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Euphausia pacifica brood sizes: a North Pacific synthesis

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Euphausia pacifica occupy a remarkably wide range of ecosystems. We examined the differences in brood sizes from eight regions of the North Pacific to explore how variation in the brood size might contribute to their success over such a range. We show a compilation and analysis of short-term *E. pacifica* brood size incubations from around the North Pacific rim, ranging from the Yellow Sea (YS) (Korea) to southern California (SC), USA. Brood sizes for *E. pacifica* are highly variable in all regions and range from 5 to 697 eggs overall. Median brood sizes were largest in the YS and off Newport, Oregon and the maximum brood sizes were greatest in the regions off the coasts of Oregon and Washington, USA followed by the YS. Quantile regression analysis revealed that there was a significant relationship between the female length and the maximum brood size (95% quantile) for broods from SC, Oregon, and Washington, USA as well as Toyama Bay, Japan, indicating that the maximum brood size is limited by the female length in these regions. This suggests that other factors, hydrographic conditions, food quantity/quality or physiological condition of females, may limit maximum brood sizes in the other regions examined here.

INTRODUCTION

Euphausia pacifica are found throughout much of the North Pacific Ocean (Fig. 1). This species thrives in environments from sub-tropical to sub-arctic and in regions characterized as open-ocean, coastal upwelling/downwelling and seasonally stratified semi-enclosed bays and marginal seas (Gómez-Gutiérrez *et al.*, 2006). *Euphausia pacifica* are important secondary producers in these oceanic and coastal ecosystems, where they are key grazers on phytoplankton (primarily) and are major prey items for many commercially harvested fish (e.g. Brodeur, 1998; Sugisaki and Kurita, 2004; Chae *et al.*, 2008) as well as seabirds and whales (e.g. Xu *et al.*, 1983; Croll *et al.*, 2005; Abraham and Sydeman, 2006). Given the essential trophic role of this species it is critical for scientists, modelers and managers to understand its population dynamics, including consistencies and differences among regions. This will allow us to better understand, and potentially predict, variability in euphausiid biomass and production in relation to the environments in which they live.

Euphausia pacifica is often the dominant species of euphausiid in the regions where it is found (Brinton, 1962). In the northern California Current off Oregon and Washington, USA it is one of two dominant euphausiid species, but extensive sampling off Newport, Oregon has revealed that the densities of adult *E. pacifica* were an order of magnitude greater than the next most common species, *Thysanoessa spinifera* (Shaw, unpublished). *Euphausia pacifica* is also the most abundant euphausiid off Southern California (Brinton, 1976). In the Gulf of Alaska, *E. pacifica* is one of three dominant species and is the most abundant species over the outer shelf region (Pinchuk and Hopcroft,

2006). Of the 10 euphausiid species found in the central and southern Japan Sea (Endo and Komaki, 1979; Dolganova, 2011) *E. pacifica* is again the dominant one. In the Oyashio Current region off northeastern Japan this one species at times comprises over 90% of total euphausiid abundance (Okazaki, unpublished). *Euphausia pacifica* is also the dominant euphausiid in the Yellow Sea, making up 50–80% of the large crustacean biomass depending on the season (Sun *et al.*, 2011). At more northerly locations such as the Sea of Okhotsk and the Bering Sea, *E. pacifica* is abundant but is sub-dominant to one of several *Thysanoessa* species (Ponomareva, 1966; Pinchuk and Coyle, 2008; Dolganova, 2011; Shaw, personal observation).

Efforts to study the distribution, biomass and life-history of *E. pacifica* have increased in the last decade through targeted studies by the US GLOBEC Northeast Pacific program, PICES Working Group 23 and China GLOBEC. Among life-history traits, brood size is one metric of reproductive output that is relatively simple to measure and thus is the most widely available for comparison among multiple regions. Brood size is only one element of reproductive output and while comparisons of brood sizes among regions yield useful information, we cannot extrapolate to a comparison of fecundity without data on inter-brood period and length of spawning season. There are data available in the literature to determine the approximate spawning seasons for many of the regions discussed as well as the estimates of inter-brood periods for a few regions.

A comparison of brood sizes of *E. pacifica* from three regions was published by Gómez-Gutiérrez *et al.* (Gómez-Gutiérrez *et al.*, 2006). One conclusion was a recommendation to compare the brood size data from a
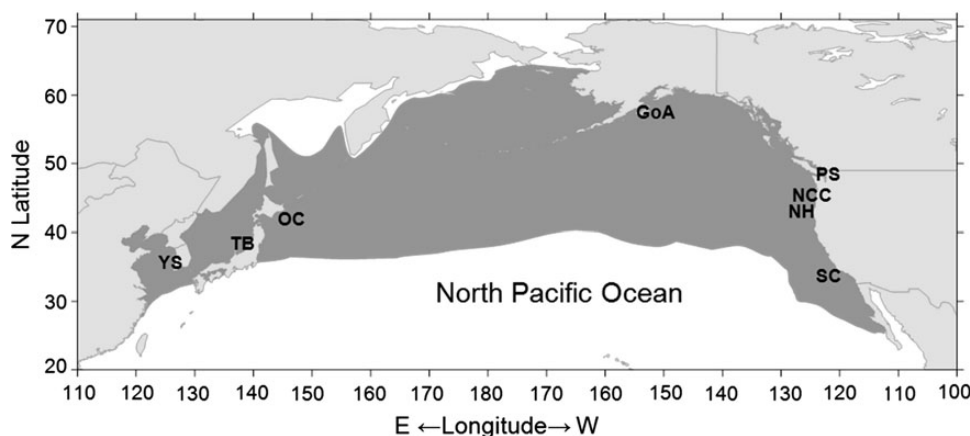
Fig. 1. An *Euphausia pacifica* map of North Pacific Ocean showing the extensive species range (shaded in gray, as defined in Gómez-Gutiérrez *et al.* (2006) with updates from Dolganova (2011) as well as the locations of all the study areas used for the synthesis. SC, M. Décima; NH, Feinberg; Shaw and Peterson; NCC, Feinberg; Shaw and Peterson; PS, Ross *et al.* (1982); GoA, Pinchuk and Hopcroft (2006); OC, Okazaki; TB, Iguchi and Ikeda (1994); YS, Ju.

wider range of environments around the North Pacific. Such data did not exist at the time, but since then, more studies with comparable methods have become available from a wider array of locations. In the current analysis we examine how body size limits brood size capacity using broods measured only during the main spawning seasons in eight different regions. The female length is a proxy for body size and the 95% quantiles of measured brood size are considered as proxies for maximum brood capacity for each size class of females. In addition, we explore the question of how this cosmopolitan species thrives in so many diverse environments (Fig. 1) and how differences in a life-history trait such as brood size might affect their success in the different study regions. Brood sizes that fall below the 95% quantile, or are not significantly related to female size in this upper range of brood size distributions, are likely limited by factors other than female size, such as female condition or environmental factors (i.e. lipid reserves, water temperature and salinity, food quantity and quality). This vital information is not available from all eight regions, thus we cannot perform a meta-analysis of all possible contributors to brood size. Instead, we observe differences between environmentally diverse regions, comparing their suites of conditions to the representative brood sizes for the area. In this way, we attempt to observe the relationships between brood size and the physical environment among the large range of habitats where *E. pacifica* is found.

METHOD

The *E. pacifica* brood sizes compared in this study are from a combination of previously published (Ross *et al.*, 1982; Iguchi and Ikeda, 1994; Pinchuk and Hopcroft, 2006) and unpublished data sets from a diverse range of environments around the North Pacific (Fig. 1, Table I).

Description of study regions

The studies conducted in the California Current along the West Coast of the USA included southern California (SC), Newport Hydrographic (NH) and NCC. They were carried out in areas of strong seasonal upwelling with highly productive and well-mixed water columns and temperatures consistently within the 5–20°C range which is associated with successful spawning, hatching and survival of *E. pacifica* eggs (Iguchi and Ikeda, 1994). The upwelling season is generally earlier and more intense to the south and progresses northward (Bograd *et al.*, 2009). The shelf region is also narrower to the south and relatively wide off the coast of Washington. Hence, the SC study periods occurred earlier in the year and at many deeper stations than the NH and NCC studies. The Puget Sound (PS) study was conducted in a shallow, enclosed, estuarine environment characterized by large spring and smaller fall phytoplankton blooms and temperatures consistently within the tolerance for *E. pacifica* (Ross *et al.*, 1982). The YS study area is also quite shallow with a strong spring bloom, but it is considered to be semi-enclosed and more open to the Pacific than the PS study area. The YS study area becomes highly stratified in the summer and autumn months and surface temperatures well over 20°C force *E. pacifica* to take refuge in deeper, colder waters during these seasons (Sun *et al.*, 2011; Ju *et al.*, 2011). Though much deeper than YS, the Toyama Bay (TB) study area is similar to YS because it is also characterized by seasonal stratification and prohibitively warm surface temperatures in summer and autumn.

Table I. Euphausia pacifica *brood size studies from the North Pacific, published and unpublished*

North Pacific region	Study location	Data Source	Incubation temp. (°C)	Station depth (m)	Timing of experiments	Number of broods	Incubation duration (h)
SC, USA	33.6–34.8°N × 120.8–123.1°W	Décima	12–14°C	88–4368	May 2006, April 2007	84	24
NH, OR, USA	44.7°N × 124.2–124.9°W	Feinberg, Shaw, Peterson	10.5°C	60–435	June–September 2000–2011	246	48
NCC, OR/WA, USA	45.0–47.0°N × 124.0–126.2°W	Feinberg, Shaw, Peterson	10. 5°C	38–750	June–September 2004–2010	244	48
PS, WA, USA	48.6°N × 122.2°W	Ross *et al.* (1982)	8 &12°C	~80	April–June 1976, 1977	84	24
GoA, USA	58.1–59.85°N × 147.8–149.5° W	Pinchuk and Hopcroft (2006)	8,10,12°C	145–1525	July–October 2001–2004	79	96[a]
OC, Japan	39.0–42.3° N × 144.0–146.8°E	Okazaki	3–10°C	1760–5251	April–July 2007	58	48
TB, Japan	37.0°N × 137.1°E	Iguchi and Ikeda (1994)	11°C	1000	March–April 1992	77	24
YS, S. Korea	35.0–35.3°N × 124.5–124.7°E	Ju	6–9°C	54–90	April 2010–2012	53	48

[a]Only two individuals spawned after 48 h in the 96 h GoA incubations.

As in YS, animals live deeper in the water column, in cooler water, during the excessively warm summer months. The OC study was carried out in a deep, oceanic region off the coast of Northeastern Japan where temperatures are cool (generally <11°C; Okazaki, unpublished data) and there is a spring phytoplankton bloom. Finally, the GoA study was conducted in an area known for downwelling, with a wide continental shelf, mixed-layer water temperatures from 3 to 12°C and relatively low primary productivity (Pinchuk and Hopcroft, 2006).

We do not have direct measurements of the food availability in all regions during the brood size incubations. *Euphausia pacifica* are omnivores, but their primary periods of spawning activity tend to coincide with phytoplankton blooms (Ross and Quetin, 2000). It is possible to compare seasonal chlorophyll *a* (chl *a*) peaks from the different regions in order to determine whether we should expect large differences in feeding conditions for the females. The OC has peaks in chl *a* up to $10\,\mu g\,L^{-1}$, with an average of $\sim 4.7\,\mu g\,L^{-1}$ during blooms (Okazaki and Tadokoro, 2009). Spring chl *a* values in the YS range from 0.3 to $5.65\,\mu g\,L^{-1}$ with an average of $1.4\,\mu g\,L^{-1}$ (Sun *et al.*, 2011). In the NCC, the mean surface chl *a* concentration during brood size incubations was $5.5\,\mu g\,L^{-1}$ with a range of $0.5{-}13\,\mu g\,L^{-1}$. The NH mean surface chl *a* value during euphausiid collection for brood size experiments was $4\,\mu g\,L^{-1}$ with a range of $0.3{-}39\,\mu g\,L^{-1}$ (Feinberg, Shaw, Peterson, unpublished data). In the GoA, the values of $0.5{-}1.3\,\mu g\,L^{-1}$ were reported for the area where females were collected for incubations (Pinchuk and Hopcroft, 2006). The sampled regions of the California Current Ecosystem cruises had surface chl *a* values at the euphausiid collection locations of $0.7{-}6.4\,\mu g\,L^{-1}$ (Landry *et al.*, 2009), with no significant difference between brood sizes from the highest and lowest chl *a* source waters. In PS we do not have chlorophyll values from the exact location of female collection, but Bollens *et al.* (Bollens *et al.*, 1992) published values for a nearby bay showing a range of $\sim 0.67{-}4\,\mu g\,L^{-1}$ during the *E. pacifica* spawning season. In TB the surface chl *a* values at the station where females were collected varied from 1 to $4\,\mu g\,L^{-1}$ in 1997–1999 (Takahashi and Uchiyama, 2007).

Brood Size Incubations (by region)

The brood sizes and female lengths compared in this study are all from short-term (24–96 h) controlled temperature incubations of gravid *E. pacifica* females, carried out using natural seawater either aboard research ships or in laboratories on shore. Incubations always occurred during the main spawning season for each region. In all studies, gravid females were identified by a purple band under the pericardial area of the thorax, as described by

Ross *et al*. (Ross *et al*., 1982). The female lengths are reported here in mm of 'total length' for all studies, defined as the distance from just behind the eye to the posterior tip of the telson. There are many different methods used for measuring euphausiids. We standardized length data from SC and the GoA to make 'total length' comparable among all data sets. A brood size is defined as the total number of eggs released by a female during an incubation.

Euphausia pacifica from SC were collected at night by M. Décima during two California Current Ecosystem process cruises (May 2006 and April 2007) as part of the US National Science Foundation Long-term Ecological Research program. The study region is an area of active upwelling off of southern California, USA (Fig. 1) and the cruises coincide with the typical upwelling season (April–September) and the peak of *E. pacifica* spawning off southern California (Brinton 1976). Gravid females were collected using oblique Bongo tows lowered to a target depth of 50 m (roughly the depth of the mixed layer). Tows were conducted between 2000 h and midnight, with the ship speed maintained at 1–2 knots. Station locations were all in the vicinity of Point Conception, California. Individual gravid females were incubated in 1-L jars containing 0.2-μm filtered seawater at 12–14°C in a shipboard cold room for 24 h.

Data collected by Feinberg, Shaw and Peterson from off the coasts of Oregon and Washington, USA were split into two regional sub-sets of incubations for this analysis, but the collection and incubation methods were identical. Brood size incubations were conducted in conjunction with two major plankton sampling efforts. Firstly, there is a long-term, biweekly time series of plankton samples on an East-West transect off Newport, OR (Table I). This transect is called the Newport Hydrographic line and designated as NH. On these cruises, gravid females are typically collected with 0.6-m diameter bongo nets towed obliquely to ~25 m after dark. Gravid females are sorted into 1-L bottles of 200-μm filtered surface seawater. The animals are kept in the dark in a cooler during transport (<5 h) to a 10.5°C cold room. Incubation water is sieved (63 μm) every 12 h to remove eggs and all eggs are counted using a dissecting microscope. After 48 h, the females are removed and measured. The second sampling effort consists of longer cruises covering a broader area off the coasts of northern Oregon and Washington (Table I). This set of incubations is designated as NCC. Females were collected and processed in the same manner and maintained in a shipboard incubator for the 48 h incubation. The methods for checking experiments and counting eggs were the same as for the shore-based incubations. Based on our year-round sampling program off of Newport, Oregon, we have established that *E. pacifica*

spawning off the Oregon and Washington, USA coasts occurs most consistently during the summer upwelling season (Feinberg and Peterson, 2003; Gómez-Gutiérrez et al., 2007) and thus the data sets included here were limited to broods produced during peak spawning from June to September.

The methods for the incubations described above were published on the PICES website in 2005 (http://www.pices.int/projects/Euphasiid/PICES%20Protocols%20COMPLETE.pdf) and these protocols were followed directly by other researchers from Korea and Japan whose data are included in this synthesis. Data from the YS, South Korea, were collected by S.-J. Ju. Females were collected from shallow, well-mixed stations in the YS (90 m, 7.5°C in 2010, 54 m, 6°C in 2011, 54 and 90 m, ∼9°C in 2012). Females were collected during spring, the peak E. pacifica spawning season (mainly April), in the YS (Sun et al., 2011). Female E. pacifica from the OC region off Japan were collected by Y. Okazaki from near the surface of several very deep (1760–5251 m), oceanic stations and incubated at a range of seasonally appropriate temperatures (Table I). In this region, spawning occurs nearly year-round, but the main peak is from April to June and is thus represented by the incubations carried out in this study which spanned these months in 2007.

In PS, euphausiids were collected from a relatively shallow (80 m), estuarine location near Port Susan, WA (Ross et al., 1982). Though the incubations and data collected were quite similar to the other studies, there were some methodological differences. Females were fed cultured diatoms and the incubations lasted only 24 h. The brood sizes and female lengths were calculated from data presented in Fig. 2 of Ross et al. (Ross et al., 1982). A female dry weight (DW), in mg, was transformed to female total length (designated as 'L' in the original

paper) in mm using their published equation: $DW = 1.45L - 18.06$ ($r^2 = 0.943$, $n = 41$) (Ross et al., 1982).

Euphausia pacifica from the GoA were collected using a 1-m² MOCNESS. Gravid females were incubated individually in 750-mL tissue culture flasks filled with seawater from the collection site and incubated at the ambient temperature of the mixed layer (Pinchuk and Hopcroft, 2006). Incubations for this study lasted 96 h but were checked every 12 h and nearly 98% of broods were released within the first 48 h of incubation. Carapace lengths were measured at the end of the incubations and TL was calculated using the equation $TL = 3.75CL + 0.92$ (Pinchuk and Hopcroft, 2006).

Females from TB were collected from the upper 200 m at a deep station of ∼1000 m depth during the spring-time (Iguchi and Ikeda, 1994) peak spawning period for that area (February–early June; Iguchi et al., 1993). Gravid females were incubated in 900-mL bottles of seawater collected from 250 m. Bottles were maintained in the dark in a tank of water at 11°C for 24 h (Table I). In Iguchi and Ikeda's (Iguchi and Ikeda, 1994) study, females were measured at the end of the incubation. The data were provided to us by Iguchi for a previous publication (Gómez-Gutiérrez et al., 2006).

Data sets do not include brood sizes of 'zero eggs' because we are interested in the relationship between the brood size and female length for those females that spawned successfully within the short incubation period. Broods smaller than five eggs were excluded from the analyses in order to minimize the chance of error as it is possible that on occasion very small numbers of eggs might be retained unnoticed in a sieve or counting chamber, causing slight contamination between samples. We chose a minimum brood size of five eggs because this was the smallest number of eggs released per daily observation in long-term (several month) fecundity experiments for *E. pacifica* (Feinberg et al., 2007 and unpublished data). We assumed that cannibalism was minimal as Pinchuk and Hopcroft (Pinchuk and Hopcroft, 2006) noted that in their experiments it accounted for a loss of <11% and in the recent studies empty egg shells would have been noted when the contents of the experimental containers were sieved.

Analyses

Statistical comparisons between brood sizes and female lengths were carried out using the non-parametric Kruskal–Wallis test since these data are not normally distributed. Differences between individual regions were identified using the median notch function of the Statgraphics Box-and-Whisker plots. Comparisons of brood sizes in four different female size classes
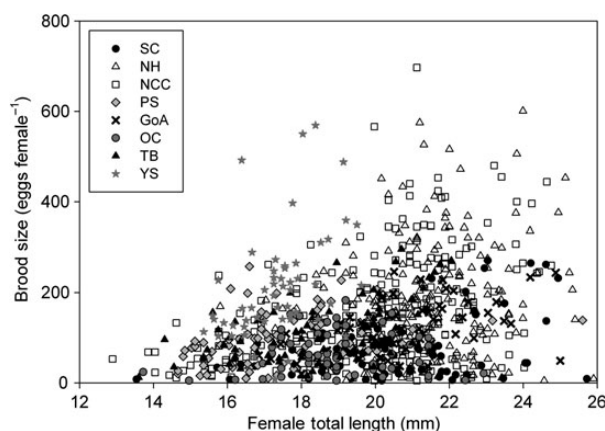

Fig. 2. The *E. pacifica* total length (mm) versus brood size for all females producing broods of five or more eggs in all regions included in this synthesis.

(<15 mm, 15–17.99 mm, 18–20.99 mm and ≥21 mm) were conducted in the same manner.

The relationship between body size (female length) and brood capacity was explored using quantile regression. Quantile regression is used to estimate a functional relationship between variables for all parts of a probability distribution and defines a best fit model for each quantile class by minimizing absolute deviations (Koenker, 2005). Quantile regression describes the relationship between a set of predictor variables and specific quantiles of the response variable, but it differs from using an ordinary linear regression on subsets of data from specific regions of response variables, because all of the observations are used to determine which observations are selected for each quantile class through the conditional probability process.

Quantile regression is often used as a method of estimating rates of change for functions along or near the upper boundary of the conditional distribution of responses (Cade and Noon, 2003). The key concept behind this method is that if an ecological factor acts as a constraint on the response variable, then the estimated effects for the measured predictor variables will not be well represented by changes in the response variable distribution means, especially when there are other unmeasured predictor variables that are potentially limiting (Cade and Noon, 2003). Unequal variance in a data set, as seen in Fig. 3, suggests that more than one predictor variable influences the response variable (brood size in this analysis). Specifically, there are many ecological factors that may affect *E. pacifica* brood sizes, such as female length, age, physiological condition, and food quantity and quality. Some of these factors, such as female age and food quality during the inter-brood period, are extremely difficult to measure for euphausiids (Harvey *et al.*, 2010). Other measureable information on environmental conditions, such as food quantity associated with each female incubated, was not always available for all data sets in this study. For the purpose of this study, and given the limitations with the available data, we tested the basic ecological assumption that brood capacity (i.e. the maximum brood size) should be a function of body size (female length) if there are no other limiting factors. This suggests that, when length is considered as a limiting factor in conjunction with many other unmeasured factors, a relationship between length and brood size is likely to be evident in the upper quantile class. Quantile regression (Equation 1) was conducted using the experimental procedure QUANTREG in SAS (SAS Institute 2005).

$$Q_y(\tau|x) = \beta_0(\tau) + x\beta_1(\tau) + F_\mu^{-1}(\tau) \qquad (1)$$

where τ is the τth quantile, y the response variable, x the predictor variable, $\beta_0(\tau)$ and $\beta_1(\tau)$ are the estimated

coefficients for τth quantile, $Q_y(\tau|x)$ is the τth quantile functions of y conditional on x, and F_μ denotes the common distribution of the errors. The associated confidence limits were constructed through a bootstrap resampling technique (Koenker, 2005). In this study we show estimated lines for the 50 and 95% quantiles in order to examine the middle and uppermost regions of the distribution.

In regional studies where females were collected from multiple station depths or incubated at more than one temperature (Table I), linear regression analysis was used to determine the relationship between station depth or temperature and brood size. The regional chl *a* values were categorically summarized as high, medium and low productivity. These rankings were compared with daily egg production rates for each region. Daily egg production was calculated using a median brood size divided by 5 days which is the median inter-brood period from available long-term *E. pacifica* fecundity studies in the Eastern Pacific (Feinberg *et al.*, 2007; Feinberg and Peterson, 2012).

RESULTS

Sample sizes varied between study areas, from 53 females producing broods in the YS to 244 and 246 for NCC and NH, respectively (Table I). This was primarily a result of the relative effort allocated towards these studies rather than the potential availability of spawning females. Incubation temperatures (a reflection of *in situ* temperatures) ranged from 3 to 12°C and station depths (where females were collected) ranged from ~40 to 5251 m (Table I).

The female lengths differed between regions, but all spawning females were between 12 and 26 mm total length (Fig. 2, Table II). With a total sample size of 921 females from around the North Pacific, this suggests a minimum size at first reproduction of ~12 mm for *E. pacifica*. Despite a large range in brood sizes for most areas, the largest broods in this analysis (>400 eggs) were from the Oregon and Washington coasts of the USA or from the YS. There is a weak positive correlation between the female length and brood size for all regions combined ($r = 0.3$). Small brood sizes are common for females of all lengths while brood sizes appear to level off or even decrease slightly for the largest females (≥22 mm, Fig. 2). Although there is a weak positive relationship between the female length and brood size, this is not an absolute physical constraint as some females <20 mm TL from the YS produced broods in excess of 400 eggs (Fig. 3).
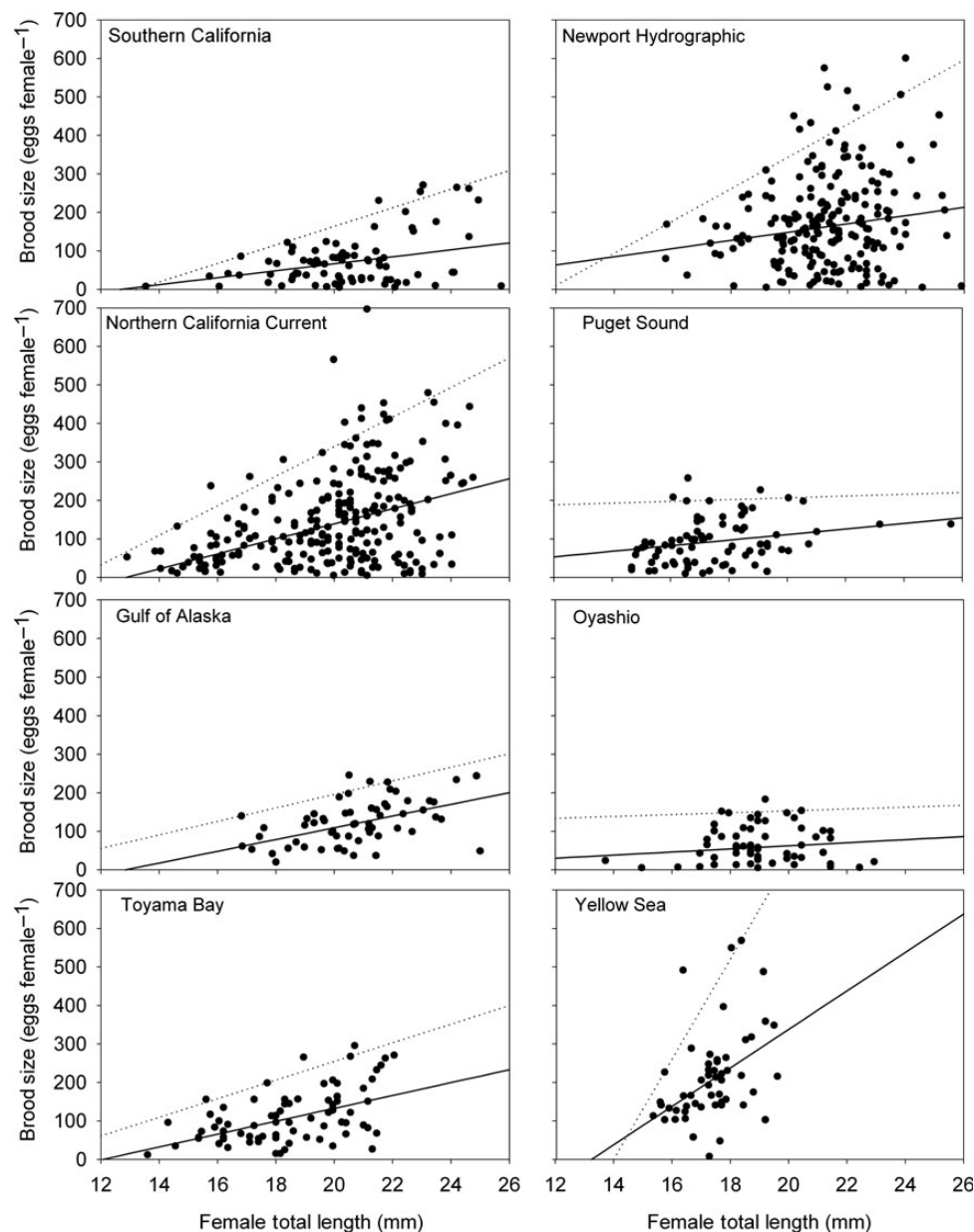
Fig. 3. Total length (mm) versus brood size of *E. pacifica* for incubations by region. The dotted line is the estimate of the regression line for the 0.95 quantile and the solid line is the estimate for the 0.50 quantile. See Table III for equations and levels of significance.

Median brood sizes and female total lengths differed significantly among regions (brood size: Kruskal–Wallis = 153.4, $P < 0.001$; length: Kruskal–Wallis = 266.6, $P < 0.001$). Median brood size for YS and NH was significantly greater (193 and 163 eggs respectively) than all other regions. With a median brood size of 56 eggs, OC had the smallest broods, significantly smaller than every region except SC and PS (Fig. 4). Females from NH (median length = 21.3 mm) were longer than all others except for those from GoA. The female lengths for NH and GoA grouped with NCC and SC were significantly longer than all other regions, and YS and PS females were significantly shorter than females from OC and TB, which were not significantly different from each other (Fig. 5). While the lengths of females incubated for these experiments do not necessarily represent the full length range of reproductive females from the various regions, it is important to recognize these differences among regions within this data set since we are interested in the relationship between length and brood size.

In order to further investigate the overall differences in the female lengths and brood sizes among regions,

Table II. Euphausia pacifica *descriptive statistics for brood size studies*

North Pacific region	Female TL (mm)						Brood size (eggs female^{-1})					
	n	Median	Mean	STD	SE	Range	n	Median	Mean	STD	SE	Range
SC, USA	82	20.28	20.48	2.24	0.25	13.54–25.72	82	64	75.5	66.08	7.30	5–271
NH, OR, USA	203	21.31	21.30	1.78	0.12	15.76–25.90	246	163	182.0	122.51	7.81	5–601
NCC OR/WA, USA	239	20.35	19.89	2.47	0.16	12.90–24.75	244	114.5	149.04	118.9	7.61	5–697
PS, WA, USA	81	17.10	17.48	1.89	0.21	14.66–25.60	81	86.7	95.4	58.5	6.5	10–258
GoA, USA	60	20.66	20.71	1.90	0.25	16.82–25.00	79	116	117.2	56.7	6.38	20–246
OC, Japan	59	18.95	19.02	1.70	0.22	13.72–22.9	59	56	65.6	47.9	6.23	5–183
TB, Japan	77	18.45	18.48	2.04	0.23	13.60–22.05	77	96	112.8	69.04	7.87	12–296
YS, S. Korea	53	17.45	17.38	1.05	0.14	15.4–19.6	53	193	214.0	119.1	16.36	8–569

In some instances, *n* (number of measurements) is greater for the brood sizes than for female lengths, as in some circumstances a female measurement was not available.
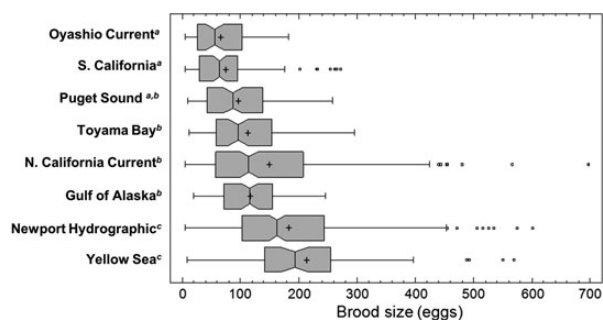

Fig. 4. The *E. pacifica* box-and-whisker plot of brood sizes by region. Horizontal gray bar = median 50%, vertical line in box = median, + = mean, range of notch = 95% confidence interval for median, □ = outliers >1.5 times width of the median box. Region with the same superscripts (*a–c*) indicate statistically indistinguishable brood sizes.
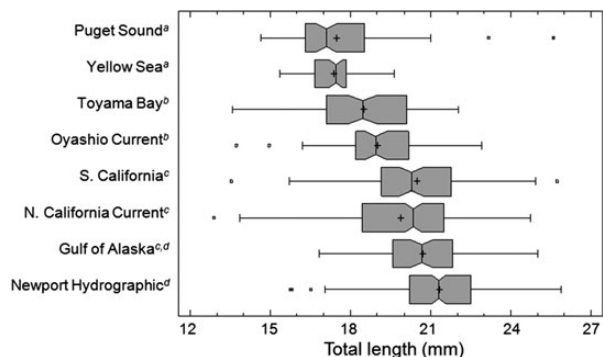

Fig. 5. The *E. pacifica* box-and-whisker plot of female lengths by region. Horizontal gray bar = median 50%, vertical line in box = median, + = mean, range of notch = 95% confidence interval for median, □ = outliers >1.5 times width of the median box. Regions with the same superscripts (*a–d*) indicate statistically indistinguishable female lengths.

females from each region were divided into four size classes by total length: <15, 15–17.99, 18–20.99 and ≥21 mm. Some regions did not have females in all four size classes. Comparisons of brood sizes in relation to

these size classes of females yielded results similar to the overall comparison with a few notable differences. The smallest size class comprised females from only SC, TB, OC and NCC and the sample size ($n = 19$) was too small for differences in brood size to be statistically significant. Brood sizes from females in the 15–17.99-mm size class ($n = 193$) from all regions were significantly different (Kruskal–Wallis = 57.05, $P < 0.001$). YS broods were significantly larger than all but NH broods. However, NH broods from this size category were only significantly larger than broods from SC, which were significantly smaller than broods from YS, PS and NCC as well. There was also a significant difference among the eight regions in the 18–20.99-mm size class ($n = 359$, Kruskal–Wallis = 74.05, $P = 0$). In this size class, YS females had the largest median brood size by far of all the regions. However, broods from NH, TB, NCC and GoA were also significantly larger than broods from SC and OC. Finally, for the largest size class of females (≥21 mm) all regions except YS were represented and once again there was a significant difference between brood sizes ($n = 280$, Kruskal–Wallis = 28.18, $P < 0.001$). The median brood size from TB was the largest overall, but was only significantly larger than the smallest median broods of the analysis from OC and SC, which were significantly smaller than all other regions.

Quantile regression was used to investigate the relationship between the female length and brood size. There was a significantly positive relationship with the upper 50% quantile of brood sizes and total length for all regions except PS, OC and SC (Table III). There was also a significantly positive relationship with the maximum brood size (95% quantile) and the female length for the incubations from NH, NC, SC and TB (Table III, Fig. 3). This suggests that in these regions the female length might indeed be the main factor limiting the maximum brood size. Brood sizes from PS and OC showed no evidence of being limited by female length, as

Table III. Euphausia pacifica *quantile regression results for individual studies of total length versus brood size in the eight study regions*

North Pacific region	Quantiles	Intercept	t-value	P-value	Coefficient	t-value	P-value
SC, USA	0.5	−114.777	−1.25	0.21	9.068	1.9	0.06
	0.95	−318.41	−2.03	0.04	24.108	3.49	<0.01
NH, OR USA	0.5	−65.153	−0.61	0.54	10.706	2.05	0.042
	0.95	−492.897	−1.24	0.21	41.897	2.24	0.02
NCC OR/WA, USA	0.5	−251.167	−4.6	<0.01	19.523	6.62	<0.01
	0.95	−428.427	−2.06	0.04	38.409	4.05	<0.01
PS, WA, USA	0.5	−33.634	−0.38	0.7	7.25	1.4	0.17
	0.95	160.783	0.33	0.74	2.289	0.08	0.94
GoA, USA	0.5	−195.643	−1.82	0.07	15.236	2.98	<0.01
	0.95	−155.403	−0.74	0.47	17.565	1.74	0.08
OC, Japan	0.5	−18.097	−0.13	0.89	4.017	0.55	0.584
	0.95	104.741	0.26	0.79	2.41	0.11	0.91
TB, Japan	0.5	−201.946	−2.74	<0.01	16.739	3.9	<0.01
	0.95	−229.526	−0.99	0.33	24.211	2.01	0.04
YS, S. Korea	0.5	−646.1	−2.37	0.03	49	3.01	<0.01
	0.95	−285.4	−0.88	0.39	32.533	1.8	0.08

Table IV. Regional chlorophyll a ranking and E. pacifica estimated daily fecundity

North Pacific region	Chl a ranking by region	~Eggs female^{-1} day^{-1}	Primary spawning season (months)	Source
SC, USA	H	13	All year (12)	Brinton (1976)
NH, OR, USA	H	33	April–October (6.5)	Feinberg and Peterson (2003)
NCC, OR/WA, USA	H	23	April–October (6.5)	Feinberg, unpublished
PS, WA, USA	M	17	April–June (3)	Ross et al. (1982)
GoA, USA	L	23	July–September (3)	Pinchuk and Hopcroft (2006)
OC, Japan	H	11	April–May, August–October (5)	Taki (2004)
TB, Japan	M	19	February–May (4)	Iguchi et al. (1993)
YS, S. Korea	M	39	March–May (3)	Sun et al. (2011)

Euphausia pacifica estimated daily egg production based on a median IBP of 5 days from Eastern Pacific studies, (Feinberg et al., 2007; Feinberg and Peterson, 2012) and assumed main spawning seasons for females in various regions of the North Pacific based on the associated study. Regional chlorophyll a ranking (H, high; M, medium; L, low)

the slope estimates for the 50 and 95% quantiles were not significant (Table III, Fig. 3). GoA and YS brood sizes were significantly related to the female length for the upper 50% of brood sizes, but not at the 95% level, suggesting that length played a substantial role in determining brood sizes but was not the only factor influencing the maximum brood sizes in those areas.

For individual studies where different incubation temperatures were used, there is no indication that differences in the brood size were related to temperature ($r^2 = 0.02$, 0.04 and 0.12 for the relationships between temperature and brood size for OC, YS and GoA, respectively). In this synthesis, the relationship between station depth and brood size for individual studies where depth varied was very weak ($r^2 = 0.005$, 0.03, 0.006, 0.04, 0.009, 0.06, respectively for the relationships between station depth and brood size for OC, SC, NCC, NH, YS and GoA, respectively).

Chlorophyll a ranking by study area showed OC, NH, NCC and SC having relatively high seasonal chl a values, TB, PS and YS in the middle range and GoA having the lowest chl a values during the respective *E. pacifica* spawning seasons (Table IV). Daily egg production rate does not appear to match the rankings of chl a as the two lowest and two of the highest estimated daily egg production rates are all associated with regions of high chl a (Table IV).

DISCUSSION

Previous studies have suggested the need for a more geographically comprehensive comparison of brood sizes for *E. pacifica*. Therefore, the goal of this synthesis was to summarize and compare the female lengths and brood sizes from all existing data in the North Pacific. Our results indicate significant differences in median brood sizes between the eight study regions, as well as some differences in the relationship between the female length and brood size. While it is not surprising to observe differences in the reproductive output between animals across a wide range of marine environments, some of the observed differences

were unexpected. Individual euphausiid fecundity is generally considered to be a function of female size and nutritional conditions prior to and during the spawning season (Ross and Quetin, 2000). Thus, larger broods are expected in regions with high and prolonged primary productivity since those environmental conditions are physiologically favorable. However, our results did not always appear to fit this pattern.

Differences in brood sizes among regions

It was not unexpected that the largest maximum brood sizes were from the productive upwelling areas off the Oregon and Washington coasts (NH and NCC, Table II). More unexpectedly, the maximum brood sizes from the YS were the next largest, and median brood sizes from that region were the highest overall (Table II) as well as the highest for the two female length subcategories present in the YS study. This was unexpected because the YS was considered to be a somewhat marginal environment for *E. pacifica* since its very warm, seasonally stratified surface waters force them to reside at the depth of the YS Bottom Cold Water mass for most of the summer and autumn months (Sun *et al.*, 2011).

The next largest broods from other regions were less than half the size of the largest broods from these areas. Given the relative rarity of large broods (Fig. 2), one might surmise that the chance of observing these largest broods was enhanced by the greater sample size off of Oregon and Washington. However, similarly large broods were also observed in the YS incubations, the study with the smallest sample size. The presence of large broods in the YS does not seem to be an artifact of small sample size either. These brood sizes were strongly corroborated by Sun *et al.* (Sun *et al.*, 2011) whose Western YS study reported a range in brood sizes of 2–617 from 164 broods and an overall average of 189.4 eggs. This range is nearly identical to YS broods reported in the current analysis (as is the mean, Table II) and is very similar to NH and NCC brood size data as well. Unfortunately, the Western YS data could not be included in the current analysis due to the lack of data on female length. However, the similarities between these data sets support the idea that these larger brood sizes are a real phenomenon in the YS.

While the females from the YS, Oregon and Washington (NH and NCC) produced notably large broods, females from the OC and SC consistently produced small broods. These smaller broods were not just associated with smaller females as both of these studies incubated females in the middle size range of the entire study (Table II). There was no relationship between female size and brood size from the OC study (Fig. 3), suggesting

that brood sizes in that region are likely more closely tied to environmental factors. The OC and SC studies both collected females from stations at greater depths than other studies and it might be expected that these females were in poorer condition due to collection from more oligotrophic waters; however, the OC and SC are generally considered to be productive regions and are ranked as 'high' on our relative chl *a* scales along with NH and NCC (Table IV). Despite the greater station depths, females were still collected from the upper 50 m in nighttime sampling for these studies, leaving no reason to expect that smaller broods are a function of greater collection stress on the females. It is more likely that temperature might limit brood sizes in these areas as OC has the coldest incubation temperatures of the group and SC the warmest (Table I). With the exception of the lowest incubation temperature from the OC, these temperatures still fall within the 5–20°C range associated with successful spawning (Iguchi and Ikeda, 1994) and thus we suggest only that temperature may have inhibited the maximum brood sizes for a given female length in these regions.

Variability in brood sizes within size classes of females

In nearly all regions there was great variability in brood sizes for females of any given length (Fig. 3). This result was anticipated since long-term laboratory studies showed similar results, even for individual *E. pacifica* females maintained for months under constant conditions of 10.5°C and fed mixed algal species *ad libitum* (Feinberg *et al.*, 2007). Results from the long-term incubations suggest that differences in the brood size were independent of diet, water temperature and salinity and female length. In these laboratory incubations, brood sizes ranged from >900 to as few as 5 eggs (Feinberg *et al.*, 2007; Feinberg and Peterson, 2012). While the maximum brood sizes of this magnitude were not observed during the shorter field incubations, these experiments included large broods, small broods and all sizes in between. We now know with certainty that individual *E. pacifica* can spawn multiple times within a spawning season (Feinberg *et al.*, 2007), a reproductive strategy which should increase the chances for reproductive success, especially in inconsistent environments where adequate food and conditions for egg production do not always occur. It has been documented for at least three species of euphausiids (*E. pacifica*, *E. superba* and *Meganyctiphanes norvegica*) that the numbers of eggs released by individual females in successive spawning events are not equal (Ross and Quetin, 2000; Feinberg *et al.*, 2007). A brood may be more accurately defined as the total number of eggs released over a period of days during multiple successive spawning episodes, and this

metric might correlate more strongly with the body size, as has been observed for *M. norvegica* and *Euphausia superba* (Ross and Quetin, 2000). This might help explain some of the variability observed in the brood size from short-term incubations in this study, even among females of the same length, but suggests that in order to improve upon the relationship between female size and brood size we should collect eggs during an entire molt cycle (Cuzin-Roudy and Buchholz, 1999). However, this method is impractical for a synthesis since molt cycles for the incubation temperatures used in these studies would range from ∼6 to 10 days (Shaw *et al.*, 2010). This period is far too long to maintain females without food, the addition of which would introduce sampling artifacts from an artificial feeding and living environment. For the purposes of a large-scale comparison between many regions with differing research programs and capabilities, the shorter term incubations compared in this paper are the best data available. Moreover, the large range in brood sizes for females of a given length suggests that quantile, rather than linear, regression is a more appropriate way to examine the relationship between the female length and the maximum brood size because it allows us to consider specific regions of the distribution, rather than just the central tendency.

An alternate method for estimating brood size is to count the eggs in the ovaries. This method could lead to an overestimation of the brood size because it is unknown how many ovarian eggs are actually released from the ovary, how long it takes them to fully mature and

whether they are all released as one larger batch or several smaller ones. Brinton (Brinton, 1976) counted the number of eggs in the ovaries of preserved female *E. pacifica* from southern California waters and published a figure (his Fig. 3) relating the female length to the number of ripe eggs in her ovary. A plot of our combined TL (mm) versus brood size data from similar California Current upwelling regions (SC, NH and NCC) shows a very similar pattern, with the mean brood size increasing linearly up until the very largest females where brood sizes drop slightly (Fig. 6). The drop in the brood size for the largest females in both studies could be an artifact of the relative scarcity of females in this size range (Fig. 2 and 4). Alternatively, one might assume that the largest females are the older females, but it is not prudent to assume that broods from these largest females come from the oldest females since length cannot be equated with age for euphausiids (Harvey *et al.*, 2010). This similarity between results is surprising given the uncertainties of ovarian egg counts. The maximum female length (21 mm) from Brinton's (Brinton, 1976) data is smaller than in the current study, even when we just compare it with animals from the nearest vicinity to his study, SC (Table II). Brinton (Brinton, 1976) did not count the small or partial broods because he only estimated 'potential' brood size. However, the overall shape of the curve and the means and standard deviations for each female length bin are strikingly similar between these two data sets. Mean and median values are useful for modeling and if that is the
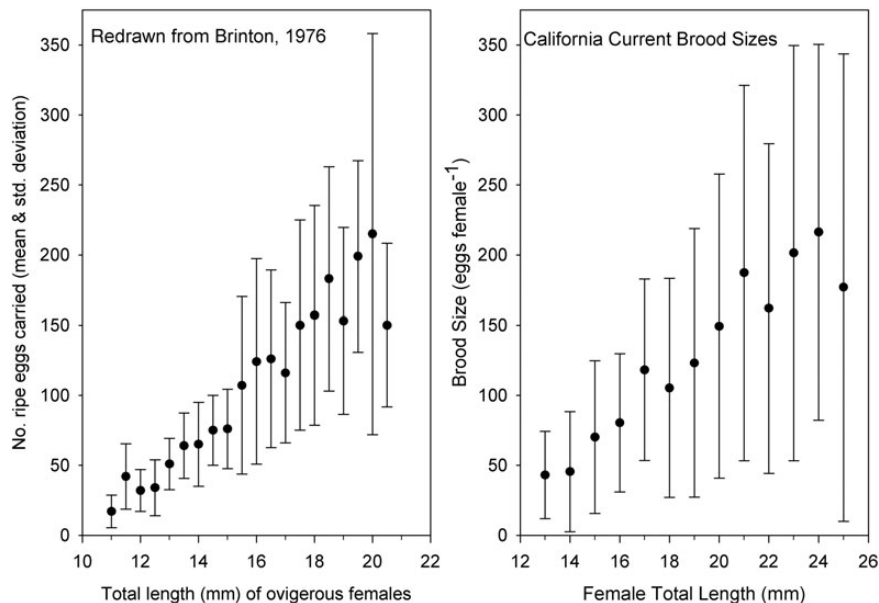

Fig. 6. The *E. pacifica* mean (±1 SD) brood size by 1-mm female length bins for females from the California Current (SC, NH, NCC) from our current synthesis and the number of ripe eggs counted in the ovaries of female *E. pacifica* from SC, USA (Brinton 1976; Fig. 3). The body length in Brinton's 1976 study is equivalent to the total length in the current study.

goal, ovarian egg counts might yield useful data. However, variability is very high and it is likely that small broods are under-represented with this method.

Influence of environmental conditions on brood size

The high variability in the female length versus brood size relationship for all regions (Fig. 2) suggests that the female length is not the only factor influencing *E. pacifica* brood size. Many factors, beyond just the possibility of incomplete spawning events described above, could limit a maximum potential brood size. Several likely candidates are food quality, food quantity, temperature (and relationship to molt cycle), past spawning behavior and female condition (such as lipid reserves or parasite infection). In order to minimize any effect of food-related differences within and among data sets, only incubations completed during the peak spawning timeframe (when gravid females are found consistently and eggs and larvae are abundant in the water column) in each region are included in the study reported here. Peak spawning activity typically corresponds with peaks in chlorophyll *a* (chl *a*), as the timing and duration of euphausiid spawning are based on the local period of elevated food production such as annual spring blooms or the blooms associated with upwelling events (Ross and Quetin, 2000; Feinberg and Peterson, 2003). Our experience has been that discrete chl *a* measurements taken at the time of an experiment are not generally good predictors of the food environment contributing to a brood of eggs since euphausiids produce broods approximately every 5 or more days (Feinberg *et al.*, 2007; Feinberg and Peterson, 2012) and thus are integrating their feeding environment over a period of days to weeks for each brood. Daily measurements of chl *a* (or other measures of food quantity or quality) might be required to adequately represent the feeding environment. This would especially be the case in highly advective environments, such as those studied here (with the exception of PS), where peak upwelling speeds of coastal currents transporting water offshore and alongshore can be quite high and cause conditions to change rapidly within an inter-brood period. Surface chl *a* is known to be a poor predictor of euphausiid brood size (Feinberg and Peterson, 2003; Taki, 2007) and this appears to be the case here, as available chl *a* data do not seem to correspond with observed regional differences in brood sizes (Table IV).

Known differences between physical environments in the different study areas could have impacted brood size as well. However, for individual studies where different incubation temperatures were used, there was no significant relationship with temperature. Brinton (Brinton,

1976) found that temperatures of 9–16°C were optimal for *E. pacifica* spawning and egg hatching, and Iguchi and Ikeda (Iguchi and Ikeda, 1994) found that these organisms could tolerate a range of 5–20°C without a significant increase in egg or larval mortality. All but one small batch of incubations from OC fell within that temperature range and even the OC incubations done at 3°C produced eggs, though these broods were somewhat smaller than broods from the other temperatures in the OC. There is no reason to believe that station depth would be a factor, beyond the assumption that greater depths may correspond with greater distances from shore where we would naturally expect lower productivity, or phytoplankton communities dominated by smaller cells. The relationship between station depth and brood size for individual studies where depth varied was very weak, indicating that depth differences between regions were not likely to be a significant factor contributing to differences in the brood size.

Factors influencing maximum brood size

Our ability to explain the differences among regional brood sizes is hindered by a lack of proper data on food quantity and by the fact that individual animals exhibit inherently high levels of variability regardless of feeding conditions. Because there are so many contributing factors, the use of quantile regression to look at maximum brood size (95% quantile) is very useful. The areas with a significant relationship between the female length and the maximum brood size were NH, NC, SC and TB. This suggests that in these regions the female size is the primary factor limiting the maximum brood size. The first three regions (NH, NC and SC) are within the California Current upwelling zone and are characterized by a prolonged spawning period (6+ months) during a highly productive upwelling season with prolonged successions of phytoplankton blooms. In these areas it is not unexpected that females produce broods that are primarily limited by their body size rather than by ocean conditions during the upwelling season when phytoplankton concentrations are consistently high and food limitation is unlikely. TB has a ~4 month long spawning season which ends in early June with the onset of much warmer surface temperatures which force the *E. pacifica* to reside at depth (Iguchi *et al.*, 1993; Iguchi and Ikeda, 1994). From February through at least May, temperatures in the upper 100 m are 10–14°C (Iguchi *et al.*, 1993), and in the appropriate range for peak egg production. There is also a prolonged spring bloom of ~1–4 µg L^{-1} of chl *a* from February through April (Takahashi and Uchiyama, 2007). Though these chl *a* levels are slightly lower than for the California Current

regions, perhaps they were consistent enough to sufficiently sustain the slightly smaller females incubated in this area and allow for the maximum brood sizes to be limited primarily by female size.

Morphometric comparison of *E. pacifica* eggs among regions

There was a striking difference in the appearance of *E. pacifica* eggs among regions. Eggs from NH and NCC had a very narrow perivitelline space with a mean width of 14 μm (n = 3891) (Gómez-Gutiérrez, 2003) similar to that described by Brinton *et al.* (Brinton *et al.*, 2000) for *E. pacifica* from the Eastern Pacific in general. The perivitelline space of *E. pacifica* eggs in the YS was extremely wide (∼240 μm) (Suh *et al.*, 1993, Shaw, personal observation) as it was in the northern Japan Sea (Pogodin, 1982). The GoA study found broods of both small and large diameter eggs (Pinchuk and Hopcroft, 2006), though the relative proportions or locations of these types of broods were not reported. Diameters of actual embryos were more similar between all regions. The perivitelline space provides buoyancy to the egg and studies suggest that this space is smaller for oceanic species than it is for neritic species (Marschall, 1983; Harrington and Thomas, 1987; Lindley, 1997) though this trend is disputed by Gómez-Gutiérrez (Gómez-Gutiérrez, 2003). This theory makes sense biologically, since eggs released in shallower water will need increased buoyancy to maintain them in the water column and prevent benthic predation before hatching while oceanic eggs would benefit from sinking below the highly populated surface waters where they are released. YS water temperatures were similar to temperatures from the NH study during the spawning season, suggesting that hatching time might also be similar (∼38 h). Sinking rates measured for *E. pacifica* from the California Current are on the order of 120 m day^{-1} (Gómez-Gutiérrez, 2003). YS eggs would need to be far less dense to avoid reaching the bottom (54–90 m in this study) in 38 h if indeed their hatching times are the same. Previous studies postulated that the size of the perivitelline space is species specific (Timofeev, 2006) but this may be a function of most euphausiid species inhabiting a particular environment rather than a wide range of habitats like *E. pacifica*. For *E. pacifica*, perivitelline space is clearly more environment specific. The extremely large perivitelline spaces in eggs from the YS, Northern Japan Sea and Gulf of Alaska show one clear instance of a way that *E. pacifica* may be able to adapt to local environmental conditions (in order to reduce sinking rates in shallower water). This difference in the total egg volume adds to the surprising similarities (median and maximum brood sizes) and differences (female size, environment) between females from the YS

and the California Current. Not only did the YS females have some of the largest broods of very large eggs but they also had the smallest total lengths of any group of females in the entire study, suggesting that perhaps a larger portion of their energy is allocated to reproduction than growth and a larger portion of the body cavity might be allocated to reproduction in the YS females. These hypotheses should be considered in future studies.

Brood size and fecundity

It is important to emphasize that the brood size and fecundity are not equivalent. *Euphausia pacifica* can spawn multiple times over one or more spawning seasons (Ross and Quetin, 2000; Feinberg *et al.*, 2007). Fecundity refers to the number of eggs a female will produce during a spawning season or throughout her lifetime, while the brood size is the number of eggs produced in a single spawning event and is indicative of environmental and physiological conditions during the previous inter-brood period (IBP). In order to calculate seasonal fecundities for individual females, it is necessary to know the IBP and the duration of the spawning season. For *E. pacifica*, these measurements require prolonged laboratory experiments (>2 months) and a regular and frequent field sampling program, preferably of greater than 1 year in duration. IBP measurements are available for only a few of the regions in this study, and even for those regions the results are highly variable (Feinberg *et al.*, 2007; Feinberg and Peterson, 2012). Given the lack of data and the inherent variability, we cannot estimate seasonal fecundities for each area. Instead, we compare hypothetical daily egg production for individual females and the duration of spawning seasons among the different regions (Table IV). If we divide the median brood sizes for each region (Table II) by an IBP of 5 days, which is the median from all long-term fecundity experiments available for *E. pacifica*, (Feinberg *et al.*, 2007; Feinberg and Peterson, 2012), we arrive at an hypothetical number of eggs produced by each female per day (Table IV). Females do not produce eggs daily, but this number is helpful for comparison. These values range from 11 to 39 for OC and YS, respectively. While this is more than a 3-fold difference, one must consider differences in the duration of the spawning season in order to consider the impact on seasonal fecundity. The spawning season is limited in areas such as the YS, PS, TB and GoA where it typically lasts only 3–4 months. In contrast, in areas such as NCC and NH and SC, the season can last well over 6 months (Table IV). These variations in spawning season duration can result in substantial differences in seasonal fecundity estimates for regions with similar median brood sizes (e.g. ∼3500 eggs season^{-1} female^{-1} for YS versus ∼6500 eggs season^{-1} female^{-1} for NH).

Longer spawning seasons can also boost overall fecundity for areas with smaller median brood sizes such as SC ($\sim$4700 eggs season^{-1} female^{-1}) assuming that individual females continue to spawn for the entire season. These results could be compared more accurately and effectively with IBPs to go along with each brood size study area.

CONCLUSIONS

The minimum size for spawning *E. pacifica* females appears to be $\sim$12-mm total length. There is a wide distribution of brood sizes associated with all lengths, suggesting that factors beyond the female length affect brood size. *Euphausia pacifica* as a species shows evidence of great reproductive plasticity and there do seem to be differences regarding the maximum brood size and its relationship to female length among studies, and likely among regions. Despite the range of study sites and slight differences in experimental methodologies, we are encouraged by the overall success of the studies and the similar relationships between female size and brood size observed from different regions. To make *E. pacifica* fecundity estimates more rigorous and applicable, more work on better defining spawning seasons and IBPs, as well as total female biomass from around the North Pacific, would be necessary. For ease of future comparisons, we would recommend a minimum of monthly cruises for at least 2 years with 300-μm mesh (or smaller) net tows and acoustic surveys for determination of spawning season and adult biomass, respectively. For the determination of IBP, we suggest future studies follow the methods described by Feinberg *et al.* (Feinberg *et al.*, 2007). Finally, we acknowledge that what we considered to be a marginal environment for *E. pacifica* reproduction, where seasonally stratified waters force them to reside at depth for part of the year (YS, TB), may not ultimately have a detrimental impact on reproduction.

ACKNOWLEDGEMENTS

FUNDING

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