INTRODUCTION

_Euphausia pacifica_ Hansen, 1911 is distributed widely within the subarctic and transition zones of the North Pacific and is the only North Pacific _Euphausia_ species living at northern temperate latitudes (Johnson 1956, Brinton 1962, Brinton et al. 2000). It occurs from the warm eastern coast of Korea, and from the Yellow Sea, East China Sea and the Japan/East Sea, into the cool Oyashio Current off Sanriku Japan (Chae et al. 2005, Wang et al. 2005, Xu & Chen 2005), and northward and eastward to the Gulf of Alaska and southward into the California Current System where, during cold years, it can extend its distribution further south to the tip of the Baja California peninsula (Brinton 1962, Gómez-Gutiérrez et al. 2005). This species is also present in the southern parts of the Sea of Okhotsk and the Bering Sea (Batten et al. 2005, Brodeur & Yamamura 2005) (Fig. 1).

_Euphausia pacifica_ from different locations seems to have varying tolerances to changes in temperature and salinity, suggesting significant regional differences among populations (Reagan 1968, Gilfillan 1972). Given its broad distribution over regions with very different seasonal production cycles, we wondered if life history characteristics of _E. pacifica_ were flexible enough to show differences in reproductive activity (spawning duration and spawning season, brood size,
and/or perhaps interbrood period). Moreover, if there were large differences in brood size for example, we should be able to detect them in populations from contrasting regions such as oceanic waters, continental shelf waters and protected inland waters.

We know that there are differences in spawning duration and spawning season for several populations of *Euphausia pacifica* (reviewed by Ross & Quetin 2000). In higher latitudes (49 to 51° N) of the eastern North Pacific in the Strait of Georgia (British Columbia), spawning is intense from May to June and less so from July to September. In Puget Sound and Dabob Bay, Washington populations (48° N), high intensity spawning occurs between March and mid-May and continues at lower intensity until September (Ross et al. 1982, Bollens et al. 1992). In the Japan/East Sea (35 to 37° N), spawning is restricted to the period March to May (Ponomareva 1963, Iguchi et al. 1993). Spawning occurs year-round in the Oyashio Current off the Sanriku region of Japan and off central and southern California (35 to 37° N), but the most intense spawning activity is between February and August (Brinton 1976, Iguchi et al. 1993, Iguchi & Ikeda 1994, 1999, Taki 2004, Dorman et al. 2005). Off the Oregon coast (45°N), Smiles & Pearcy (1971) deduced from larval abundance that intense spawning occurs in the fall; however, recent observations indicate that spawning starts as early as February and extends through October (Feinberg & Peterson 2003, Gómez-Gutiérrez 2003, Gómez-Gutiérrez et al. 2005).

These differences in spawning intensity and spawning season among regions motivated us to compare the geographical differences in brood size of *Euphausia pacifica*. Unfortunately, no other reproductive index (interbrood period, egg volume/energy content) is available for more than 2 *E. pacifica* populations, making brood size the only useful reproductive proxy for quantitative comparative purposes. The available data sets are quite limited and only include observations made on individuals from Puget Sound (PS), WA, USA (Ross et al. 1982), Toyama Bay (TB), Japan (Iguchi & Ikeda 1994, 1999), and the Oregon coast (OC), USA (Gómez-Gutiérrez 2003). We used a meta-analysis of brood size (eggs brood⁻¹) and the female total length (mm) to examine scaling of brood size among these 3 *E. pacifica* populations in the North Pacific. Theoretically, the scaling of brood size among females of varying length within the same species should have a substantially lower slope than interspecific scaling among species (Mauchline 1988, Gómez-Gutiérrez 2003). However, except for the studies by Reagan (1968) and Gilfillan (1972) on temperature and salinity tolerance, no quantitative intraspecific comparison of any vital rate has been attempted with euphausiids. Our aim was to test the hypothesis that the brood sizes of *E. pacifica* females from 3 different North Pacific populations differ significantly after accounting for female size. Our study may offer a new understanding of reproductive adaptation of *E. pacifica* to local conditions.

**MATERIALS AND METHODS**

*Euphausia pacifica* brood size estimation. We used both published (Ross et al. 1982, Iguchi & Ikeda 1994) and our own data on brood size and female length measured from shipboard and laboratory incubations from 3 regions of the North Pacific (Table 1). In PS,
euphausiids were collected near Port Susan (48.6° N, 122.22° W; station depths of approximately 80 m), representing a shallow, estuarine environment (Ross et al. 1982). In Japan, euphausiids were collected in TB, a large deep bay (>1000 m) with a wide mouth at its connection with the Japan Sea. The sampling station was located at 37.0° N, 137.14° E near the 1000 m isobath, thus representing an oceanic environment (Iguchi et al. 1993, Iguchi & Ikeda 1994). The OC sampling area included continental shelf, shelf-break and offshore waters (42 to 44.65° N, 124.3 to 126.2° W) and ripe euphausiids were collected between April and September 1999 to 2004. The sampling area includes a significant inshore–offshore habitat gradient in both phytoplankton and copepod biomass (high biomass inshore, low biomass offshore) (Peterson et al. 2002, Lamb & Peterson 2005). Thus, the area was divided into inshore (<200 m depth) and offshore (>200 m depth) regions. The 4 data sets thus include a gradient of 

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Puget Sound, USA</th>
<th>Toyama Bay, Japan</th>
<th>Oregon coast, USA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oceanographic cruises</td>
<td>5</td>
<td>2</td>
<td>29</td>
</tr>
<tr>
<td>Period of sampling</td>
<td>April to June 1976–1977, sampled every 2 wk</td>
<td>March and April 1992</td>
<td>Sampled seasonally and every 2 wk on the Newport Hydrographic line from 1999 to 2004 (44.18° N, 124°10’ W). Ripe females were found only between March and September</td>
</tr>
<tr>
<td>Location</td>
<td>48.6° N, 122.22° N, shallow inlet waters at ~80 m depth</td>
<td>37.0° N, 137.14° E, oceanic waters 1000 m depth</td>
<td>42.0 to 44.65° N, 124.3 to 126.2° W, inshore (&lt;200 m) and offshore (&gt;200 m) environment</td>
</tr>
<tr>
<td>Sampling gear</td>
<td>1 m net or NIO net, both 571 µm mesh net</td>
<td>1.83 m² Isaacs-Kidd Mid Water Trawl (IKMT) and 1.3 m net diameter 500 µm mesh net</td>
<td>1 m diameter, 300 µm mesh net with 0.7 length × 0.25 diameter closed cod end (live net), 1 m² MOCNESS, and 0.6 m diameter Bongo net 333 µm mesh net</td>
</tr>
<tr>
<td>Incubation method</td>
<td>Bottles 1 l, 8 and 12°C, fed with suspension of cultured diatoms</td>
<td>Bottles 0.9 l, 11°C, fed with natural seston</td>
<td>Bottles 1 l, 10°C, fed with natural seston</td>
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<tr>
<td>Incubation time</td>
<td>24 h, inspected every 6 h</td>
<td>24 h, inspected daily</td>
<td>≤48 h, inspected every 12 h</td>
</tr>
<tr>
<td>Female length measurement</td>
<td>Total length calculated from dry weight data</td>
<td>Total length</td>
<td>Total length</td>
</tr>
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E. pacifica females from the OC region were collected at night between July 1999 and September 2004 (29 oceanographic cruises) using a variety of plankton nets (Table 1). Contents of the cod ends of these nets were poured into a cooler with 20 l of surface seawater. Mature females with purple ovaries were removed from the catch and placed individually into 1 l transparent polypropylene bottles filled with 200 µm filtered seawater. At 12 h intervals for a 48 h period, each bottle was examined and, if eggs were present, the female was removed, the water was sieved to remove the eggs (which were then preserved with 5% formalin) and the female was returned to the bottle. Eggs were counted with the aid of a binocular dissecting microscope. Brood size was calculated as the cumulative number of eggs produced during the 48 h period. At the end of the experiment, female total length was measured from the posterior edge of the eye to the tip of the telson. All uses of the term length (L) in this paper refer to total length. E. pacifica brood size data from literature were used for PS and TB regions. There were some slight differences in the methods of measuring brood size among studies (Table 1).

For the PS region, the brood size and female lengths were calculated directly from data presented in Fig. 2 of Ross et al. (1982) by transforming female dry weight (DW), expressed in mg, to female total length (mm) using their equation: DW = 1.45 L – 18.06 (r² = 0.943, n = 41). For the TB region, the original brood size and female total length data set was kindly provided by Naoki Iguchi (pers. comm.; from Iguchi & Ikeda 1994). For some comparisons of length and brood size among populations we used the same length range intervals.
as Ross et al. (1982) as follows: <17 mm, 17 to 19 mm and >19 mm.

**Analysis of covariance of Euphausia pacifica brood size.** To test for differences in brood size as a function of female size among Euphausia pacifica populations in the North Pacific, we conducted a meta-analysis of covariance using multiple linear regression models to compare the relationship between brood size (eggs female\(^{-1}\)) and female length (mm) among 3 populations following methods described by Ramsey & Shafer (1996). Logarithm transformation was carried out to linearize the data and reduce variability. The effect of the brood size (explanatory variable) is the mean response that is associated with a one-unit increase in this reproductive index while holding all other variables constant. In this case, the constant variables are female length and population region.

We set the intercept of multiple linear regression models as the minimum female length at first maturity recorded in any of the 3 populations (~12 mm, as presented in the original analysis for females with young oocytes stage I). We tested a parallel line full model \(\text{Log BS} = \beta_0 + \beta_2 \text{LogL} – 12 \text{ mm} + \beta_3 \text{Toyama} + \beta_4 \text{Oregon}\), and a reduced model \(\text{Log BS} = \beta_0 + \beta_2 \text{LogL} – 12 \text{ mm}\) to test for differences in the intercepts for the association of brood size and female length by regions (see Table 3) where \(\text{Log BS}\) is the logarithm of the brood size (eggs female\(^{-1}\)). \(\text{LogL} – 12 \text{ mm}\) is the logarithm of the female length after subtracting the length at first maturity and Toyama and Oregon are indicator variables for each region. The PS population was treated here as the reference level. The intercept for PS is the coefficient \(\beta_0\); for TB it is \(\beta_0+\beta_2\) and for OC it is \(\beta_0+\beta_3\). Thus, if the last 2 are equal to zero, the intercepts for all the 3 populations are statistically the same.

Additionally, we fitted a non-parallel full model, incorporating different intercepts and slopes expressed as interaction terms, to test that the regression lines are indeed parallel. The separate full model is \(\text{LogBS} = \beta_0 + \beta_1 \text{LogL} – 12 \text{ mm} + \beta_2 \text{Toyama} + \beta_3 \text{Oregon} + \beta_4 (\text{LogL} – 12 \text{ mm} \times \text{Toyama}) + \beta_5 (\text{LogL} – 12 \text{ mm} \times \text{Oregon})\). The reduced model was \(\text{LogBS} = \beta_0 + \beta_1 \text{LogL} – 12 \text{ mm} + \beta_2 \text{Toyama} + \beta_3 \text{Oregon}\) (see Table 3).

**Interspecific comparison of egg size as a function of total length in euphausiids.** Brood size in broadcast spawning euphausiids has been estimated for only a few species (reviewed in Ross & Quetin 2000), but average egg sizes have been reported more frequently (Mauchline 1988, Gómez-Gutiérrez 2003). Assuming that the brood size has a direct association with the length of each euphausiid species (and thus with the volume of the ovary), then the egg diameter (ED) could be a proxy for relative female brood size. To provide a general perspective about the interspecific variability of egg diameter and the relationship between female size and reproductive investment (expressed as egg size) among the species of the Order Euphausiacea, we compared egg diameters (Mauchline 1988, Brinton et al. 2000, Gómez-Gutiérrez 2003) and the adult maximum total length (MTL) (Baker et al. 1990) for broadcast-spawning euphausiids around the world.

**RESULTS**

For the 3 *Euphausia pacifica* populations, there was a relatively similar increase in brood size as a function of body length up to 23 mm, with slopes ranging between 10.0 for PS and 17.7 for TB (Fig. 2A–D). For larger females, brood size tended to decrease with body length (Fig. 2C–D, black circles). The average brood size was marginally smaller for PS (96 eggs female\(^{-1}\)) than for TB (113 eggs female\(^{-1}\)) (t-test, \(p < 0.0514\)); however, the average brood sizes of both regions were significantly smaller than for the OC population (152 eggs female\(^{-1}\)) for all size classes (t-test, \(p < 0.0002\)) (Table 2). However, the average brood sizes of females in inshore (<200 m) and offshore (>200 m) regions of the OC were statistically indistinguishable (161 vs. 147 eggs female\(^{-1}\), respectively; t-test, \(p > 0.099\)). Females were significantly smaller in PS (mean L = 15.9 mm) than in TB (mean L = 18.5 mm) (t-test, \(p < 0.0001\)). On average, females in TB were also significantly smaller than those at OC (mean L = 20.1 mm for whole data set; t-test, \(p < 0.0001\)). In the OC region, the average length of females recorded inshore (<200 m) was significantly longer than for offshore females (>200 m) (t-test, \(p < 0.0007\)) (Table 2).

When females were separated into 3 size classes, <17 mm, 17 to 19 mm and >19 mm, the brood sizes of females were statistically indistinguishable among any of the 3 locations (t-test, \(p > 0.106\)) except for PS where the females between 17 and 19 mm produced smaller brood sizes than the corresponding females in the OC region (t-test, \(p < 0.009\)). Also, OC-inshore females <17 mm produced more eggs than the same size class in the OC-offshore region (t-test, \(p < 0.008\)). Analysis of female size indicated that those from TB and OC were statistically larger than those from the other 2 regions for the >19 mm size range (t-test, \(p < 0.003\)).

**Analysis of covariance of Euphausia pacifica brood size**

The multiple linear regression models to test whether median brood sizes (intercepts) were signifi-
cantly different among regions indicate that, independently of region and environmental conditions, females of similar length produced the same number of eggs. Thus, there were no regional differences in brood size, and the variability is well explained by female length ($p > 0.05$; extra-sums-squares $F$-test $= 0.537$). The 95% confidence interval for the brood size multiplicative effect, accounting for length, indicates that TB females produce between 0.70 and 1.16 times less or more eggs than PS females and that OC females produce between 0.80 and 1.24 times less or more eggs than PS females (Table 3).

After establishing that the median brood sizes (intercepts) were not statistically different, we employed a multiple linear regression model to test if there were statistical differences in the slopes among regions. This model accounted for the observed differences in brood size among regions, and the results indicated that the slopes were not statistically different ($r^2 = 0.1087$ for PS, $r^2 = 0.0693$ for OC, and $r^2 = 0.0756$ for OC, $r^2 = 0.2754$ for TB). The slope of the regression lines for PS, OC, and TB populations were 0.006, 0.005, and 0.007, respectively, indicating that the brood size increased linearly with female length in all regions.

Table 2. *Euphausia pacifica*. Comparison of the average female total length (mm) and brood size (eggs female$^{-1}$) among 3 populations of euphausiids in the North Pacific: Puget Sound, WA, USA, (Ross et al. 1982), Toyama Bay, Japan (Iguchi & Ikeda 1994) and along the Oregon coast, USA (1999 to 2004). STD: standard deviations; $S_x$: standard error (shown in parentheses). The total length and brood size data from the Oregon Coast region was divided into inshore (<200 m depth) and offshore (>200 m depth) regions. Females that produced brood sizes of <10 eggs female$^{-1}$ were removed from the statistical analysis ($n = 37$ females; 4 from Puget Sound, 33 from the Oregon coast population).
analysis produced no statistical evidence that the slopes of the association between brood size among the 3 regions differed after accounting for female length ($p > 0.05$; extra-sums-squares $F$-test = 1.489) (Table 3). Similar results were obtained when the OC population was divided into OC-inshore (<200 m) and OC-offshore (>200 m) regions (multiple regression models not shown).

To estimate the average rate of increase of brood size at intervals of female length and explore the inherent capability of *Euphausia pacifica* females to produce larger brood sizes as they become larger, we calculated the simple linear regression model using all the available data: $BS = 8.51 \times L + 41.83$ ($r^2 = 0.56$, $p = 0.0012$, $n = 600$ females) (Fig. 3). The highest variability in brood size occurred in females 19 to 22 mm long. Small broods (<100 eggs female$^{-1}$) could be produced by females of any size within the entire size range of mature females observed in this study, i.e. 12 to 25 mm. Intermediate broods (≤250 eggs female$^{-1}$) were produced by females ranging from 14 to 18 mm in length. For broods >250 eggs female$^{-1}$, the range in female length was quite large at 17 to 24 mm (Fig. 3). The largest females, 25 mm, produced fewer eggs than females ranging in length from 14 to 24 mm.

**Table 3. ANCOVA using an inferential-multiple linear regression model to compare the minimum brood sizes per population (intercepts) and rate of increase of brood size (slopes) of the association between brood size (BS, eggs female$^{-1}$) and female total length minus the total length of females at first maturity ($L = 12$ mm) of *Euphausia pacifica* among 3 populations in the North Pacific: Puget Sound, WA, USA (Ross et al. 1982), Toyama Bay, Japan (Iguchi & Ikeda 1994) and along the Oregon coast, USA (this study). All of the coefficients and the 95% confidence interval of the coefficients are expressed as $\log_{10}$**

| Model to test differences between intercepts (parallel model) | Coefficients ($\pm 95\%$ CI) | Error | $t$-value | $p = (>|t|)$ | $r^2$ | df |
|---|---|---|---|---|---|---|
| Full model | Intercept ($\beta_0$) | 1.486 (1.346 to 1.626) | 0.071 | 20.833 | 0.000 | 0.0965 | 596 |
| | LogL – 12 mm ($\beta_1$) | 5.106 (3.559 to 6.653) | 0.787 | 6.484 | 0.000 | 0.988 |
| | Toyama ($\beta_2$) | –0.043 (–0.152 to 0.065) | 0.055 | –0.781 | 0.435 | 0.562 |
| | Oregon ($\beta_3$) | –0.001 (–0.096 to 0.095) | 0.049 | –0.015 | 0.988 |
| Reduced model | Intercept ($\beta_0$) | 1.4722 (1.336 to 1.610) | 0.070 | 21.133 | 0.000 | 0.0978 | 598 |
| | LogL – 12 mm ($\beta_1$) | 5.174 (3.923 to 6.426) | 0.637 | 8.118 | 0.000 | 0.988 |

| Model to test differences between intercepts and slopes (non-parallel model) | Coefficients ($\pm 95\%$ CI) | Error | $t$-value | $p = (>|t|)$ |
|---|---|---|---|---|
| Full model | Intercept ($\beta_0$) | 1.471 (1.174 to 1.767) | 0.151 | 9.740 | 0.000 |
| | LogL – 12 mm ($\beta_1$) | 5.3027 (1.602 to 9.003) | 1.884 | 2.814 | 0.005 |
| | Toyama ($\beta_2$) | –1.436 (–3.878 to 1.007) | 1.244 | –1.154 | 0.249 |
| | Oregon ($\beta_3$) | 0.378 (–1.345 to 2.102) | 0.878 | 0.431 | 0.668 |
| | LogL – 12 mm × Toyama ($\beta_4$) | 1.097 (–0.877 to 3.072) | 1.005 | 1.092 | 0.275 |
| | LogL – 12 mm × Oregon ($\beta_5$) | 0.297 (–1.712 to 1.118) | 0.720 | –0.412 | 0.681 |
| Reduced model | Intercept ($\beta_0$) | 1.486 (1.346 to 1.626) | 0.071 | 20.833 | 0.000 |
| | LogL – 12 mm ($\beta_1$) | 5.106 (3.559 to 6.653) | 0.787 | 6.484 | 0.000 |
| | Toyama ($\beta_2$) | –0.043 (–0.152 to 0.065) | 0.055 | –0.781 | 0.435 |
| | Oregon ($\beta_3$) | –0.001 (–0.096 to 0.095) | 0.049 | –0.015 | 0.988 |

Interspecific comparison of egg size as a function of total length in euphausiids

Our analyses indicate that there is no difference in brood size among 3 populations of *Euphausia pacifica* (we did not observe intraspecific variability). However, we would expect to see larger interspecific variability in brood size. Since egg diameter is the only reproduc-
average index commonly reported in euphausiid species, we used it for an interspecific comparison. A simple linear regression model indicates that there is a significant direct association between average ED and MTL: \( ED = 0.1208 + 0.0156 \times \text{MTL} \) (\( r^2 = 0.8129, p < 0.0001 \)). The slope of the relationship is 0.016, meaning that there is an increase of about 0.02 mm in the ED per mm increase in the MTL of euphausiids (Fig. 4). For euphausiids of a given length, data points above the line in Fig. 4 indicate species with larger eggs than those below the line. Therefore, assuming similar body volumes, females above the line should produce fewer eggs than those below the line. We do not know if there is any relationship between egg diameter and brood size, but if larger eggs indicate smaller brood sizes, then this would suggest that epipelagic oceanic brood size, but if larger eggs indicate smaller brood sizes than those below the line. We do not know if there is any relationship between egg diameter and brood size, but if larger eggs indicate smaller brood sizes, then this would suggest that epipelagic oceanic species like Thysanoessa longipes, Euphausia similis, Thysanopoda tricuspidata, and Euphausia gibboides, which have relatively large egg sizes may have proportionally smaller brood sizes than \( E. \text{pacifica} \). The epipelagic species Euphausia diomedeae, Thysanoessa longicaudata, Thysanoessa inspinata, Nematobrachion flexipes and Meganyctiphanes norvegica seem to have egg diameters proportionally similar to \( E. \text{pacifica} \) because they are close to the regression line. The euphausiids Euphausia triacantha, Thysanoessa spinifera and Euphausia superba apparently have proportionally smaller egg size than \( E. \text{pacifica} \), after accounting for female length. \( T. \text{longipes} \) is the species with the largest egg size proportional to its maximum adult length.

**DISCUSSION**

One goal of this study was to test for differences in brood size among 3 Euphausia pacifica populations living in regions with different seasonal cycles of primary productivity. We initially expected that females from the Oregon continental shelf might be more fecund than females inhabiting relatively enclosed water bodies, like PS, simply due to differences in seasonal availability of phytoplankton food for the adult euphausiids. Both PS and TB have earlier and shorter spawning seasons (March to May) compared to the populations in the OC upwelling zone (April to September). A relatively short period of primary production could supposedly give the euphausiids comparatively little time to feed and invest energy in reproduction. Longer spawning seasons resulting from frequent phytoplankton blooms as a result of upwelling (Feinberg & Peterson 2003) should contribute to an increase in the maximum potential fecundity at each female body size interval, thus maximizing the overall population reproductive effort. However, what appeared to be large differences in mean brood sizes among populations could be accounted for by differences in body size: OC females were larger than those from PS or TB; thus, they produced larger broods. This suggests that euphausiids living in regions characterized by intense phytoplankton blooms over relatively short periods of time in spring are equally as likely to produce size-specific brood sizes as those living in regions with prolonged primary production cycles. The only difference between the 3 populations may be in lifetime fecundity; this life history trait should be higher for OC females because the period over which primary production occurs is longer (up to 6 mo compared to 1–2 mo in PS and TB). Fecundity is the product of brood size and interbrood period. To test the hypothesis that fecundity is different, one would need measurements of interbrood period from all 3 regions, and such measurements are lacking in most studies.

An intriguing feature of the brood size–body length relationship was that females of intermediate size (19 to 22 mm) produced the greatest number of eggs (bell-shaped distribution). This could be the result of a reduction in fecundity among larger (and presumably older) females. An alternate hypothesis comes from
one of our unpublished experiments (L. R. Feinberg et al. unpubl.), in which we maintained more than 30 female Euphausia pacifica in the laboratory and checked the egg production of each individual daily for 4 to 9 mo. Each female in this experiment was in the 19 to 22 mm size range, and brood sizes ranged from a few eggs up to a maximum of 800 eggs female\(^{-1}\). We found that 41 of 284 broods (14\%) produced in the laboratory contained >250 eggs female\(^{-1}\). For the shipboard incubation data reported in the present study, we found a similar proportion: 73 broods out of 600 (12\%) produced in our OC incubations contained >250 eggs female\(^{-1}\). Thus, the range observed in our OC incubations is matched by our unpublished laboratory observations, suggesting that any apparent ‘bell-shaped’ relationship may be due solely to natural variability within individual females in the 19 to 22 mm size class, and that among any given set of females within this size class one can expect that about one in 7 broods from the same female will contain >250 eggs. Therefore, a population of euphausiids does not necessarily contain females with anomalously high fecundity, because all females seem capable of producing large or small broods.

Lack of brood sizes >250 eggs female\(^{-1}\) for very large females (>23 mm) may simply be due to the fact that we do not often catch large females, perhaps reflecting their relatively reduced abundance caused by age- or size-dependent mortality. For example, a recently discovered parasitoid apostome ciliate species (Collinia oregonensis) infects Euphausia pacifica and can cause mass mortality events (Gómez-Gutiérrez et al. 2003). These ciliates tend to infect mostly larger females, so as to maximize the ciliate reproductive process from the biomass of the host (Gómez-Gutiérrez et al. 2006), and along with other better known euphausiid predators may significantly reduce the likelihood of E. pacifica females attaining sizes larger than 23 mm.

We do not know why brood sizes of >300 egg female\(^{-1}\) were not observed in the PS and TB populations, but perhaps the phytoplankton blooms in both regions were not of sufficient duration or magnitude to result in large euphausiid brood sizes. This supports the hypothesis that females in regions with short production seasons have smaller brood sizes. Another possibility, as suggested above, is that there was a relatively smaller sample size of females in the PS and TB regions than in the OC region, and the resultant data sets may not reflect the range of variability in brood size and fecundity for those locations.

Seasonal variations in water temperatures may also affect egg production. In TB, egg production occurs from February to May when the SST is <12\°C (Iguchi & Ikeda 1999). SST increases significantly from 12 to 26\°C between July and October, and a strong thermocline develops between 50 and 75 m depth. The magnitude of the nighttime vertical migration is reduced after May because of the temperature barrier (>20\°C) located at approximately 50 m depth, probably reducing feeding activity in the euphotic zone (Iguchi et al. 1993). Similarly, in the Oyashio Current, highest abundances of eggs in the water column were observed from April through June, when SST ranged from 5 to 12\°C; however, eggs were found only rarely in the Kuroshio, where temperatures were always >15\°C (Taki 2004). In PS, intense spawning usually occurs during April and May, which is earlier than on the OC, but continues at a low level throughout most of June (Ross et al. 1982). Since temperature in PS does not usually rise above 12\°C in spring, the decrease in brood size after May is likely due to reduced phytoplankton concentrations, rather than temperature. In the OC region, spawning extends from March through October, with greatest intensity from July to September. The later and more intense spawning season here compared to the PS and TB regions is a result of the coastal upwelling. Upwelling benefits euphausiids in 2 ways: (1) by keeping the waters cool throughout the summer months (commonly <14\°C) and (2) by promoting frequent phytoplankton blooms during the summer upwelling season (Feinberg & Peterson 2003).

Brood size has been estimated for only a few other broadcast-spawning euphausiid species (Ross & Quetin 2000). In the Benguela Current off South Africa, individual female Euphausia lucens Hansen (<18 mm female length) produced brood sizes up to 80 eggs female\(^{-1}\) with relatively large eggs (550 to 600 \(\mu\)m egg diameter) (Stuart & Nicol 1986); thus, given the small body size compared to E. pacifica smaller brood sizes would be expected. Using counts of mature oocytes in the ovary as an estimate of brood size for Euphausia hanseni, E. lucens and Nyctiphanes capensis, Stuart & Nicol (1986) found that ‘potential’ brood sizes were quite small: between 19 and 138 eggs for females ranging in length from 8 to 27 mm. Using the same approach of counting mature oocytes in ovaries, Brinton (1976) found a significant linear relationship between number of E. pacifica ripe oocytes and body length for individuals off southern California, but found an average of 150 ripe oocytes in 17 to 21 mm E. pacifica females and a maximum of 350 oocytes. He also found that the largest size class of females (21 mm) had a reduced number of oocytes, ~140 per ovary, similar to our bell-shaped brood size distribution. Brinton’s data on mean number of oocytes (on the order of 150 oocytes per ovary) are similar to our average E. pacifica brood size for females from the northern end of the California Current off Oregon state. However, his maximum number of oocytes (350)
was far less than our direct measurements (800 eggs female\(^{-1}\)) from females maintained in the laboratory (L. R. Feinberg et al. unpubl.). These data suggest a common pattern among species from 2 upwelling systems related to embryo size and brood size: *E. lucens* and *E. hansenii* have larger diameter eggs than *E. pacifica*, resulting in reduced brood size. However, comparing the interspecific size continuum of *E. lucens* (small size), *E. pacifica* (intermediate) and *E. superba* (large size), there is a clear pattern of larger brood sizes in larger individuals.

Finally, we showed interspecific differences in egg diameter: on average, larger species have larger eggs (Fig. 4). The more interesting relationship in Fig. 4 is the large range in egg diameter among species of the same length. This suggests that some species with large eggs—for example, epipelagic oceanic species like *Thysanoessa longipes*, *Euphausia similis*, *Thysanopoda tricuspidata*, and *Euphausia gibboidea*—have proportionally larger egg diameter but perhaps smaller brood sizes than *Euphausia pacifica*. Egg size is sometimes the only index that allows one to qualitatively evaluate the variations in maximum brood size among species (Timofeev & Sklyar 2002). Because egg size information is available for only 23 of 57 broadcast-spawning euphausiid species, our analysis highlights the current gap in knowledge of egg biometry within the Order Euphausiacea.

### CONCLUSIONS

When comparing brood sizes among euphausiids from different populations, length must be taken into account. Comparisons of brood size among populations can be confounded by the duration of the primary production season and potentially by temperature. If we are to determine whether *Euphausia pacifica* has differential reproductive investment under different environmental conditions, future studies devoted to estimating brood size are needed from other regions, particularly from those near the limits of the distribution range (i.e. East China Sea, Bering Sea and Baja California peninsula). Those inter-population differences cannot be addressed adequately without measurement of brood size, egg volume or diameter, interbrood period and spawning duration. Additional studies similar to ours need to be carried out for other euphausiid species in order to gain further insights into relationships between brood size and female length. If such studies are coupled with measurement of interbrood period, comparison of fecundity (determined from embryo energy content, interbrood period and spawning season) will be possible.

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