm 95%CI	n	IP \pm 95%CI	n	IP \pm 95%CI	n	IP \pm 95%CI	n	IP \pm 95%CI	n	IP \pm 95%CI	n	IP \pm 95%CI	n
Egg	2.5 \pm 0.2	112	1.5 \pm 0.4	25	–	–	2.6 \pm 0.3	69	1.8 \pm 0.2	160	1.2 \pm 0.3	70	1.1 \pm 0.56	32
N1	1.8 \pm 0.2	89	1.5 \pm 0.4	25	0.7 \pm 0.5	47	1.6 \pm 0.3	69	1.2 \pm 0.2	159	1.1 \pm 0.3	70	0.9 \pm 0.5	28
N2	4.1 \pm 0.2	84	–	–	1.6 \pm 0.5	47	3.6 \pm 0.3	69	1.5	3	1.0 \pm 0.3	70	1.1 \pm 0.5	28
MN	4.3 \pm 0.7	9	–	–	2.8 \pm 0.4	69	6.4 \pm 0.2	144	–	–	2.9 \pm 0.3	70	2.3 \pm 1.0	7
C1	6.9 \pm 0.8	8	–	–	4.8 \pm 0.3	44	13.4 \pm 0.2	144	–	–	6.9 \pm 0.3	70	5.1 \pm 1.3	4
C2	6.9 \pm 0.8	7	–	–	5.8 \pm 0.4	31	9.2 \pm 0.2	118	–	–	7.5 \pm 0.4	53	4.3 \pm 1.5	3
C3	6.3 \pm 0.8	7	–	–	5.9 \pm 0.4	33	9.1 \pm 0.3	86	–	–	6.9 \pm 0.7	16	–	–
F1	–	–	–	–	5.3 \pm 0.7	9	9.4 \pm 1.0	7	–	–	–	–	–	–

high (over 90%). However, a few clutches consisted completely of non-viable eggs, which failed to develop. Such clutches were occasionally found throughout the egg production season. Eggs usually hatched into N1 stage. Occasionally, we observed delayed hatching of *E. pacifica*, when an embryo developed to the C1 stage within the egg membrane, but the occurrence of such events was very rare. Mean mortality of non-feeding *E. pacifica* larvae, calculated for 10 viable clutches, was 40% when they reached the first feeding C1, 61% for C1, 23% for C2 and 11% for C3.

The mean developmental time for *T. inermis* to reach C1 stage from hatching was 10.04 ± 1.55 days (95% CI) at 5 °C and 5.36 ± 0.05 days (95% CI) at 12 °C; for *E. pacifica* 11.5 ± 0.47 days (95% CI), 5 ± 0.44 days (95% CI) and 4.2 ± 0.11 days (95% CI) at 5 °C, 10 °C and 12 °C, respectively. All stages of both species showed shorter intermolt period (IP) at higher temperatures and appeared to have similar growth patterns (Table 3). The IP of non-feeding nauplii (N1 and N2) and metanauplii (MN) was significantly shorter than those of feeding calyptopis stages (C1–C3). The mean IP of *E. pacifica* C1 at 5 °C of 13.4 days was probably overestimated, since, during that experiment, incubation temperature dropped down to 2 °C for 6–8 h with surprisingly long-term consequences. Development times from egg to the first furcilia (F1) stage as estimated from stage specific IP ranged between 20 and 33 days for *T. inermis*, and 15 and 45 days for *E. pacifica* at 12 °C and 5 °C, respectively.

4. Discussion

Our findings of breeding *E. pacifica* in the northern GOA from July through October suggest that its spawning season coincides with development of the seasonal stratification where mixed layer temperature rise from 5–6 °C in May, to 12–14 °C in July and August, and decreases through late October to ~10 °C (Weingartner et al., 2005). This warm layer contains relatively high post-bloom chlorophyll-*a* concentrations (~0.95 mg m⁻³) in July and August, while in October the chlorophyll-*a* content is generally lower (~0.72 mg m⁻³), but may substantially vary between years (Childers et al., 2005). Water temperature of 9–16 °C and abundant food are thought to facilitate the spawning of *E. pacifica* (Brinton, 1976; Nicol and Endo, 1997; Lu et al., 2003) along the central North American coast. Thus, *E. pacifica* breed year-around with peaks in May–July off southern California (Brinton, 1976), June through September off Oregon (Smiles and Percy, 1971), from February through May in the southern Japan Sea (Igu-

chi et al., 1993) and in June in the colder Okhotsk Sea (Ponomareva, 1966). The *E. pacifica* reproduction in the northern GOA, the northernmost part of its range, also appears to follow local temperature and chlorophyll-*a* seasonal dynamics, resulting in a delayed spawning as compared to the southern areas. In contrast, spawning of *T. inermis* in the northern GOA coincided with the spring bloom of large diatoms in April and May and lasted about two month, similar to the other regions of the subarctic Atlantic and Pacific (Kulka and Corey, 1978; Hanamura et al., 1989; Asthorson, 1990; Smith, 1991; Nicol and Endo, 1997; Dalpadado and Skjoldal, 1991; Timofeev, 1996).

We found brood size poorly correlated to female body size, a trend often observed in pelagic crustaceans, including euphausiids (e.g. Ross et al., 1982; Ross and Quetin, 1983; Harrington and Ikeda, 1986; Iguchi and Ikeda, 1994; Nicol et al., 1995; Thatje et al., 2004). This indicates that the number of eggs released during spawning is influenced by factors other than body size.

The strong functional relationship between brood size and ambient chlorophyll-*a* concentration in *E. pacifica* (Fig. 3) indicates that the reproductive rates in this species are closely coupled with availability of phytoplankton. In contrast, the lack of similar relationship over a broad range of chlorophyll-*a* concentrations (0.35–5.71 mg m⁻³) in *T. inermis* suggests that either the species relies on substantial lipid reserves for reproduction, or prey items other than phytoplankton are important in their diet. Therefore, the tight coupling of *T. inermis* reproduction with the start of the spring phytoplankton bloom would provide additional advantage not to spawning adults, but rather to their first feeding larval stages, which would appear in the northern GOA system within 10 days after hatching to find the resources of the bloom available for consumption. Curiously, similar observations were made on *Metridia* copepods from the same area: *M. pacifica* and *M. okhotensis*, which adopt contrasting reproductive strategies analogous to this study's euphausiids. While egg production rates of *M. pacifica*, which spawns throughout the production season from spring till late fall, were closely related to chlorophyll-*a* concentrations, those of *M. okhotensis*, spawning in April and May, were not (Hopcroft et al., 2005).

Our observations show that *E. pacifica* from the GOA is capable of having 11–15 spawning episodes assuming their reproductive season lasting from 3 to 4 months. Applying these (presumably the highest possible) laboratory rates to the natural population in the GOA would yield potential individual fecundity of 1148–1530 eggs per season. Our projection is similar

to estimates for *E. pacifica* in Puget Sound (Ross et al., 1982) and the Japan Sea (Ponomareva, 1966), but substantially lower than those made off the Oregon coast (Feinberg and Peterson, 2003; Feinberg et al., 2004). In contrast, *T. inermis* are assumed to release eggs only once in a spawning season and they may breed in two or more successive years (e.g. Timofeev, 1996). Both the mean and maximum brood sizes of *T. inermis* are larger than those of *E. pacifica*, falling well within their reported range (Zelikman, 1958; Ponomareva, 1966; Dalpadado and Ikeda, 1989; Dalpadado and Skjoldal, 1991), but, for the first time, we document that the egg release of *T. inermis* can take up to 3 days.

Euphausiid spawning strategies appear to be linked to the differences in food supply in specific environments. In *Meganyctiphanes norvegica*, from the Mediterranean, the ovary appears to continually produce new yoke throughout the season, and oocyte development is progressive, allowing rapid successive production of smaller batches of eggs (Cuzin-Roudy and Buchholz, 1999). Alternatively, in the Antarctic *E. superba*, the yoke develops in successive batches at the start of ovarian maturation, with the possibility of different stages of oocytes occurring simultaneously in the ovary, leading to pulsed oocyte production with larger batches of eggs per individual (Ross and Quetin, 2000). The former strategy is effective when food availability is sufficient during a longer spawning season, while the latter works better when food supply oscillates between brief peaks of excess and long periods of deficiency. The morphology of the *E. pacifica* feeding basket allows effective retention of particles >5 μm (Suh and Choi, 1998), thus enabling these oceanic animals to feed on smaller diatoms, dinoflagellates and microzooplankton, which are usually abundant throughout the summer in the North Pacific. In contrast, coastal *T. inermis* consume larger diatom cells comprising nearshore spring phytoplankton blooms in northern latitudes (Ponomareva, 1966), and it also uses accumulated lipid reserves for spring reproduction (Falk-Petersen et al., 1999, cited after Ross and Quetin, 2000). Therefore, the observed differences in timing, frequency, magnitude and factors controlling *E. pacifica* and *T. inermis* reproduction may reflect distinctive spawning strategies they employ to maximize the spawning success in oceanic and coastal habitats.

We found that *E. pacifica* in the northern GOA produced two distinct types of eggs with embryo/egg capsule ratios of 0.52 and 0.78 (Table 2). Larger egg capsules with a thicker perivitelline space (embryo/egg capsule ratio of 0.55–0.59) were reported from the western Pacific (Pogodin, 1982; Suh et al., 1993), while those

with the greater ratio were observed only in the eastern Pacific (embryo/egg capsule ratio of 0.83) (Brinton et al., 2000). The perivitelline space protects the embryo (Pechenik, 1979; Rass, 1982; Timofeev, 1996) and increases buoyancy of the egg (Timofeev, 1990). The development of perivitelline space is thought to be controlled by environmental conditions (e.g. temperature and salinity), rather than genetics (Marschall, 1983; Timofeev, 1996). It is tempting to suggest that the appearance of larger eggs in the northern GOA results from exposure to the harsh subarctic environment, facilitating better protection and dispersal. However, the occurrence of larger *E. pacifica* eggs in the warm Yellow Sea (Suh et al., 1993) implies that some other factors influence the determination of egg size in this species. The documented occurrence of eggs belonging to the same species but of drastically different proportions indicates that extreme caution must be exercised when identifying the eggs in zooplankton samples based on size proportions.

The general lack of data on rates of early development of the North Pacific euphausiids is probably explained by uncertainties in identification of eggs and larvae collected in the field. Pogodin (1980) reported development times for *Thysanoessa* spp. larvae from egg to C1 as 12–13 days at 7 to 8 °C in the northern Sea of Japan, without discriminating them by species. The alternative incubation of eggs produced in the laboratory at various temperatures was applied to *E. pacifica* from the Puget Sound and the southern sea of Japan (Ross, 1981; Iguchi and Ikeda, 1994). It was concluded that *E. pacifica* early stages can tolerate wide range of temperature (5–20 °C), but that these

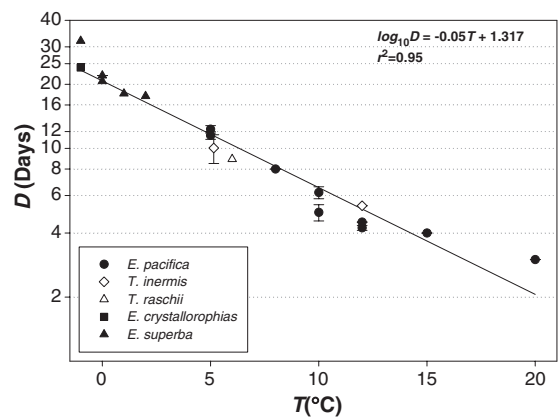


Fig. 6. Development time (D , days with 95% confidence intervals) from hatching to calyptopis 1 and temperature (T , °C) based on our results and on data available in literature (*Euphausia pacifica* from Ross, 1981; Iguchi and Ikeda, 1994; *E. superba* from Ikeda, 1984; Ross et al., 1988; *E. crystallorophias* from Ikeda, 1986; *Thysanoessa raschii* from Smith, 1991).

rates required further confirmation from other regions (Iguchi and Ikeda, 1994).

This study confirms that the cumulative duration of non-feeding stages of *E. pacifica* from hatching till molting into C1 was temperature dependent, and allows quantification of this relationship (Fig. 6). Other measurements done on *E. pacifica* from other parts of the North Pacific also fit close to the regression line. The available data for *E. pacifica*, therefore, suggest that this species has a consistent temperature–stage duration relationship. Our data for *T. inermis*, and data for other broadcast spawning euphausiid species from the literature, appear to fit the trendline as well, suggesting this relationship may be applied to a variety of euphausiid species inhabiting temperate waters.

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References

- Armstrong, J.L., Boldt, J.L., Cross, A.D., Moss, J.H., Davis, N.D., Myers, K.W., Walker, R.V., Beauchamp, D.A., Haldorson, L.J., 2005. Distribution, size, and interannual, seasonal and diel food habits of northern Gulf of Alaska juvenile pink salmon, *Oncorhynchus gorbuscha*. *Deep-Sea Res.*, II 52, 247–265.
- Astthorson, O.S., 1990. Ecology of the euphausiids *Thysanoessa raschi*, *T. inermis* and *Meganyctiphanes norvegica* in Isafjord-deep, northwest-Iceland. *Mar. Biol.* 107, 147–157.
- Bargu, S., Marinovic, B., Mansergh, S., Silver, M.W., 2003. Feeding responses of krill to the toxin-producing diatom *Pseudonitzschia*. *J. Exp. Mar. Biol. Ecol.* 284, 87–104.
- Boden, B.P., 1950. The post-naupliar of the crustacean *Euphausia pacifica*. *Trans. Am. Microsc. Soc.* 69, 373–386.
- Brinton, E., 1976. Population biology of *Euphausia pacifica* off southern California. *Fish. Bull.* 74, 733–762.
- Brinton, E., Ohman, M.D., Townsend, A.W., Knight, M.D., Bridgeman, A.L., 2000. Euphausiids of the World Ocean. ETI World Biodiversity Database CD-ROM Series. Springer-Verlag Electronic Media.
- Brodeur, R.D., 1998. Prey selection by age-0 walleye Pollock, *Theragra chalcogramma*, in nearshore waters of the Gulf of Alaska. *Environ. Biol. Fishes* 51, 175–186.
- Childers, A.R., Whitley, T.E., Stockwell, D.A., 2005. Seasonal and interannual variability in the distribution of nutrients and chlorophyll across the Gulf of Alaska shelf: 1998–2000. *Deep-Sea Res.*, II 52, 193–216.
- Coyle, K.O., Pinchuk, A.I., 2003. Annual cycle of zooplankton abundance, biomass and production on the northern Gulf of Alaska shelf, October 1997 through October 2000. *Fish. Oceanogr.* 12, 327–338.
- Coyle, K.O., Pinchuk, A.I., 2005. Seasonal cross-shelf distribution of major zooplankton taxa on the northern Gulf of Alaska shelf relative to water mass properties, species depth preferences and vertical migration behavior. *Deep-Sea Res.*, II 52, 217–245.
- Cuzin-Roudy, J., Buchholz, F., 1999. Ovarian development and spawning in relation to the moult cycle in Northern krill, *Meganyctiphanes norvegica* (Crustacea: Euphausiacea), along a climatic gradient. *Mar. Biol.* 133, 267–281.
- Dalpadado, P., Ikeda, T., 1989. Some observations on moulting, growth and maturation of krill (*Thysanoessa inermis*) from the Barents Sea. *J. Plankton Res.* 11, 133–139.
- Dalpadado, P., Skjoldal, H.R., 1991. Distribution and life history of krill from the Barents Sea. *Polar Res.* 10, 443–460.
- Einarsson, H., 1945. Euphausiacea: 1. North Atlantic species. "Dana" Rep. 27, 1–185.
- Falk-Petersen, S., Hagen, W., Kattner, G., Clarke, A., Sargent, J., 1999. Lipids—key components of dominant species of Arctic and Antarctic krill. Paper Presented at the Second International Symposium on Krill, Santa Cruz CA, August 23–27, 1999.
- Feinberg, L.R., Peterson, W.T., 2003. Variability in duration and intensity of euphausiid spawning off central Oregon, 1996–2001. *Prog. Oceanogr.* 57, 363–379.
- Feinberg, L.R., Shaw, C.T., Peterson, W.T., 2004. Long-term laboratory observations of *Euphausia pacifica* fecundity: a comparison of two populations. Abstract Book, ASLO/TOS Ocean Research 2004 Conference, February 15–20, 2004, Honolulu, Hawaii, p. 47.
- Gillooly, J.F., Charnov, E.L., West, G.B., Savage, V.M., Brown, J.H., 2002. Effects of size and temperature on development time. *Nature* 417, 70–73.
- Hanamura, Y., Kotori, M., Hamaoka, S., 1989. Daytime surface swarms of the euphausiid *Thysanoessa inermis* off the west coast of Hokkaido, northern Japan. *Mar. Biol.* 102, 369–376.
- Harrington, S.A., Ikeda, T., 1986. Laboratory observations on spawning, brood size and egg hatchability of the Antarctic krill *Euphausia superba* from Prydz Bay, Antarctica. *Mar. Biol.* 92, 231–235.
- Hart, J.L., 1973. Pacific fishes of Canada. *Fish. Res. Board Can. Bull.* 180. Ottawa.
- Hopcroft, R.R., Clarke, C., Byrd, A.G., Pinchuk, A.I., 2005. The paradox of *Metridia* spp. egg production rates: a new technique and measurements from the coastal Gulf of Alaska. *Mar. Ecol. Prog. Ser.* 286, 193–201.
- Iguchi, N., Ikeda, T., 1994. Experimental study on brood size, egg hatchability and early development of a euphausiid *Euphausia pacifica* from Toyama Bay, southern Japan Sea. *Bull. Japan Sea Natl. Fish. Res. Inst.* 44, 49–57.
- Iguchi, N., Ikeda, T., Imamura, A., 1993. Growth and life cycle of euphausiid crustacean (*Euphausia pacifica* Hansen) in Toyama Bay, southern Japan Sea. *Bull. Jpn. Sea Natl. Fish. Res. Inst.* 43, 69–81.
- Ikeda, T., 1984. Development of the larvae of the Antarctic krill (*Euphausia superba* Dana) observed in the laboratory. *J. Exp. Mar. Biol. Ecol.* 75, 107–117.

- Ikeda, T., 1986. Preliminary observations on the development of the larvae of *Euphausia crystallorophias* Holt and Tattersall in the laboratory. Mem. Natl. Inst. Polar Res., Spec. Issue 40, 183–186.
- Kulka, D.W., Corey, S., 1978. The life history of *Thysanoessa inermis* (Kroyer) in the Bay of Fundy. Can. J. Zool. 56, 492–506.
- Lebour, M.V., 1924. The Euphausiidae in the neighbourhood of Plymouth and their importance as herring food. J. Mar. Biol. Assoc. U. K. 13, 402–431.
- Lebour, M.V., 1926. The Euphausiidae in the neighbourhood of Plymouth. III. *Thysanoessa inermis*. J. Mar. Biol. Assoc. U. K. 14, 1–20.
- Lu, B., Mackas, D.L., Moore, D.F., 2003. Cross-shore separation of adult and juvenile euphausiids in a shelf-break along shore current. Prog. Oceanogr. 57, 381–404.
- Marschall, H.-P., 1983. Sinking speed, density and size of euphausiid eggs. Meersforschung 30, 1–9.
- Mauchline, J., 1980. The biology of mysids and euphausiids. Adv. Mar. Biol. 18, 1–680.
- Nakagawa, Y., Ota, T., Endo, Y., Taki, K., Sugisaki, H., 2004. Importance of ciliates as prey of the euphausiid *Euphausia pacifica* in the NW North Pacific. Mar. Ecol. Prog. Ser. 271, 261–266.
- Nicol, S., Endo, Y., 1997. Krill fisheries of the world. FAO Fisheries Technical Paper, vol. 367. Food and Agriculture Organization of the United Nations, Rome, pp. 1–100.
- Nicol, S., de la Mare, W.K., Stolp, M., 1995. The energetic cost of egg production in Antarctic krill (*Euphausia superba* Dana). Antarct. Sci. 7, 25–30.
- Pechenik, J.A., 1979. Role of encapsulation in invertebrate life histories. Am. Nat. 114, 859–870.
- Peterson, W., 2001. Patterns in stage duration and development among marine and freshwater calanoid and cyclopoid copepods: a review of rules, physiological constraints, and evolutionary significance. Hydrobiologia 453/454, 91–105.
- Pogodin, A.G., 1980. On the development of euphausiid larvae from the northern Tatar strait in aquaria (in Russian). Izvestia TINRO 104, 70–76.
- Pogodin, A.G., 1982. Some developmental stages of *Euphausia pacifica* (in Russian). Biologiya Morya 2, 72–75.
- Ponomareva, L.A., 1966. The euphausiids of the North Pacific, their distribution, ecology, and mass species. Israel Program for Scientific Translations, Jerusalem.
- Rass, T.S., 1982. On some eco-morphological aspects of fish embryology (in Russian). Problems in Animal Developmental Morphology, Moscow, pp. 172–182.
- Roff, J.C., Hopcroft, R.R., 1986. High precision microcomputer based measuring system for ecological research. Can. J. Fish. Aquat. Sci. 43, 2044–2048.
- Ross, R.M., 1981. Laboratory culture and development of *Euphausia pacifica*. Limnol. Oceanogr. 26, 235–246.
- Ross, R.M., Quetin, L.B., 1983. Spawning frequency and fecundity of the Antarctic krill *Euphausia superba*. Mar. Biol. 77, 201–205.
- Ross, R.M., Quetin, L.B., 2000. Reproduction in Euphausiacea. In: Everson, I. (Ed.), Krill: Biology, Ecology and Fisheries. Blackwell Publishing, Oxford, pp. 150–181.
- Ross, R.M., Daly, K.L., English, T.L., 1982. Reproduction cycle and fecundity of *Euphausia pacifica* in Puget Sound, Washington. Limnol. Oceanogr. 27, 304–314.
- Ross, R.M., Quetin, L.B., Kirsch, E., 1988. Effect of temperature on development times and survival of early larval stages of *Euphausia superba*. J. Exp. Mar. Biol. Ecol. 121, 55–71.
- Sigler, M.F., Rutecki, T.L., Courtney, D.L., Karinen, J.F., Yang, M.-S., 2001. Young of the year sablefish abundance, growth, and diet in the Gulf of Alaska. Alaska Fish. Res. Bull. 8, 57–70.
- Suh, H.-L., Choi, S.-D., 1998. Comparative morphology of the feeding basket of five species of *Euphausia* (Crustacea, Euphausiacea) in the western North Pacific, with some ecological considerations. Hydrobiologia 385, 107–112.
- Suh, H.-L., Soh, H.Y., Hong, S.Y., 1993. Larval development of the euphausiid *Euphausia pacifica* in the Yellow Sea. Mar. Biol. 115, 625–633.
- Smiles, M.C., Pearcy, W.G., 1971. Size structure and growth rate of *Euphausia pacifica* off the Oregon coast. Fish. Bull. 69, 79–86.
- Smith, S.L., 1991. Growth, development and distribution of the euphausiids *Thysanoessa raschii* (M. Sars) and *Thysanoessa inermis* (Kroyer) in the southeastern Bering Sea. Polar Res. 10 (2), 461–478.
- Thatje, S., Lovrich, G.A., Anger, K., 2004. Egg production, hatching rates, and abbreviated larval development of *Campylonotus vagans* Bate, 1888 (Crustacea: Decapoda: Caridea), in subantarctic waters. J. Exp. Mar. Biol. Ecol. 301, 15–27.
- Timofeev, S.F., 1990. Vertical distribution of eggs and early larvae of euphausiids in the Barents Sea (in Russian). Biology of Marine Plankton. Vladivostok, pp. 102–107.
- Timofeev, S.F., 1996. Ontogenetic Ecology of Euphausiid Crustaceans (Crustacea, Euphausiacea) of the Northern Seas (in Russian). Nauka, St.-Petersburg.
- Weingartner, T.J., Coyle, K.O., Finney, B., Hopcroft, R.R., Whitley, T.E., Brodeur, R., Dagg, M., Farley, E., Haidvogel, D., Halderson, L., Hermann, A., Hinckley, S., Napp, J., Stabeno, P., Kline, T., Lee, C., Lessard, E., Royer, T., Strom, S., 2002. The Northeast Pacific GLOBEC program: coastal Gulf of Alaska. Oceanography 15 (2), 48–63.
- Weingartner, T.J., Danielson, S.L., Royer, T.C., 2005. Freshwater variability and predictability in the Alaska Coastal Current. Deep-Sea Res., II 52, 169–191.
- Zelikman, E.A., 1958. On gonad ripening and female fecundity in mass euphausiid species of the Barents Sea (in Russian). Dokl. Akad. Nauk SSSR 118 (1), 201–204.