

Euphausiids in the Eastern Bering Sea: A synthesis of recent studies of euphausiid production, consumption and population control

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Abstract

Euphausiids are an important component of the eastern Bering Sea marine ecosystem. We synthesized information on the ecological roles of two species, *Thysanoessa raschii*, which predominates over the Middle and Inner Shelf Domains, and *T. inermis*, which predominates over the Outer Shelf Domain. Although estimates of euphausiid biomass across the shelf are not well constrained, we estimated that, between April and July, 2004 - 2010, euphausiid biomass was $3.08 - 5.25 \text{ g C m}^{-2}$ on the outer shelf and $1.95 - 3.92 \text{ g C m}^{-2}$ on the middle shelf. Modeled estimates of euphausiid production, for spring and summer combined, varied between $0.043 \text{ g C m}^{-2} \text{ d}^{-1}$ and $0.051 \text{ g C m}^{-2} \text{ d}^{-1}$, depending on location, with a mean of $0.048 \text{ g C m}^{-2} \text{ d}^{-1}$. Recently reported field measurements of annual primary production over the southeastern Bering Sea in 2008 – 2009 vary between 0.06 and $6.65 \text{ g C m}^{-2} \text{ d}^{-1}$, with a mean of $1.262 \text{ g C m}^{-2} \text{ d}^{-1} \pm 2.049 \text{ g C m}^{-2} \text{ d}^{-1}$ in spring and summer combined, a level sufficient to support euphausiids, at least on an annualized basis. Walleye pollock (*Gadus chalcogrammus*, hereafter pollock) is the single most important consumer of euphausiids over the eastern Bering Sea shelf. We estimated that pollock consumed between 0.0042 and $0.019.7 \text{ g C m}^{-2} \text{ d}^{-1}$ of euphausiids, depending on year, with a mean of $0.011 \text{ g C m}^{-2} \text{ d}^{-1}$ in summer averaged over 1999 – 2009. This consumption is equivalent to between 17% and 29% of summer euphausiid production, depending on location.

Over the period for which data were available (2004 – 2012), we observed a strong negative relationship between euphausiid biomass as determined in acoustic surveys and pollock biomass as estimated in the eastern Bering Sea pollock stock assessment ($r^2 = 0.82$). During this time period, sea-surface temperature was the

second strongest predictor of euphausiid biomass, ($r^2 = 0.63$). However, for the period 2004 – 2010, bottom temperature ($r^2 = 0.94$) was the strongest predictor, followed by pollock biomass from the pollock stock assessment ($r^2 = 0.82$), and sea-surface temperature ($r^2 = 0.82$) were stronger predictors of euphausiid biomass than pollock biomass from the pollock stock assessment ($r^2 = 0.81$). Mean pollock density in the acoustic surveys was not a powerful predictor of euphausiid biomass during either period. In spatially explicit multiple regression analyses for the periods 2004 – 2012 and 2004 – 2010 those formulations that included sea-surface and bottom temperatures as well as survey estimates of pollock had the greatest explanatory value. However, when either or both temperature terms were dropped, the explanatory value of the models dropped considerably. When pollock biomass was dropped from the models, there was little change in explanatory value compared to the full model. Euphausiid production and pollock consumption data coupled with a negative relationship between euphausiid biomass and stock assessment estimates of pollock biomass indicate a top-down predation effect. However, strong negative relationships between euphausiid biomass and water temperatures indicate the influence of a bottom-up mechanism. The apparent differences in these results may relate to the different spatial and temporal scales used to assess the pollock biomass used in the analyses. Alternatively, euphausiid biomass may be strongly controlled during a restricted portion of the year, such as spring, if critical food needs are not met in some years. We lack the data necessary to resolve these alternative hypotheses.

- 82 Key words: Bering Sea, euphausiids, krill, *Thysanoessa*, walleye pollock, *Gadus*
83 *chalcogrammus*, top-down/bottom-up control

1.Introduction

Euphausiids (also known as krill) play a central role in the pelagic food-web of the eastern Bering Sea marine ecosystem. They consume phytoplankton, micro-zooplankton, and detritus, and “repackage” these small particles into lipid-rich bodies that then become an important source of energy for fish, seabirds and baleen whales (Aydin and Mueter, 2007). Despite their central role in the pelagic food web, Bering Sea euphausiids have remained little studied, perhaps because they are sufficiently large and fast swimmers to avoid most scientific plankton nets, and small enough that they are not sampled during fishery surveys using either bottom or mid-water trawls. In recent years, acoustic methods for estimating their abundance in the Bering Sea have been developed, and these have allowed improved estimates of euphausiid distribution and abundance (De Robertis et al., 2010; Ressler et al., 2012, 2014a). In this contribution, we consider both new data and information from the literature on the ecology of euphausiids in the eastern Bering Sea (Fig.1). These new data were obtained in the Bering Ecosystem Study (BEST), and the Bering Sea Integrated Ecosystem Study (BSIERP), which together are now known as the Bering Sea Project (<http://www.nprb.org/bering-sea-project>). We focus primarily on synthesizing the new information available on euphausiid population biology to assess the factors that control euphausiid abundance in the region.

In particular, our investigation examines the relative importance of top-down and bottom-up factors in the control of euphausiid biomass. The general consensus has been that most secondary production in the eastern Bering Sea is consumed by

predators (Smith, 1991; Springer, 1992; Aydin et al., 2007). Springer (1992) and Ressler et al. (2012) have suggested that the biomass of euphausiids in the eastern Bering Sea could be determined in part through top-down control by walleye pollock (*Gadus chalcogrammus*, hereafter, pollock) predation. Ressler et al. (2012) used biomass data from a new acoustic-trawl survey of euphausiids, as well as acoustic-trawl and bottom trawl surveys of pollock, to demonstrate a negative correlation between pollock and euphausiid biomass. They hypothesized that pollock predation, in addition to forcing by water temperature or ice cover as suggested by other work (e.g., Coyle et al., 2011; Hunt et al., 2011), might provide a significant control of eastern Bering Sea euphausiid standing stocks.

Predation by pollock is a key focus of our investigation because this species contributes the largest source of planktivorous fish biomass in the eastern Bering Sea (Aydin and Mueter, 2007). Pollock are also the single most important predator of euphausiids in the eastern Bering Sea, accounting for 37% of the euphausiid biomass taken by predators, more than double the amount taken by shrimp (14%), the second most important predator of euphausiids (Aydin et al., 2007). Juvenile Pacific cod (*Gadus macrocephalus*) are also important consumers of euphausiids in the southeastern Bering Sea, particularly in cold years (Farley et al., This Volume).

The top-down control of euphausiids by pollock in the Bering Sea has recently been brought into question. When Ressler et al. (2014a) compared the effects of pollock predation and water temperature on local euphausiid densities in regression models

using data from the summers of 2004-2010, they found that water temperature was a far better predictor of euphausiid biomass than was pollock biomass. They interpreted this result as inconsistent with strong top-down control of euphausiid populations by pollock predation.

Investigation of the relative importance of bottom-up and top-down control of euphausiids by pollock requires knowledge of the biomasses of pollock and euphausiids and how they vary with respect to one another, the rate of consumption of euphausiids by pollock, the rate of production of biomass by euphausiids, and the temporal and spatial availability of food for euphausiids. Field data are available for pollock biomass, euphausiid biomass, consumption, and production, and consumption of euphausiids by pollock. Recent modeling efforts also provide estimates of euphausiid biomass, production and food consumption. In this paper, we synthesize these sources of information to examine the potential for pollock to exert top-down pressure on euphausiids in the Bering Sea. We also attempt to examine the potential for bottom-up limitation of euphausiid productivity. However, estimates of the timing and magnitude of euphausiid food requirements relative to the availability of their prey are largely lacking. In particular, we lack data on the food requirements of euphausiids in early spring when they are producing eggs, and when the larval and juvenile euphausiids begin foraging.

In this paper, we present background on the euphausiids commonly found in the eastern Bering Sea (Section 2). After a presentation of data sources and analysis methods (Section 3), we provide a synthesis of data on primary production and its

export (Section 4.1), the distribution and abundance of euphausiids (Section 4.2), interannual variation in their biomass (Section 4.3), their food consumption (Section 4.4), and their production in the eastern Bering Sea (Section 4.5). We then provide a brief review of pollock biomass fluctuations in the eastern Bering Sea (Section 5.1) and their consumption of euphausiids (Section 5.2). In Section 6, we investigate the impacts of pollock predation and variability in sea surface and bottom temperatures on the distribution and abundance of euphausiids at the meso-scale and at the scale of the southeastern Bering Sea. Finally, we discuss the reliability of the data available to us (Section 7.1), annual and seasonal variability in the availability of food for euphausiids (Section 7.2), predation and temperature as predictors of the spatial and temporal distribution of euphausiid biomass (Section 7.3), and the relative importance of bottom-up and top-down control of euphausiids (Section 7.4).

2. Background on eastern Bering Sea Euphausiids

At least five species of euphausiids are found in the eastern Bering Sea: *Thysanoessa raschii*, *T. inermis*, *T. longipes*, *T. spinifera* and *Euphausia pacifica* (Vidal and Smith, 1986). *T. raschii* occurs over most of the eastern Bering Sea shelf, but is most abundant in cold, fresher mid- and inner-shelf waters shallower than 100 m (Coyle and Pinchuk, 2002a) i.e. the Middle and Inner Shelf Domains (Coachman, 1986) outlined in Fig. 1. This species accounts for 70 – 90% of the crustacean zooplankton biomass in the Middle Shelf Domain in early spring, with this percentage declining to < 50% of the biomass after the abundance of the copepod *Calanus marshallae*/*glacialis* (there is uncertainty as to which species of *Calanus* is present)

begins to increase rapidly in early June (Vidal and Smith, 1986). *T. inermis* occurs most commonly over deeper (100 to 200 m), more saline, shelf-edge waters (the Outer Shelf Domain and the top of the Shelf-slope Domain). The proportion of *T. inermis* and *T. raschii* in stomach samples of groundfish collected between January - December 1981 to 2013 where euphausiid prey (n=52296) could be identified as either *T. inermis* or *T. raschii* (n=6025), show a distribution similar to that described for the corresponding euphausiid species in the eastern Bering Sea (Fig.2). Only 9% of the stomach samples collected contained both species. The other euphausiid species occur primarily in the deeper water of the Shelf-slope Domain and the Aleutian Basin (Vidal and Smith, 1986; Smith, 1991; Ressler et al., 2012), although *T. longipes* is sometimes abundant in the Outer Shelf Domain (Bi et al., 2015). These distributions may reflect the individual species' oceanographic habitat preferences (e.g., Smith, 1991; Pinchuk and Coyle, 2008; Bi et al., 2015).

Both *T. raschii* and *T. inermis* are widespread in the Arctic marginal seas, the North Pacific, and the North Atlantic Oceans, and their distributions in the eastern Bering Sea are consistent with their patterns of distribution elsewhere (Fukuchi, 1977; Smith, 1991; Coyle and Pinchuk, 2002a; Pinchuk and Coyle, 2008; Bi et al., 2015). *T. raschii* is abundant in shallow coastal waters and fjords of the southern Barents Sea (Dalpadado and Skjoldal, 1991; Drobysheva, 1979, 1994); *T. inermis* is more abundant farther offshore (Dalpadado and Skjoldal, 1991).

198 *T. inermis* stores lipids to fuel overwinter survival and reproduction in the spring
 199 and, at 18 months of age, they contain about twice the amount of lipid per individual as
 200 *T. raschii*(Falk-Petersen et al., 1981, 2000; Harvey et al., 2012). *T. raschii* instead
 201 appears to rely more heavily on detrital feeding to overwinter, and upon the spring
 202 phytoplankton bloom to support spawning (Falk-Peterson et al., 2000; Harvey et al.,
 203 2012). These different strategies are reflected in the timing of reproduction for these
 204 species: *T. inermis* apparently spawns earlier in the year than *T. raschii* (Hopkins et al.,
 205 1984; Smith, 1991), perhaps because *T. raschii* needs to feed before spawning. Recent
 206 work based on the accumulation of lipofuscin in the eyes of euphausiids as a function of
 207 body length shows that both *T. raschii* and *T. inermis* are likely to live to age three or
 208 four years in the Bering Sea (Harvey, Pleuthner and Shaw, Unpubl.), similar to their life
 209 spans in cold waters elsewhere (Einasson, 1945; Hopkins et al., 1984; Dalpadado and
 210 Skjodal, 1991).

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 212 Cold water temperatures may impact the spawning activity of euphausiids. In the
 213 Bering Sea, euphausiids have been more abundant in cold years than warm years
 214 (Stabeno et al., 2012). In the very cold Arctic-influenced waters of the Barents Sea
 215 marginal ice zone, despite the presence of bloom or pre-bloom conditions, Dalpadado
 216 et al. (2008) found that few *T. inermis* were in a sexually mature state, whereas sexually
 217 mature *T. inermis* were found in the warmer, Atlantic-influenced West Spitsbergen
 218 Current. These findings, along with that of Timofeyev (1993) that *T. inermis* does not
 219 reproduce in the waters around Spitsbergen, suggest that excessively cold conditions
 220 can retard or halt reproduction by *T. inermis*. *T. raschii* reproduces in colder waters than

T. inermis and is able to reproduce in the waters of the marginal ice zone (Ponomareva, 1963; Dalpadado et al., 2008). As in the Sea of Okhotsk (Timofeyev, 1987, 1996), *T. raschii* is more abundant in the Barents Sea during years when water temperatures are cold (Drobysheva, 1979, 1994; Dalpadado and Skjoldal, 1991).

3. Data Sources and Methods

3.1. *Euphausiid* Biomass

The biomass of euphausiids per unit area is a critical variable for the estimation of euphausiid production, which is the product of individual growth rates and euphausiid standing stock (Kimmerer, 1987). In the eastern Bering Sea, euphausiid biomass has been measured by two methods, net hauls and multi-frequency acoustic surveys. Both methods have inherent sampling errors. Euphausiids are adept at avoiding plankton nets, especially during daylight hours (e.g., Clutter and Anraku, 1968; Sameoto et al., 2000). Acoustic-based abundance estimates are highly sensitive to the estimates of the acoustic reflectivity, or target strength of the organism (Stanton et al., 2000). In Appendix A, we develop methods for adjusting both the initial net-derived and acoustic-derived estimates to provide what we reason are the most likely values for euphausiid biomass. Thus, in addition to presenting non-adjusted values for euphausiid biomass in Table 1, in the text and in Table 2 we present net-based euphausiid biomass estimates adjusted upward for net avoidance by a factor of 5 and acoustic estimates adjusted downward by a factor of 8.

3.1.1 Net sampling

In 2004 (August) and 2008-2010 (April – June), euphausiids were collected at night using a 1 m² MOCNESS fitted with black 505 µm mesh nets towed at 2 knots (1.0 m s⁻¹); details on spatial coverage and sample processing protocols are presented elsewhere (Pinchuk and Coyle, 2008; Bi et al., 2015). To obtain biomass estimates, euphausiids were weighed in the laboratory and their weights were later converted to g C m⁻² using species-specific dry/wet weight and carbon/dry weight relationships (Harvey et al., 2012). For comparison, the species-specific euphausiid abundance data of Smith (1991) were converted to units of carbon biomass by multiplying the average number of adult euphausiids m⁻² from the stations in the Middle and Outer Shelf Domains in 1980 (Table 1 in Smith, 1991) by the mean dry weights of adult euphausiids caught in these regions in 1980 (Table 3 in Smith, 1991), and then applying the same dry mass to carbon ratio (Harvey et al., 2012).

3.1.2 Acoustic-trawl survey

Our analysis draws on acoustic survey data collected in the eastern Bering Sea from 2004 – 2012. Acoustic-trawl survey estimates of euphausiid biomass involved classification of multifrequency acoustic backscatter (18, 38, 120, and 200 kHz) measured by vessel-mounted echosounders and concurrent sampling with targeted, daytime Methot trawls (Methot, 1986). Details of these analyses are given by DeRobertis et al. (2010) and Ressler et al. (2012). Euphausiids were numerically and acoustically dominant in trawl catches from layers of euphausiid backscatter in the eastern Bering Sea (Ressler et al., 2012); thus, their vertically integrated abundance per m⁻² (N_{euph}) was computed from acoustic backscatter by the following:

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$$N_{eup\ h} = z \left(\frac{Sv_{eup\ h}}{10^{(TS_{eup\ h}/10)}} \right) \quad \text{Equation 1}$$

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270 where $Sv_{eup\ h}$ is the mean volume backscattering coefficient for euphausiids (m^2/m^3),
 271 $TS_{eup\ h}$ (target strength) represents the length-weighted average backscatter from a
 272 single euphausiid (dB re 1 m^2), and z is water column depth (m). $TS_{eup\ h}$ was estimated
 273 using a scattering model parameterized for the eastern Bering Sea (Ressler et al., 2012,
 274 Smith et al., 2010, 2012) and the distribution of euphausiid lengths from trawl catches.
 275 $N_{eup\ h}$ was converted to carbon using species-specific length-carbon relationships for
 276 Eastern Bering Sea euphausiids (Harvey et al., 2012).

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278 Both net sampling and acoustic-trawl techniques may have substantial biases,
 279 and a low bias in model-estimated euphausiid $TS_{eup\ h}$ (Equation 1) could inflate acoustic-
 280 trawl estimates and explain some of the discrepancy. For comparison, an alternative
 281 estimate of mean euphausiid $TS_{eup\ h}$ was obtained by dividing the observed volume
 282 backscatter by the number of euphausiids in the observation volume as estimated by a
 283 trawl catch (e.g., Sameoto et al., 1993). Using this approach, we estimated euphausiid
 284 $TS_{eup\ h}$ by regressing daytime, avoidance-adjusted Methot trawl catches of
 285 euphausiids with concurrently observed euphausiid backscatter, and obtained a $TS_{eup\ h}$
 286 value 8-fold higher than the scattering model estimate (further details are given in
 287 Appendix A).

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289 *3.1.3 NPZ model*

We also considered euphausiid biomass computed with a Nutrient-Phytoplankton-Zooplankton (NPZ) model developed in BEST (hereafter BEST-NPZ Model) for estimating lower trophic level ecosystem dynamics over the Bering Sea shelf. This model (see Gibson and Spitz, 2011 for details) computes euphausiid biomass ($E \text{ mg C m}^{-2}$) based on estimates of temperature-dependent euphausiid consumption ($Graz_E$) and respiration ($Resp_E$) rates, assimilation efficiency (γ_E) and losses due to explicitly defined higher predators (jellyfish, $Pred_{JE}$), as well as in-explicitly defined losses including losses ($Mort_E$) to higher trophic levels (i.e. pollock) that are not explicitly represented in the model, natural mortality, and molting.

$$\frac{\partial E}{\partial t} = \gamma_E \cdot Graz_E - Resp_E - Pred_{JE} - Mort_E \quad \text{Equation 2}$$

The predation term $Pred_E = p_E(E^2)f(t)$ is a temperature (t) dependent quadratic function, reflecting the assumption that, if there are more euphausiids in an area (higher biomass), they will experience higher predation than euphausiids in an area (or time) with fewer euphausiids. The modulation of the predation rate parameter (p_E) by temperature (increasing with increasing temperature), reflects the assumption that fish will consume more euphausiids, to meet their higher metabolic demands when they are in warmer water. When considering the BEST-NPZ model results, it should also be noted that winter survival of euphausiids may be underestimated, and thus the cumulative influence of consecutive 'good' or 'bad' years on the euphausiid standing stock may not be well captured.

3.2. Euphausiid ingestion rates:

In the 1980s, Smith (1991) estimated euphausiid ingestion rates using net-measured biomass, assuming an assimilation efficiency of 70%. Smith did not account for the effects of net avoidance or temperature on these rates. In the Bering Sea Project, euphausiid food consumption was modeled as a function of the available prey field (small (PS) and large phytoplankton (PL) and microzooplankton (MZ)), euphausiid biomass (E) and temperature (f_t). The grazing formulation followed the approach by Ryabchenko et al. (1997) to extend a Holling type III grazing formulation to multiple prey resources (Gibson and Spitz, 2011), where f represents the preference of euphausiids for each prey type.

$$Graz_E = \gamma_E \frac{e_E \cdot (fp_{PS} \cdot PS^2 + fp_{PL} \cdot PL^2 + fp_{MZ} \cdot MZ^2)}{k + fp_{PS} \cdot PS^2 + fp_{PL} \cdot PL^2 + fp_{MZ} \cdot MZ^2} \cdot E \cdot f_t$$

Following Smith (1991), we assumed an assimilation efficiency (γ_E) of 70%. A large range for zooplankton ingestion rates can be found in the modeling literature with typical values ranging from 0.5-1.5 d^{-1} (Doney et al., 1996 and references there-in). Here we assume a slightly lower mass specific ingestion rate (e_E) for Bering Sea euphausiids of 0.3 $mg\ C\ (mg\ C)^{-1}\ d^{-1}$. This value is still considerably higher than the maximum ingestion rate of 4% of body weight determined by Campbell et al., this volume.

3.3 Euphausiid production rates:

Production of euphausiids has been estimated from egg production and somatic growth rates. Using shipboard incubations of female euphausiids, Smith (1991) measured euphausiid egg production rates in the Bering Sea during spring and summer

in 1980 and 1981. In August, 2004, Pinchuk and Coyle (2008) measured egg production rates of euphausiids in the vicinity of the Pribilof Islands. Somatic growth rates were also measured by these investigators. Smith (1991) computed mass-specific growth rates ($\% d^{-1}$) of older euphausiid life stages from the average dry weights of a population at initial and subsequent time periods. Pinchuk and Coyle (2008) measured somatic growth rates using the instantaneous growth rate technique (Ross et al., 2000; Pinchuk and Hopcroft, 2007).

In the BEST-NPZ model, euphausiid production is estimated as a function of food availability ($Graz_E$) and euphausiid 'preference' for the different prey types, euphausiid mass specific grazing rate (e_E), temperature, Q^{10} rates, assimilation efficiency (γ_E), and the biomass of the euphausiid population to which the growth equations were applied (Gibson and Spitz, 2011). The NPZ model is a 'complete' lower trophic level model and food availability (i.e. phytoplankton and microzooplankton biomass) was estimated within the model.

3.4. Consumption of euphausiids by pollock

We estimated the spatial distribution of pollock consumption of euphausiid biomass in the southeastern Bering Sea using detailed data on the spatial distribution of stomach contents of pollock of known size collected during the NOAA Alaska Fisheries Science Center annual bottom trawl survey (Ianelli et al., 2011). The daily ration of a pollock of a given size was calculated as a function of temperature (Holsman and Aydin, 2015) and then apportioned among the prey species found in its stomach (Buckley et

al., this volume). To assess the impact of ocean temperature and the timing of ice retreat on pollock consumption of euphausiids, the consumption calculations were made separately for years when ice retreat was “early” and “late”. Early-ice-retreat-years were: 1983, 1987, 1993, 1998, 2003, 2004 and 2005; and late-ice-retreat-years were: 1985, 1992, 1995, 1999, 2008, 2010, and 2012. Early- and late-ice-retreat-years were selected based on an updated version of Figure 3 from Hunt et al. (2011), as the thirds of the ice record with the earliest and latest dates of ice retreat in the period from 1982 – 2010, when stomach samples were available.

3.5. Euphausiid biomass as a function of temperature and pollock biomass

To assess trends in euphausiid biomass as a function of temperature and pollock biomass, we used several different sources of information to construct single and multiple regression models. For these models, we used pollock and euphausiid acoustic-trawl survey data sets as described by Ressler et al. (2012, 2014a,b) and in section 3.1.2. Briefly, the data consist of euphausiid biomass per area (kg ha^{-1}) for the entire water column on a 37 x 37 km (20 x 20 nmi) grid covering the middle and outer shelf of the eastern Bering Sea (Fig. 1). Survey pollock biomass is the sum of age-1+ biomass from bottom trawl and acoustic-trawl survey estimates at each station; euphausiid estimates are available only from the acoustic-trawl survey. Surface temperature and bottom temperatures ($^{\circ}\text{C}$) were also measured at each bottom-trawl station. In addition, stock assessment model estimates of age-1 and older pollock biomass (metric tons, t) for the eastern Bering Sea shelf in January of each year were available from Ianelli et al. (2013). Finally, two indices of ice cover for the eastern Bering Sea were obtained

from <http://www.beringclimate.noaa.gov/>. The “Ice retreat index” represents observations of the number of days after March 15 when 10% or more of a 2° x 2° box (56-58°N, and 163-165°W) on the southeast Bering Sea shelf was covered with ice in each year. The “Ice cover index” combines observations of ice cover throughout the Bering Sea from several sources; results are expressed as the standard deviation from the long term mean. Larger values for both indices indicate more ice.

For single variable regressions predicting euphausiid biomass, a functional regression equation was used to compute the coefficient of determination (r^2) (Ricker, 1973). For spatially explicit multiple regressions, generalized additive models (GAMs) were fit using the mgcv toolbox (Wood, 2006) in R (R Development Core Team, 2012). This model is described in detail by Ressler et al. (2014a) and was of the form:

$$\log_{10}(E + 10) \sim s[\log_{10}(P + 10)] + s(t_b) + s(t_{ast}) + s(longitude, latitude) \text{ Equation}$$

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where E and P are the euphausiid and pollock biomass respectively, $s()$ indicates a spline function for the effect of each covariate on log euphausiid biomass, t_b is the bottom temperature, and t_{ast} is the annual average surface temperature. Each covariate represents the estimate of the quantity at a survey station, except annual average surface temperature, which is an average for all survey stations in each year. The $s(longitude, latitude)$ term served to control for the average spatial pattern in the observations for each year and removed autocorrelation in model residuals. Note that

these regression models treat euphausiid abundance as a relative index, and the inferences drawn from the models would not be altered by the adjustments to the acoustic abundance estimates described in section 3.1.2 and Appendix A.

We evaluated several hypotheses using these regression models. First, we hypothesized that temperature would remain a better predictor of local euphausiid density when the GAM from Ressler et al. (2014) was updated with 2012 summer survey observations. Second, we hypothesized that if ice-associated primary production was the mechanism by which temperature affects euphausiid biomass, then annual indices of winter-spring ice cover would be better predictors of annual changes in euphausiid biomass than temperature. Finally, we hypothesized that annual pollock abundance from the stock assessment model of eastern Bering Sea pollock (Ianelli et al., 2013) might serve as an alternative annual index of shelf-wide pollock consumption of euphausiids, and thus be associated with annual variation in euphausiid abundance.

4. Results:

4.1. Primary production in the southeastern Bering Sea and its export:

The amount and timing of primary production are potentially important variables in controlling the growth and biomass of euphausiids. Field measurements of primary production in the Bering Sea are variable in space and time, and past estimates of primary production over the outer and middle domains of the southeastern shelf have ranged between $162 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the Outer Shelf Domain and $166 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the Middle Shelf Domain (Fig. 7 in Walsh and McRoy, 1986) to $145 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the

Outer Shelf Domain and $150 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the Middle Shelf Domain (Rho and Whitley, 2007).

The BEST-NPZ model's average annual production estimate of $154 \pm 4 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the Southern Outer Shelf Domain (Region 4, Fig. 1) for the 1999-2009 period, falls well within this observed range. The average annual production estimate of $123 \pm 4 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the southern middle shelf (Region 3) likely underestimates the true extent of the production. Daily net primary production over the southeastern Bering Sea shelf, as estimated in the BEST-NPZ model for the years 1999-2009, averaged $0.57 \text{ g C m}^{-2} \text{ d}^{-1}$ for spring (1 April – 14 June) and summer (15 June – 31 August), combined (Table 3). Modeled estimates of daily mean gross primary production by Liu et al. (This volume) were $0.950 \text{ g C m}^{-2} \text{ d}^{-1}$ in “warm” years and $0.859 \text{ g C m}^{-2} \text{ d}^{-1}$ in “cold” years. Net production estimates, which take into account losses due to respiration, were not provided, but would be lower.

Recently, Lomas et al. (2012) assessed the average production rates from all previous field efforts in an attempt to improve the quantification of primary production in the southeastern Bering Sea. An average of prior estimates of annual averages (Table 2 in Lomas et al., 2012) for the Middle Shelf and Outer Shelf Domains, combined, was $1.00 \text{ g C m}^{-2} \text{ d}^{-1} \pm 50\%$. This would result in a yearly rate of $153 \text{ g C m}^{-2} \text{ yr}^{-1} \pm 50\%$, assuming a production period of 153 days (1 May - 30 September). Daily production estimates obtained in 2008 - 2010 ranged from 0.06 to $6.65 \text{ g C m}^{-2} \text{ d}^{-1}$, with a mean of $1.262 \text{ g C m}^{-2} \text{ d}^{-1} \pm 2.049 \text{ g C m}^{-2} \text{ d}^{-1}$ in spring and summer combined ($n=85$) (M. Lomas, pers.

comm.), which is equivalent to an annual rate of 193 g C m^{-2} , assuming a 153 day growing season.

Export of primary production to the benthos has been estimated from both field measurements of the amount of material settling to the bottom, as measured in sediment traps and thorium losses, and by modeling based on estimates of annual primary production and annual consumption by zooplankton (Lomas et al., 2012; Moran et al., 2012). Based primarily on model output, Walsh and McRoy (1986) estimated that direct annual export of primary production to the benthos was $130 \text{ g C m}^{-2} \text{ y}^{-1}$ over the Middle shelf Domain and $94 \text{ g C m}^{-2} \text{ y}^{-1}$ over the Outer Shelf Domain.

More recently, Baumann et al. (2013a,b), measuring carbon export to the benthos with both sediment traps and thorium deficits, observed daily rates ranging from $0.048 - 0.072 \text{ g C m}^{-2} \text{ d}^{-1}$ in spring to $0.36 - 0.60 \text{ g C m}^{-2} \text{ d}^{-1}$ in summer. Annual export was estimated to be $\sim 60 \text{ g C m}^{-2} \text{ y}^{-1}$ using the seasonal interpolation scheme of Cross et al. (2014). Carbon export, as a proportion of net primary production (*e*-ratio), averaged 0.46 ± 0.48 in spring and 0.33 ± 0.26 in summer, which were not statistically distinct (Moran et al., 2012, Baumann et al., 2013b). Thus, based on these estimates of the *e*-ratio, 60% to 70% of annual primary production was available to support the pelagic community. This is likely an underestimate, as some of the export was likely to be fecal pellets of grazers.

Moran et al. (2012) suggested that the summer values may reflect a substantially differently structured ecosystem than in spring, with the summer ecosystem being dominated by flagellates and with significant recycling due to heavy micro-zooplankton grazing (see also Stoecker et al., 2013). Microzooplankton are consumed by mesozooplankton in spring, particularly post-bloom (Campbell et al., this volume), and become a large proportion (>50%) of euphausiid diets in the summer (Lessard et al., 2012; unpubl.).

4.2. Estimation of euphausiid biomass in the southeastern Bering Sea

Estimates of euphausiid biomass over the eastern Bering Sea shelf vary dramatically depending on the methods used (Table 1). In 2008-2010, euphausiid biomass from the uncorrected nighttime MOCNESS tows averaged 1.05 g C m^{-2} on the outer shelf in June and 0.39 g C m^{-2} on the middle shelf in April-June. Note that euphausiid biomass on the outer shelf was exceptionally large in 2010 due in part to a high abundance of *T. longipes*, which had a relatively higher carbon content than other euphausiids in that summer (Harvey et al. 2012, Fig. 4). These recent net-based estimates of euphausiid are similar to those developed for 1980 by Vidal and Smith (1986) of $0.10 - 0.90 \text{ g C m}^{-2}$ for the waters of the outer shelf and slope, and of $0.40 - 0.50 \text{ g C m}^{-2}$ for the Middle Shelf Domain. In June-July 2008-2010, uncorrected acoustically-derived estimates of euphausiid biomass averaged 24.7 g C m^{-2} on the outer shelf and 31.4 g C m^{-2} on the Middle Shelf (23 and 81 times higher than the corresponding MOCNESS estimates quoted above; Table 1).

When the net-derived estimates are adjusted upward for net avoidance by a factor of 5, and the acoustic-derived estimates adjusted downward by a factor of 8 (see section 3.1.2 and Appendix A for a rationale for corrections), MOCNESS and acoustic-trawl estimates agree to within a factor of 2 of each other (Table 2). The BEST-NPZ model estimates for euphausiid biomass ranged from 1.77-3.87 g C m⁻² depending on domain, season and year (Table 1). Thus, the adjusted MOCNESS and acoustic-trawl estimates of euphausiid biomass were of the same order of magnitude as BEST-NPZ model estimates for spring and summer. We do not know if our adjustments are correct, but they are plausible and bring acoustic and net estimates of euphausiid standing stock into line with one another and with the primary and secondary production estimates from the NPZ model. Averaging the results from corrected net sample and acoustic sampling with the output from the BEST-NPZ model, the summer estimates of euphausiid biomass are ~ 4.01 g C m⁻² for the Outer Shelf Domain and ~ 3.17 g C m⁻² for the Middle Shelf Domain for the period 2008 to 2010 (Table 2).

4.3. Interannual variability in euphausiid biomass

The net sampling, acoustic surveys and the BEST-NPZ model all showed considerable inter-annual variability, but the variability captured by the net surveys (2008 vs. 2010; +750%) was considerably greater than that seen in the acoustic data (2008 vs. 2010; -77%) for the Outer Shelf Domain (Table 1). The biomass estimates of euphausiids from the model output (Fig. 3) and the acoustic surveys (Fig. 4) both suggest an increase in summer biomass between 2004 and 2010 (250% in the acoustic signal, Table 1). The acoustic surveys were conducted using the same methods and at

the same time each year, giving us added confidence that the interannual differences are real.

Both model and acoustic results indicate that euphausiid biomass was low in 2004/2005 (see also Coyle et al., 2011; Hunt et al., 2011). 2004 was the first year of the acoustic euphausiid biomass time series and the third consecutive year of unusually high sea temperatures and early ice retreat in the eastern Bering Sea. Euphausiid biomass increased from 2006 to 2009, during a stanza of colder than average temperatures and late ice retreat (2006-2012; Stabeno et al., 2012). Acoustic measurements indicate a steep decline in euphausiid biomass from 2009 to 2012, the last year for which acoustic survey data are available (Fig. 4). The summer biomass from the acoustic survey and the NPZ model for the outer shelf were positively correlated between 2004 and 2009, the years for which data were available from the NPZ model ($r^2 = 0.83$, $p = 0.03$; Table 1).

4.4. Eastern Bering Sea euphausiid grazing impact

Smith (1991) estimated that euphausiid ingestion rates of phytoplankton for the spring bloom period (1 May – 10 June) in the Middle Shelf Domain varied between 0.014 and 0.193 g C m⁻² d⁻¹ in 1980 and between 0.006 and 0.037 g C m⁻² d⁻¹ in 1981. Smith estimated that this ingestion amounted to a maximum of 6% of primary production in 1980, a relatively cold and stormy year, and 1% of primary production in 1981, a relatively warm and calm year.

More recent estimates of euphausiid consumption are consistent with these historic estimates. Based on measurements of euphausiid ingestion in experimental incubations and euphausiid biomass from net tows in the Bering Sea project from 2008 -2010, euphausiid consumption was estimated to be <1 - 5% of primary production, however, when the underestimation of euphausiid biomass from net tows is taken into account this figure could be as high as 15% (Campbell et al., in press; Lessard et al., unpubl.).

4.5. Eastern Bering Sea euphausiid production

Estimates of production per unit area by euphausiids are sensitive to the area's standing stock euphausiid biomass and growth rates, which vary with food availability, water temperature, and other factors affecting metabolic rates. Smith (1991) estimated somatic growth rates of *T. raschii* adults to be 0.6 - 1.8% dry body mass d⁻¹ for adult females and 1.8% dry body mass d⁻¹ for adult males, in 1980, with sea surface temperatures in the Middle Shelf Domain of 2 - 3 °C in May. In 1981 surface temperatures of 5 -6 °C during May, she estimated the growth of *T. raschii* females to be 1.9 - 2.4% dry body mass d⁻¹ while the adult males had a rate of 1.8- 4.0% dry body mass d⁻¹; during the same year Smith (1991) found *T. inermis* to have lower somatic growth rates, estimated at -0.1% dry body mass d⁻¹ for adult females and 1.3% d⁻¹ for adult males in the Middle Shelf Domain. For both species of euphausiid, Smith (1991) found that juveniles had higher growth rates than adults.

In August, 2004, near the Pribilof Islands, where there is a combination of Middle Shelf and Outer Shelf Domain waters, Pinchuk and Coyle (2008) found mass-specific growth rates of *T. inermis* juveniles to be $7.9 \pm 1.8\% \text{ d}^{-1}$ and those of adults to be $0.09 \pm 0.4\% \text{ d}^{-1}$. During the same period, female *T. raschii* were still producing eggs (mean brood size 138.7 ± 37.5 eggs d^{-1}) corresponding to 1.1% dry body mass. Their somatic growth was slightly negative ($-0.01 \pm 0.18\% \text{ d}^{-1}$), for a total mass-specific production rate of $1.04\% \text{ d}^{-1}$. Water temperatures during this time were 10 - 13 °C above the thermocline and 2 – 4 °C below it.

Summary estimates of euphausiid production and primary production in the BEST-NPZ model are presented in Table 3. Over the period 1999 – 2009, modeled euphausiid production averaged $\sim 0.048 \text{ g C m}^{-2} \text{ d}^{-1}$ for spring and summer (1 April - 31 August) combined. This model estimate falls within the range of values for euphausiid production estimated by Smith (1991) for the southeastern Bering Sea spring ($0.002 - 0.124 \text{ g C m}^{-2} \text{ d}^{-1}$), though Smith's numbers are likely low by a factor of 5 or more, as her biomass estimates were based on uncorrected net hauls. When annual euphausiid production estimates from the ecosystem model of Walsh and McRoy (1986) are divided by an assumed 153 day growing season, the resultant daily production estimates range from $0.039 - 0.079 \text{ g C m}^{-2} \text{ d}^{-1}$ for the outer and middle Eastern Bering Sea shelf, respectively. We are unable to determine whether the above range of values represents sampling errors or interannual variation in euphausiid production.

5. Walleye pollock in the eastern Bering Sea

5.1. *Pollock biomass*

Since 1978, the biomass of age-3+ pollock in the Eastern Bering Sea has fluctuated between about 3.5 million metric tons (1978) and 13 million metric tons (1995) (Ianelli et al., 2013). In the years 2000 - 2006, pollock biomass remained above 9.5 million metric tons due to the recruitment of the strong year classes of 1996, 1999 and 2000. However, recruitment between 2001 and 2005 was weak, which combined with continued fishing effort and natural mortality led to a decline in pollock biomass from a peak in 2003 of 12.2 million metric tons (not shown) to a trough at 4.6 million metric tons in 2008 (Fig. 4). Since then, the biomass of pollock has been increasing and reached 8.3 million metric tons in 2013; this increase is primarily attributable to above average recruitments of the 2006 and 2008 year classes (Ianelli et al., 2013).

5.2 *Pollock consumption of euphausiids:*

On average, approximately 37% of the diet of pollock is composed of euphausiids, but this proportion varies with the size of the pollock, its location in the eastern Bering Sea, and year (Buckley et al., this volume). The biomass of euphausiids consumed by pollock also varies spatially (Fig. 5). In particular, in the more southerly areas, just north of the Alaska Peninsula where euphausiid abundance tends to be high (Ressler et al., 2012), consumption of euphausiids by pollock was high. Furthermore, a substantial biomass of euphausiids was consumed by pollock along a relatively broad portion of outer shelf, an area where pollock abundance is generally high (Ressler et al., 2012).

Pollock diets and consumption of euphausiids differed between cold years with late ice retreat, and warm years with early ice retreat (Fig 4) (see also Buckley et al., this volume). In cold years, a lower biomass of euphausiids was consumed, and most of this was along the peninsula and the shelf edge, with little predation over the Middle Shelf Domain. In contrast, during the warmer years, a greater biomass of euphausiids was consumed by pollock, and much of this was taken in the Middle Shelf Domain. Buckley et al. (this volume) show that in the cold years, pollock increased their consumption of copepods, but decreased it during the warm years. Although copepods are likely to have been more abundant in the cold years (Coyle and Pinchuk, 2002b; Ohashi et al., 2013), it is not known if the shift in pollock diets was due to a change in the relative availability of the different prey or to a behavioral change on the part of the pollock.

Over the period from 1999 to 2009, the mean June – July estimated consumption of euphausiids by pollock in the southeastern Bering Sea, as measured from stomach contents, (Regions 1, 3, 4, 6, 8) varied between $4.2 \text{ mg C m}^{-2} \text{ d}^{-1}$ in 2008 and $19.7 \text{ mg C m}^{-2} \text{ d}^{-1}$ in 2001 (Table 4). This level of temporal variation in the amount of euphausiids consumed by pollock was to be expected because of the fluctuating biomass of both pollock and euphausiids on the shelf (Fig. 4). On average, over Regions 1, 3, 4, 6, and 8 combined (Fig. 1), pollock consumed $0.0066 \text{ g C m}^{-2} \text{ d}^{-1}$ of euphausiids in the cold years (1999 and 2007 - 2010), which increased to $0.0133 \text{ g C m}^{-2} \text{ d}^{-1}$ of euphausiids in the warm years (2003, 2004, and 2005) (Table 4).

The proportion of modeled euphausiid production to biomass consumed by pollock varied considerably among regions and years, with the greatest interannual variation in both metrics occurring in Region 1 (Fig. 6a). There, the highest proportion of euphausiid production consumed by pollock occurred in 2001 and 2003. For all regions combined, there was an increase in the proportion of euphausiid production consumed by pollock from 1999 to 2001, and a decline in the proportion of production consumed from 2003 to 2009, the last year for which a model run was available to us.

For all years between 1999 and 2009, mean pollock consumption of euphausiids in June and July in Regions 1, 3, 4, 6, and 8, combined, was $0.011 \text{ g C m}^{-2} \text{ d}^{-1}$ (11 mg C $\text{m}^{-2} \text{ d}^{-1}$, Table 5). This is approximately 23% of euphausiid production over the same area between April and August ($0.011 \text{ g C m}^{-2} \text{ d}^{-1} / 0.048 \text{ g C m}^{-2} \text{ d}^{-1}$), as estimated in the BEST-NPZ model (Table 3), or a consumption rate of $\sim 0.34 \% \text{ d}^{-1}$ of the average summer standing stock of euphausiid biomass, as estimated in the NPZ model (Table 5). The total consumption over the 77 days (15 June and 31 August) is equivalent to the consumption of 26% of the euphausiid biomass present. (Table 5).

6. Trends in euphausiid biomass as a function of temperature and pollock biomass

In single variable regressions predicting annual average euphausiid biomass ($n = 7$ surveys), euphausiid biomass was negatively associated with bottom temperature, surface temperature, and pollock biomass (Fig.7), while relationships between

euphausiid biomass and both ice retreat and ice cover were positive. However, these relationships were not always statistically significant. In particular, r^2 values between euphausiid density and both surface and bottom temperatures, and ice cover for the 2004-2012 period were weaker compared to the shorter 2004-2010 period, while the r^2 based on survey pollock density remained about the same and was not statistically significant (Table 6).

Annual averages of euphausiid density were strongly and negatively correlated with stock assessment model estimates of pollock standing-stocks for 2004-2010 and 2004-2012 (Fig.7). Indices of ice cover and ice retreat were not strongly correlated with euphausiid density (Table 6). The relationships between annual indices of any of these quantities were very sensitive to addition or removal of a single observation. For example, each of these relationships became weaker and no statistically significant correlations remained if summer 2004 was removed from the computation (Table 6). As a very warm year when pollock standing stock was high, summer 2004 provided substantial contrast in this data set.

Analysis of the full resolution acoustic-trawl survey data set ($n=1440$ stations over 7 years) provided increased statistical power and allowed spatial analysis; however this meant stock assessment estimates could not be included in this analysis. When the spatially explicit GAM from Ressler et al. (2014a) was updated with 2012 observations (Eqn. 3), the variance explained by the model decreased (36.9%, model 1.1) compared to the model fitted to 2004-2010 observations (47%, model 2.1, see Table 7). This result

is consistent with the weakening of single variable regressions when 2012 data were added (Table 6). However, temperature still remained a stronger predictor of local euphausiid density than pollock density in the updated model (Fig. 8). The shapes of the partial effects in the GAM did not change substantially with the addition of 2012 observations: the effect of bottom temperature and annual average surface temperature were negative (Fig. 8, panels b and d), and the effect of pollock density (Fig. 8a) was relatively flat after accounting for the average spatial pattern in the data over all years (Fig. 8c).

The relative effects of pollock density and temperature on GAM predictions of euphausiid density became clearer when temperature or pollock density were removed from the 2004 – 2012 model: the variance explained by the model changed by only a small amount when the pollock term was dropped (Table 7, model 1.2), yet it decreased greatly when either or all of the temperature terms were removed (Table 7, models 1.3-1.5). Overall, removal of temperature terms caused a much larger decrease in explanatory power (reduction in deviance explained) and model fit given the number of covariates (increase in Akaike Information Criterion, AIC) than removal of the pollock term. In models with no temperature terms (Table 7, models 1.5, 2.5, and 3.5), pollock density had a negative effect on euphausiid density, but the explanatory power of these models was poor. Although the effect of pollock density was retained in the best fitting models, its effect was not strongly negative (e.g., Fig. 8a) and the models were only marginally less informative if pollock density was excluded.

As with the single variable regressions, the GAM was also sensitive to removal of 2004 observations (Table 7). In a model using data from 2006 – 2012 (there was no survey in 2005), overall deviance explained was lower. Also, the reduction in deviance explained when temperature terms were dropped from the model (Table 7, models 3.3 - 3.5) was more similar to that observed when pollock was removed (Table 7, model 3.2), though a model with either temperature term remained superior to a model without temperature (Table 7, model 3.5). Thus, data from 2004 drive much of the strength in the relationships between temperature and euphausiid abundance. The reduction in deviance explained when pollock was dropped from the models was small for all groups of years in our analysis (Table 7, models 1.2, 2.2, and 3.2).

7. Discussion:

Climate exerts a strong control on the marine ecosystem of the eastern Bering Sea (Hunt et al., 2002, 2011; Baier and Napp, 2003; Aydin and Mueter, 2007; Coyle et al., 2011; Brown and Arrigo, 2011; Brown et al., 2013; Kotwicki and Lauth, 2013). During the past decade and a half, the climate of the eastern Bering Sea has differed from that which we knew between the 1970s and 1990s, but not from what has been observed since the turn of the 20th century (Overland et al., 2012). The period from 2001 to 2012 was not only unusual in terms of extreme high and low temperatures, but also because warm and cold years were grouped in stanzas. The year 1999 saw some of the coldest conditions since the 1960s, and was followed by a stanza of unusually warm conditions with early ice retreat or no sea ice from 2001 to 2005 (Stabeno et al., 2012). In contrast, from 2006 to 2013, ice retreat was late in the spring, and except for

2006 which had intermediate water temperatures, water temperatures were unusually cold. Since 2000, we have also seen large variations in euphausiid biomass present on the Bering Sea shelf (Ressler et al., 2012, 2014a). Here, we have attempted to assimilate available data to determine if this variability is due to bottom up control by the environmental variability, or due to top down control by pollock predation.

7.1 Data reliability:

We have compared historical data on euphausiid ecology in the southeastern Bering Sea with more recent field observations gathered during the Bering Sea Program. Our investigation also incorporated new output from the BEST-NPZ model. We found that, when adjusted for plausible sampling biases, euphausiid biomass estimates from MOCNESS net sampling, acoustic surveys and the BEST-NPZ model were similar in both the Outer Shelf Domain and in the Middle Shelf Domain. Likewise, estimates of euphausiid production from the BEST-NPZ model for the Outer Shelf Domain and Middle Shelf Domain were within the range found by Smith (1991). These comparisons give us confidence that the BEST-NPZ model is providing estimates of process rates and biomass that are of the right order of magnitude.

However, especially in light of updated primary production estimates obtained from historical data, and the mean results of the 2008-2010 Bering Sea Project (M. Lomas, pers. Comm.), it seems likely that BEST-NPZ model estimates of daily primary production during the spring and summer are low. The BEST-NPZ model also appears to underestimate the inter-annual variability in euphausiid biomass, at least as

747 compared to results from the acoustic surveys. This apparent underestimate of biomass
748 variability will result in an underestimate in the interannual variability of euphausiid
749 production.

750
751 Necessary assumptions in the model may not be appropriate for all comparisons
752 with field data (Brooks and Deroba 2015). If euphausiid mortality is not closely
753 correlated with euphausiid standing stock and temperature, as the model assumes
754 (section 3.1.3, Equation 2), then interannual variation in model standing stock estimates
755 will be different than field observations, though the average values may be of the correct
756 magnitude.

757
758 Similarly, field data are subject to observation error, as we have discussed at
759 some length (sections 3.1.1, 3.1.2, Appendix A). Shifts in the progression of the
760 seasonal cycle in euphausiid abundance, or in broader scale movements of euphausiid
761 population centers or mesoscale patches, could confound interpretation of the inter-
762 annual signal. Other possibilities for the mismatch could be related to the fact that
763 Bering Sea euphausiids live 3 – 4 years (Harvey, Pleuthner and Shaw, unpubl.), and
764 the over-winter survival of the euphausiids in the model is likely under-represented.
765 Thus, care is advised in the interpretation of the interannual patterns in the comparisons
766 of pollock consumption with euphausiid production and standing stock estimates from
767 the NPZ model.

We are presently unable to fully evaluate the accuracy of the model output on spatial and seasonal variability in euphausiid biomass, as field sampling at the necessary spatial and temporal scales is not available. A more in-depth evaluation would require higher resolution temporal coverage; presently we generally only have data on euphausiid biomass at 1 or 2 times periods a year (spring and/or summer), no winter data are available, and the sampling does not extend the width of the shelf. There is still need for considerable work on these issues. In contrast, we have high confidence in the reliability of the data on pollock abundance and their consumption of euphausiids, as these are based on extensive, repeated surveys and on the analysis of the contents of thousands of pollock stomachs from fish of known size, from which daily ration can be estimated.

7.2. Annual and seasonal availability of food to support euphausiids:

At present, there is no detailed carbon budget for the southeastern Bering Sea, and thus no recent estimate of the relationship between primary production and its consumption by euphausiids. Estimates for annual primary production vary considerably, with a grand average of past averages of $153 \text{ g C m}^{-2} \text{ y}^{-1}$ and an average of spring and summer production for the 2008 – 2010 period extrapolated to an annual average of $193 \text{ g C m}^{-2} \text{ y}^{-1}$ (Lomas et al., 2012) (see section 4.1). Both of these estimates have wide confidence intervals. Estimates of export to the benthos vary between about $60 \text{ g C m}^{-2} \text{ y}^{-1}$ (31% of primary production) based on Lomas' updated estimate for annual primary production of $\sim 193 \text{ g C m}^{-2} \text{ y}^{-1}$ (Baumann et al., 2013a, 2013b; M. Lomas, pers. comm.) and $\sim 76 \text{ g C m}^{-2} \text{ y}^{-1}$ (39% of primary production) using the average value of the

e-ratios of Moran et al. (2012) and Baumann et al. (2013b). By comparison, Walsh and McCroy (1986) modeled export of $94 \text{ g C m}^{-2} \text{ y}^{-1}$ over the outer shelf and $130 \text{ g C m}^{-2} \text{ y}^{-1}$ over the middle shelf. Subtracting the export ($60 - 70 \text{ g C m}^{-2} \text{ y}^{-1}$) from the primary production would imply that between 77 (40% of annual primary production) and $133 \text{ g C m}^{-2} \text{ y}^{-1}$ (69% of annual primary production) is consumed by the pelagic grazing community including microzooplankton, copepods and euphausiids, among others.

Recent field estimates of euphausiid consumption of primary production indicate that euphausiid grazing consumes only a small proportion ($\sim 1\% - 6\%$, or up to 15% , depending on whether there was a correction for net avoidance) of annual primary production (Campbell et al., this volume; Lessard, unpubl.). This compares with the estimates of Smith (1991) that annual euphausiid consumption of primary production for 1980 was 6% , and for 1981 was 1% , both of which may be low by a factor of 5 if net avoidance was not considered in estimating the biomass of the euphausiids present. The consumption of the primary producers by the euphausiids in the BEST-NPZ model was not tracked.

The proportion of the primary production supporting euphausiids would be increased in proportion to their consumption of microzooplankton in place of phytoplankton. Recent work shows that microzooplankton consume an average of 52% and 42% of phytoplankton production during non-bloom and bloom conditions, respectively, in spring (Sherr et al., 2013) and $\geq 90\%$ in summer (Olson and Strom, 2002; Stoeker et al., 2014). Microzooplankton are an important food for euphausiids and

can comprise >50% of their diets in summer when phytoplankton biomass is low (Lessard et al. 2012, unpubl.). It remains unlikely that, on an annual basis, euphausiid population growth in the years studied was limited by the annual availability of primary production.

However, it is possible that euphausiid growth and survival could be limited if they do not have access to an appropriate food source at a critical period. For example, we know very little about the food requirements and food availability to euphausiids in spring when they are producing eggs and undergoing rapid development and growth. One indication that spring conditions may be important is the very strong relationship between bottom temperatures and the abundance of euphausiids. This relationship becomes much weaker when data from the very warm year of 2004 are excluded, suggesting that small variations in water temperature, or possibly timing of ice retreat in “cold” years are of minor importance.

The mechanisms for temperature forcing of euphausiid standing stock (bottom-up control) are poorly understood, but bottom temperatures in the southeastern Bering Sea are determined by the location and amount of ice melt that occurs in winter and spring. Thus, it is possible that temperature serves as a proxy for one or more important processes, such as the amount of ice algae present in spring, or the increased metabolic demands that warmer water places upon euphausiid metabolic processes, especially during winter under low-food conditions (Pinchuk and Hopcroft, 2008; Coyle et al., 2008, 2011; Hunt et al., 2011; Ressler et al., 2014a). Late ice melt and heavy ice

cover would lead to lower bottom temperatures (e.g., Stabeno et al., 2012), and the presence of ice algae in early- to mid-spring, and ice-edge blooms (Hunt et al., 2002, 2011; Coyle et al., 2011). These conditions have been associated with stronger recruitment in the copepod *C. marshallae/glacialis* (Baier and Napp, 2003; Campbell et al., this volume). Ice algae and ice edge blooms may also be important to euphausiids, as much for their timing as for the amount of production available to be cropped, but at present, we do not have the data necessary to assess the relative importance of these factors.

Coyle (2008) suggested that the low biomass of euphausiids and other large crustacean zooplankton on the shelf during the exceptionally warm year of 2004 was due to suppression of the summer primary production by a highly stratified water column. However, the low biomass of euphausiids present in 2004 may have been the result of successive years of low recruitment of euphausiids due to the lack of either ice algae or a diatom bloom at the time good foraging conditions were needed to support egg production. *T. raschii* requires food in spring to produce eggs (Falk-Petersen et al., 2000; Harvey et al., 2012). It is thus a reasonable hypothesis that the succession of warm years with early ice retreat between 2001 and 2005 led to repeated low recruitment rates for euphausiids (Sigler et al., this volume), as was apparently the case for the copepod, *C. marshallae/glacialis* (Baier and Napp, 2003; Coyle et al., 2011).

While little is known about the association of the Outer Shelf Domain euphausiid, *T. inermis*, and sea ice in the southeastern Bering Sea, there is evidence that in the

Middle and Inner Shelf Domains, *T. raschii* makes use of ice algae, as well as phytoplankton associated with the early bloom. Campbell et al. (this volume) cite observations of euphausiids foraging on ice algae under the ice, and experiments that showed consumption of ice algae by euphausiids. Likewise, Lessard et al. (2012, unpubl.) have documented euphausiids consuming ice algae, perhaps in preference to phytoplankton. *T. raschii* populations in the Barents Sea are known to thrive in periods of cold conditions and to decline in periods when water temperatures are warm (Drobysheva, 1971, 1984). *T. raschii* there is reported to reproduce in the vicinity of the ice edge (Ponomareva, 1963; Dalpadao and Skjoldal, 1991; Dalpadado et al., 2008). In the Barents Sea, *T. inermis* thrives best in warmer waters, and is unlikely to be able to reproduce in the sub-zero water found close to the ice edge (Timofeyev, 1993; Dalpadao, et al., 2008).

Given that *T. raschii* of the Middle Shelf Domain apparently should do well in cold conditions, and *T. inermis* of the Outer shelf Domain should do well in warm, ice-free conditions, one might expect that, during stanzas of warm years, the biomass of *T. inermis* would increase, while the biomass of *T. raschii* would decrease, all other things being equal. Conversely during stanzas of cold years, *T. inermis* might decrease while *T. raschi*would be expected to increase. The few data that we have do not support this scenario. In the acoustic data, in the one warm year for which we have data, 2004, the biomass of euphausiids was low in both the Outer Shelf Domain and the Middle Shelf Domain, while in the years with late ice retreat of 2006 – 2010, euphausiid biomass was consistently high in the Middle Shelf Domain, and moderate to high in the Outer Shelf

Domain (Table 1). In the cold year of 2012, there were reductions in the biomass of euphausiids in both domains. In 2014, an exceptionally warm year with little sea ice present in the southeastern Bering Sea, the mean biomass of euphausiids declined considerably from that in 2012 (Ressler, 2014). These data showing the similarity in interannual euphausiid biomass variation on the outer and middle shelf do not unequivocally support or refute the hypothesis that the timing of ice retreat affects the recruitment of *T. raschii* and *T. inermis* differently, but they do leave open the possibility that euphausiid biomass in the two domains is affected similarly by another factor that modifies the effects of water temperature and sea ice presence on euphausiid biomass.

Because euphausiids in the southeastern Bering Sea may live to three or four years of age (Harvey et al., unpubl.), a one-time failure of euphausiid recruitment in spring could be buffered by the presence of as many as three year-classes of euphausiids from earlier years. However, after three consecutive springs of reduced reproduction, euphausiid biomass would be expected to be severely reduced. Although field evidence supports the notion that *T. raschii* biomass shows less interannual variability than does the copepod *C. marshallae/glacialis* (Coyle and Pinchuk, 2002b), these hypotheses remain to be tested.

7.3. Predation and temperature as predictors of the spatial and temporal distribution of euphausiid biomass

Estimates of both euphausiid biomass and euphausiid production consumed by pollock and the single variable regressions of euphausiid biomass on pollock density

indicate that pollock has an appreciable impact on euphausiids. Based on the BEST-NPZ model estimates of euphausiid biomass, pollock predation appears to be able to remove 21 - 41% of the euphausiid biomass and 17 to 29% of euphausiid production during the summer, depending on the region of the shelf for which calculations are made (Table 5). Certainly the biomass of euphausiids removed would be greater if pollock consumption were considered over an entire year, but data on fall and winter consumption rates and diets are too limited at present to make interannual comparisons. In particular, the model shows high interannual variability in fall bloom production with corresponding high variability in the modeled rates of grazing down of the overwintering krill stock which may lead to top-down control. However corroborating field data are insufficient to evaluate this model result. Overall, these model- and field-based results support the contention that pollock could play a significant top-down role in the determination of euphausiid biomass on a shelf-wide, annual basis.

In the single-variable regressions of annual averages of summer acoustic-trawl survey data, euphausiid biomass was negatively associated with pollock biomass and water temperature. Euphausiid biomass was positively associated with large-scale annual indices of the amount and persistence of annual ice cover, which is consistent with the observed temperature relationship, but the predictive power of these ice-related indices was not very strong. Euphausiid biomass was also negatively associated with stock assessment model estimates of pollock standing stock, and more strongly than with survey estimates of pollock biomass, which was not statistically significant. This result must be interpreted with some caution as the survey estimate of euphausiids and

the stock assessment model estimates differ in terms of season, areal extent, and assumptions made, and as such may not be directly comparable (Brooks and Deroba, 2015). For example, the stock assessment model (Ianelli et al., 2001, 2013) estimate is from a population dynamics model that assumes fixed natural mortality and variable survey catchability for the entire standing stock of age-1+ pollock in the Bering Sea in January of each year, while the acoustic-trawl survey consists of field observations from the middle and outer shelf in June-July. In summary, the regression results are consistent with forcing by both temperature (bottom-up) and pollock predation (top-down), but were not always statistically significant. The number of annual observations was limited, and the strength of these associations depended on the years considered.

When spatially-explicit summer survey observations were included in a multiple regression model (GAM), euphausiid biomass had a strong negative relationship with temperature and temperature had much more predictive power than did pollock biomass. These results are generally inconsistent with the expected strong negative association between pollock biomass and euphausiid biomass, if pollock predation is the dominant control on euphausiid biomass. At this spatial and temporal scale, our results suggest that bottom-up forcing related to temperature is more important than predation by pollock, though the mechanism for this effect remains unclear. As suggested above, temperature may be a proxy for another important environmental variable.

952 The predictive power of water temperature in the results of Ressler et al. (2014a)
953 may have, at least in part, reflected temperature preferences by both pollock and
954 euphausiids (e.g. Kotwicki et al., 2005; De Robertis and Cokelet, 2012), rather than the
955 control (production or consumption) of the biomass of euphausiids present in their
956 survey area. However, if this were true and temperature was acting primarily as a proxy
957 for pollock predation (or the absence thereof), one would expect pollock biomass to be
958 a better proxy for predation by pollock than temperature and hence a better predictor of
959 euphausiid biomass, and this was not the case.

960
961 One possible explanation for the apparently contradictory results between the
962 single-variable regressions and the multi-variable GAMs is that the single variable
963 analyses used yearly averages of temperatures and pollock density over either the
964 entire acoustic-trawl survey area or over the entire southeastern shelf (pollock biomass
965 from the assessment model), whereas the GAM results were based on pollock and
966 euphausiid data taken at the spatial scale of 37 x 37 km grids, and examined
967 simultaneous co-occurrence of predator and prey in these grids. Both pollock and
968 euphausiids are patchily distributed, and the association between patchy distributions of
969 predators and their prey at small spatial scales is notoriously poor (e.g., Hunt et al.,
970 1990, 1992). As shown by Vlietstra (2005), the local association between predators and
971 prey may be dependent on whether, at a much larger spatial scale, prey is abundant or
972 scarce.

There have been conjectures that a switch from interannual variation in marine climate conditions to stanzas of years that are climatically similar would have important ecological consequences (e.g., Coyle et al., 2011; Hunt et al., 2011). It is possible that both euphausiids, with a life span of 3 – 4 years in the Bering Sea, and pollock, with a life span of >15 years, are able to integrate across short-term variability, whereas, the long period of warm conditions with early ice retreat in 2001 – 2005 exceeded euphausiid ability to bridge a poor year (or two) without incurring a severe population decline (Coyle and Pinchuk 2002b).

7.4. Relative importance of bottom-up and top-down control of euphausiids

Evaluating the relative importance of bottom-up and top-down control of euphausiids in the eastern Bering Sea has proven more difficult than originally envisioned. In some cases the time series of field data available for examination are short, and in other cases the data are likely biased by the methods used to collect them.

For the period 2004 to 2012, we have developed a simple diagram that describes what we think may have happened as the climate shifted from a stanza of unusually warm years to a stanza of unusually cold years (Fig. 9). In this scenario, during the years with early ice retreat, euphausiid recruitment was depressed for lack of appropriate food at a critical time in spring (and possibly summer, Coyle et al., 2008, 2011; Strom and Fredrickson, 2008), and from predation by pollock. Subsequently, both euphausiid and pollock biomass recovered from low levels with pollock lagging due to their longer life history. Eventually euphausiid biomass declined, possibly due to predation. Thus, we

argue that there may have been bottom-up control in warm years (failure of krill to recruit) and top-down control in cold years (after a lag required for pollock to rebuild their biomass). Although it seems possible that the decline in euphausiid biomass after 2009 is related to predation, we are presently not able to assign the relative importance to top-down and bottom-up factors between 2001 and 2012. It is likely that neither top-down control by pollock, nor bottom-up control by the availability of food is the sole determinant of euphausiid biomass.

A further influence on the geographic distribution and biomass of euphausiids, not directly considered in this synthesis, is the role of advection. On-shelf advection is known to play a major role in the seasonal distribution of copepods (Cooney and Coyle, 1982; Smith and Vidal, 1986) and of fish eggs and larvae (Wilderbuer et al., 2002, 2013; Siddon et al., 2013; Vestfals et al., In Press) on the southeastern Bering Sea shelf. Modeling work examining the advection of *Neocalanus* spp., large-bodied oceanic copepods, onto the eastern Bering Sea shelf found that there is a strong connection between the Gulf of Alaska and the Southern Bering Sea, and that the on-shelf advection of the zooplankton varies substantially year to year, primarily depending on wind direction (Gibson et al., 2013). It is likely that inter-annual variation in advection would also impact the eastern Bering Sea euphausiid populations as these populations would also be subjected to advective forces. The role of advection on euphausiid biomass, and its relative importance with respect to top-down and bottom-up control needs to be resolved.

Although we have made progress in developing hypotheses as to how these processes are linked, many open questions remain, and there is still much work to do. This synthesis has highlighted the need for longer time series which would allow us to determine whether the associations we observed between temperature, pollock biomass, and euphausiid biomass are robust.

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1329 Hall, Boca Raton, FL
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- 1331

1332 Table 1. Estimates of mean euphausiid biomass (g C m^{-2}) in the Outer Shelf and Middle
 1333 Domains of the eastern Bering Sea. Data from 1980 are from Smith, 1991. Net data
 1334 from 2008-2010 are from A. Pinchuk (unpubl.), and acoustic data from 2004 – 2012 are
 1335 from Ressler et al., 2012 and unpublished. Net data from 2004 were obtained in
 1336 August: OSD, 1.00 g C m^{-2} and MSD, 1.72 g C m^{-2} . See Methods, above, for the
 1337 methods used by Smith (1991), Pinchuk (unpub.), and Ressler et al. (2012). OSD =
 1338 Outer Shelf Domain; MSD = Middle Shelf Domain.

Season	Net		NPZ model				Acoustic	
	June	April-June	1 April – 14 June		15 June - 31 August		June-July	
Region	4 and 8	3 and 6	4 and 8	3 and 6	4 and 8	3 and 6	4 and 8	3 and 6
	OSD	MSD	OSD	MSD	OSD	MSD	OSD	MSD
1980		0.60						
2004			3.28	2.79	2.71	2.63	8.70	10.23
2005			2.61	2.22	2.56	2.49		
2006			2.17	2.01	3.13	3.40	17.10	21.76
2007			2.59	2.21	2.74	2.89	18.10	25.60
2008	0.28	0.49	2.47	1.77	3.54	3.67	24.21	23.19
2009	0.76	0.26	2.55	1.83	3.87	3.62	31.06	34.41
2010	2.10	0.42					18.68	36.53
2012							16.45	13.84
Mean	1.05	0.39*	2.61	2.14	3.09	3.12	19.19	23.65

1339 * Excluding 1980, to keep all comparisons in the 2004 – 2012 period. Mean is 0.44 if
 1340 1980 value is included.

1341

1342 Table 2. Summary of adjusted values for euphausiid biomass (g C m^{-2}) in the Outer
 1343 Shelf Domain and the Middle Shelf Domain based on net surveys (A. Pinchuk, unpubl.),
 1344 acoustic surveys (Ressler et al., 2012) and output from the BEST-NPZ model (Gibson
 1345 and Spitz, 2011) for June- August, 2008 – 2010 (2008 – 2009 for the NPZ model). For
 1346 the rationale and methods for adjustment of the net-based and acoustics-based
 1347 estimates, see Methods and Appendix A. Values are reported in gCm^{-2} .

Method	Outer Shelf Domain	Middle Shelf Domain
1 m^2 MOCNESS	5.25	1.95
Acoustic survey	3.08	3.92
NPZ model	3.71	3.65
Mean	4.01	3.17

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 1352
 1353 Table 3. Modeled primary production and euphausiid production, by Bering Sea Project
 1354 Regions (Fig.1), summarized for April - August 1999 - 2009. Data expressed in g C m^{-2}
 1355 d^{-1} , data for all Regions (1, 3, 6, 4, and 8) are area weighted. Data are output from the
 1356 Bering Sea Project NPZ model (Gibson et al., 2012).

Region	Primary Production	Euphausiid Production
1 (Peninsula)	0.60	0.049
4, 8 (Outer Domain)	0.58	0.051
3, 6 (Middle Domain)	0.55	0.043
1, 3, 6, 4, 8 (SE Bering Shelf)	0.57	0.048

1357

1358

1359
 1360 Table 4 Consumption of euphausiids in June and July by pollock ($\text{mg C m}^{-2} \text{ d}^{-1}$), by year
 1361 and Region based on the proportional distribution of pollock biomass by age (size) class
 1362 from the eastern Bering Sea pollock assessment and the summer diets of pollock by
 1363 size class, as determined from the NOAA AFSC Bottom Trawl Survey.

1364

Year	Regions			
	1	4, 8	3, 6	1, 3,4, 6, 8
1999	15.3	14.5	5.0	10.8
2000	18.7	14.0	15.8	15.5
2001	35.5	12.7	21.9	19.7
2002	15.9	8.8	15.6	12.2
2003	34.6	18.3	15.1	18.7
2004	10.5	3.2	12.2	10.4
2005	8.8	13.3	7.7	10.7
2006	9.5	7.3	8.3	8.2
2007	19.1	5.9	7.8	9.1
2008	14.1	3.5	3.4	4.2
2009	8.7	3.9	2.9	4.4
2010	7.7	4.1	3.1	4.3

1365

1366

1367
 1368
 1369 Table 5. Summary of euphausiid production, biomass and consumption by pollock
 1370 during a 77-day summer season. Data are the means from 1999–2009. Data for
 1371 Regions 1,3, 6, 4,8 combined are area adjusted. Data Sources: euphausiid biomass
 1372 and production,BEST-NPZ model; pollock consumption,See Table 4.

1373

Region	Euphausiid			Pollock	
	Production g C m ⁻² d ⁻¹	Biomass g C m ⁻²	Consumption g C m ⁻² d ⁻¹	Consumption/ euphausiid production	Consumption x77 days/ euphausiid biomass
1	0.058	3.23	0.017	0.29	0.41
3, 6	0.053	3.25	0.0091	0.17	0.21
4, 8	0.059	3.28	0.010	0.17	0.23
1, 3, 6, 4, 8	0.059	3.27	0.011	0.19	0.26

1374

1375

Table 6

Table 6. Coefficient of determination (r^2) for single variable functional regressions modeled on euphausiid biomass. Regression results graphed in Fig. 7. Bold indicates $p < 0.05$.

Model	Years		
	2004-2012	2004-2010	2006-2012
Pollock survey density	0.45	0.43	0.27
Pollock assessment biomass	0.82	0.82	0.57
Mean bottom temperature	0.46	0.94	0.0
Mean surface temperature	0.63	0.81	0.21
Ice retreat index	0.23	0.52	0.13
Ice cover index	0.36	0.82	0.04
n	7	6	6

Table 7. GAM of euphausiid biomass density from Ressler et al. (2014a) run with three subsets of survey years: 2004-2012, 2004-2010, and 2006-2012. Dark shading indicates superior models (higher deviance explained, lower AIC).

model	description	formulation	years included	deviance explained	AIC
1.1	Ressler et al. (2014) GAM	$\log_{10}(\text{euph} + 10) \sim s[\log_{10}(\text{pk} + 10)] + s(\text{bot_temp}) + s(\text{ann_surf_temp}) + s(\text{lon}, \text{lat})$	2004-2012	36.9	2129.08
1.2	drop pollock	$\log_{10}(\text{euph} + 10) \sim s(\text{bot_temp}) + s(\text{ann_surf_temp}) + s(\text{lon}, \text{lat})$	2004-2012	36.1	2144.659
1.3	drop annual average surface temperature	$\log_{10}(\text{euph} + 10) \sim s[\log_{10}(\text{pk} + 10)] + s(\text{bot_temp}) + s(\text{lon}, \text{lat})$	2004-2012	30.2	2263.39
1.4	drop bottom temperature	$\log_{10}(\text{euph} + 10) \sim s[\log_{10}(\text{pk} + 10)] + s(\text{ann_surf_temp}) + s(\text{lon}, \text{lat})$	2004-2012	33.5	2193.124
1.5	drop all temperature terms	$\log_{10}(\text{euph} + 10) \sim s[\log_{10}(\text{pk} + 10)] + s(\text{lon}, \text{lat})$	2004-2012	12.8	2552.75
2.1	Ressler et al. (2014) GAM	$\log_{10}(\text{euph} + 10) \sim s[\log_{10}(\text{pk} + 10)] + s(\text{bot_temp}) + s(\text{ann_surf_temp}) + s(\text{lon}, \text{lat})$	2004-2010	47	1619.598
2.2	drop pollock	$\log_{10}(\text{euph} + 10) \sim s(\text{bot_temp}) + s(\text{ann_surf_temp}) + s(\text{lon}, \text{lat})$	2004-2010	46.1	1632.7
2.3	drop annual average surface temperature	$\log_{10}(\text{euph} + 10) \sim s[\log_{10}(\text{pk} + 10)] + s(\text{bot_temp}) + s(\text{lon}, \text{lat})$	2004-2010	42.5	1712.577
2.4	drop bottom temperature	$\log_{10}(\text{euph} + 10) \sim s[\log_{10}(\text{pk} + 10)] + s(\text{ann_surf_temp}) + s(\text{lon}, \text{lat})$	2004-2010	40.2	1750.281
2.5	drop all temperature terms	$\log_{10}(\text{euph} + 10) \sim s[\log_{10}(\text{pk} + 10)] + s(\text{lon}, \text{lat})$	2004-2010	15.3	2153.045
3.1	Ressler et al. (2014) GAM	$\log_{10}(\text{euph} + 10) \sim s[\log_{10}(\text{pk} + 10)] + s(\text{bot_temp}) + s(\text{ann_surf_temp}) + s(\text{lon}, \text{lat})$	2006-2012	19.5	1558.776
3.2	drop pollock	$\log_{10}(\text{euph} + 10) \sim s(\text{bot_temp}) + s(\text{ann_surf_temp}) + s(\text{lon}, \text{lat})$	2006-2012	18.7	1566.591
3.3	drop annual average surface temperature	$\log_{10}(\text{euph} + 10) \sim s[\log_{10}(\text{pk} + 10)] + s(\text{bot_temp}) + s(\text{lon}, \text{lat})$	2006-2012	16.4	1592.742
3.4	drop bottom temperature	$\log_{10}(\text{euph} + 10) \sim s[\log_{10}(\text{pk} + 10)] + s(\text{ann_surf_temp}) + s(\text{lon}, \text{lat})$	2006-2012	18.8	1570.23
3.5	drop all temperature terms	$\log_{10}(\text{euph} + 10) \sim s[\log_{10}(\text{pk} + 10)] + s(\text{lon}, \text{lat})$	2006-2012	15.8	1602.776

1391 Figure legends:

1392

1393 Figure1. The eastern Bering Sea shelf with the BSIERP regions (numbered 1 – 16), the
1394 stations for the NOAA bottom trawl survey (dots), and the track line of the acoustic trawl
1395 survey (white lines). Bathymetry is indicated in shades of white (0-49 m, Inner Shelf
1396 Domain), light grey (50-100 m, Middle Shelf Domain), and dark grey (101 – 200 m,
1397 Outer Shelf Domain. The Shelf slope domain is a narrow strip just seaward of the Outer
1398 Shelf Domain.

1399

1400 Figure 2. Presence / absence of groundfish stomach samples with euphausiid as prey
1401 items where *T. inermis* and / or *T.raschii* were identified. Samples from Jan-Dec, 1981-
1402 2013 were divided into grids of 20 x 20 nm (37 x 37 km).

1403

1404 Figure 3. Model-derived estimates of spring (1 April – 14 June) and summer (15 June-
1405 31 August) euphausiid biomass for the Peninsular Region (1), the Outer Shelf Domain
1406 (Regions 4 and 8) and the southern Middle Shelf Domain (Regions 3 and 6), as
1407 estimated by the BEST-NPZ model as modified from the one-dimensional model in
1408 Gibson et al., 2011. Note that seasonal variation is as great or greater than interannual
1409 variation.

1410

1411 Figure4. Interannual variations in the biomass of euphausiids, walleye pollock,
1412 temperature, and ice cover on the eastern Bering Sea shelf. Survey pollock is the
1413 combined average biomass per area from bottom trawl and acoustic trawl surveys,

while survey euphausiid biomass(kg ha^{-1}) is from acoustic-trawl surveys (Ressler et al., 2012, 2014a). Assessment pollock is a stock assessment model estimate biomass (t) in January of each year from Ianelli et al. (2013). Bottom and surface temperature ($^{\circ}\text{C}$) are measured at each bottom trawl survey station. Ice retreat and ice cover indices for the eastern Bering Sea (higher values mean more ice) are described at beringclimate.noaa.gov. All series except the ice cover index are expressed relative to their value in 2004. The ice cover index is expressed as standard deviations from the mean of the time series. Shading indicates 'warm' (red) and 'cold' (blue) periods.

Figure 5. Annual pollock consumption of euphausiids based on the proportional distribution of pollock biomass by age (size) class from the eastern Bering Sea pollock assessment and the summer diets of pollock by size class, as determined from the NOAA AFSC Bottom Trawl Survey. Top: The consumption of euphausiids in years with early ice retreat. Middle: Consumption of euphausiids in years with late ice retreat.

Figure 6. Summer pollock consumption of euphausiids as a proportion of euphausiid production (empty circles) or euphausiid standing stock biomass (filled circles) for the BSIERP regions defined in Fig. 1. Pollock consumption is estimated from field measurements (Table 3), and euphausiid production and standing stock are estimated from the NPZ model (Gibson and Spitz, 2011). Consumption of biomass is calculated for a 77 day summer season. A) Region 1: Alaska Peninsula, B) Regions 4 and 8: outer shelf C) Regions 3 and 6: south and mid-north middle shelf D) Regions 1, 2,3,4,6, and 8 – the southeast outer and middle shelf.

1437

1438 Figure 7. Regressions of euphausiid biomass on a) annual averages of combined
1439 pollock biomass from NOAA acoustic and bottom trawl surveys (kg ha^{-1}), b) pollock
1440 biomass as determined by the NOAA fisheries stock assessment model for the
1441 southeastern Bering Sea Shelf (metric tons; Ianelli et al. 2013), c) annual average
1442 bottom temperatures ($^{\circ}\text{C}$) and d) sea surface temperatures ($^{\circ}\text{C}$) as determined by the
1443 NOAA bottom trawl survey in the area of the acoustic survey, 2004-2012. Year is
1444 indicated by text at each datum. R^2 for a single variable functional regression is
1445 indicated on each panel.

1446

1447 Figure 8. Effect of each term in the best generalized additive model (GAM) of
1448 euphausiid biomass density (kg ha^{-1}) over the period (2004 – 2012). Covariates shown
1449 by each panel are as follows: (a) Age 1+ pollock biomass (kg ha^{-1}), (b) bottom
1450 temperature ($^{\circ}\text{C}$), (c) latitude and longitude, and (d) annual average surface
1451 temperature ($^{\circ}\text{C}$). Note that the units of pollock and euphausiid biomass have
1452 undergone a $\log_{10}(x+10)$ transformation. In each panel, the points on the plots are
1453 residuals from the full model without the effect of the covariate on the x-axis, and the
1454 solid lines are smooth functions indicating the modeled effect of that covariate on
1455 predicted euphausiid density. In panels (a), (b), and (d), the shading denotes a 95%
1456 confidence interval around the fit; in panel (c), green dotted lines indicate +1 SE and red
1457 dotted lines indicate -1 SE.

1458

1459 Figure 9. Diagram of the potential interactions of climate, pollock biomass, euphausiid
1460 biomass and rates of biomass growth of pollock relative to takes of pollock by the
1461 fishery and natural mortality.

1462

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1464

Fig 1.

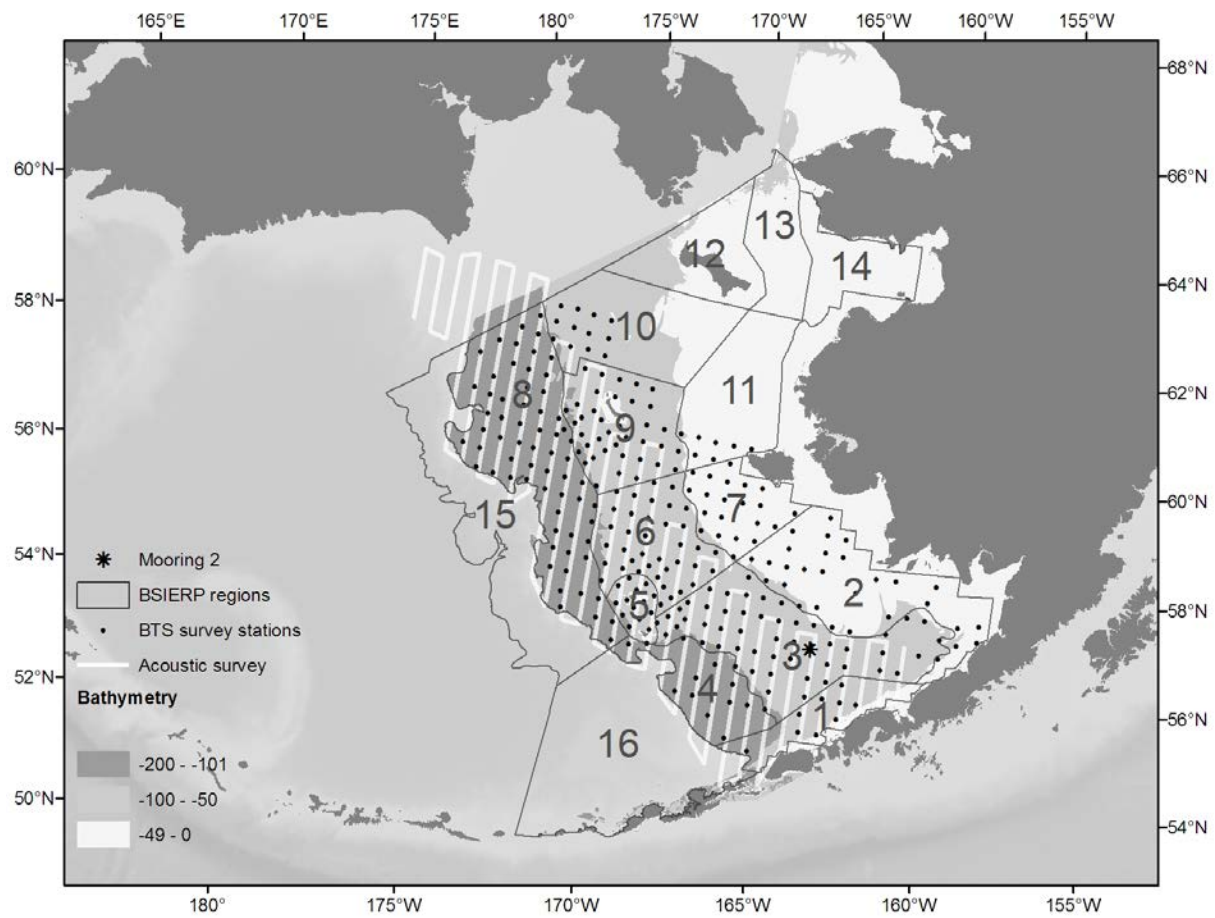
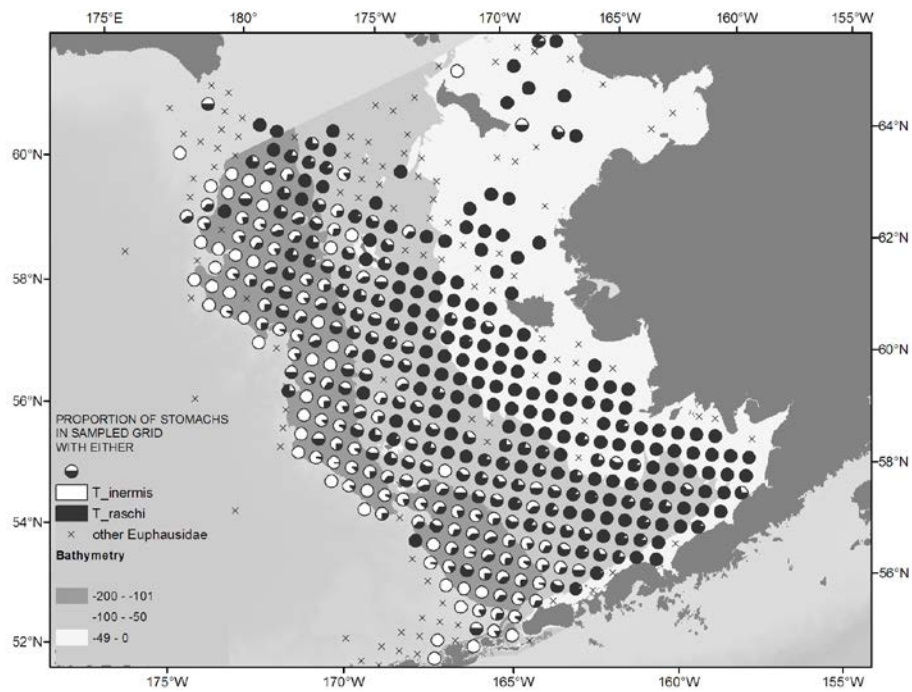


Figure1.

1472 Fig2.



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1476 Figure 2.

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Fig. 3.

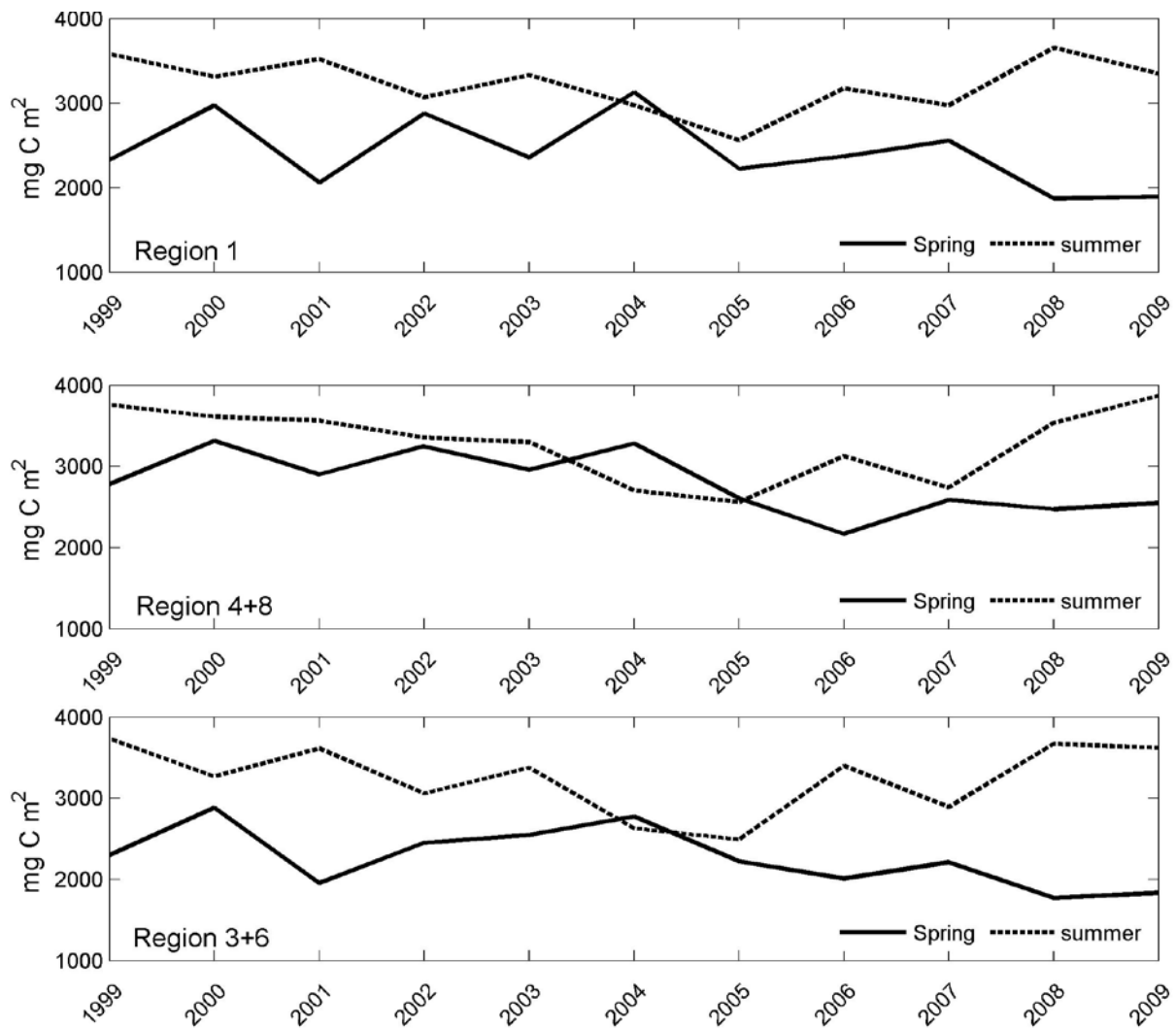
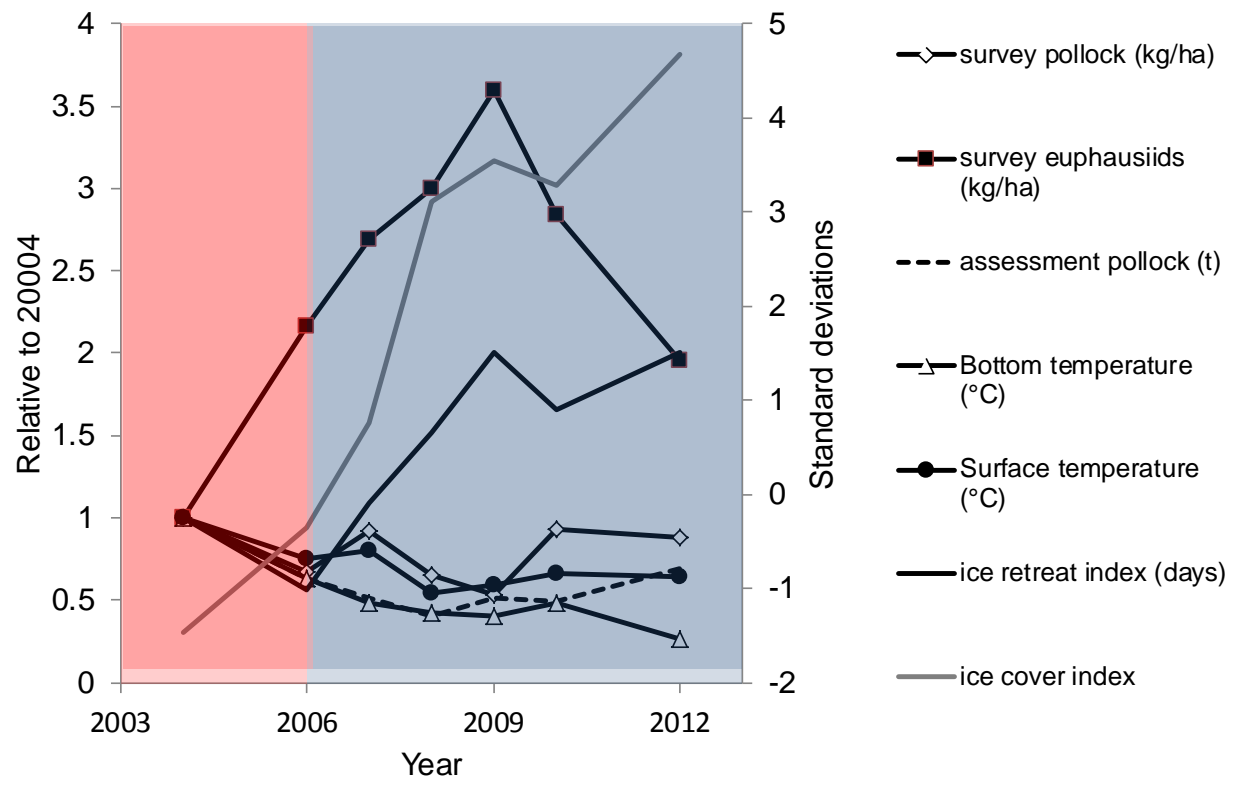


Figure 3.

1484 Fig 4

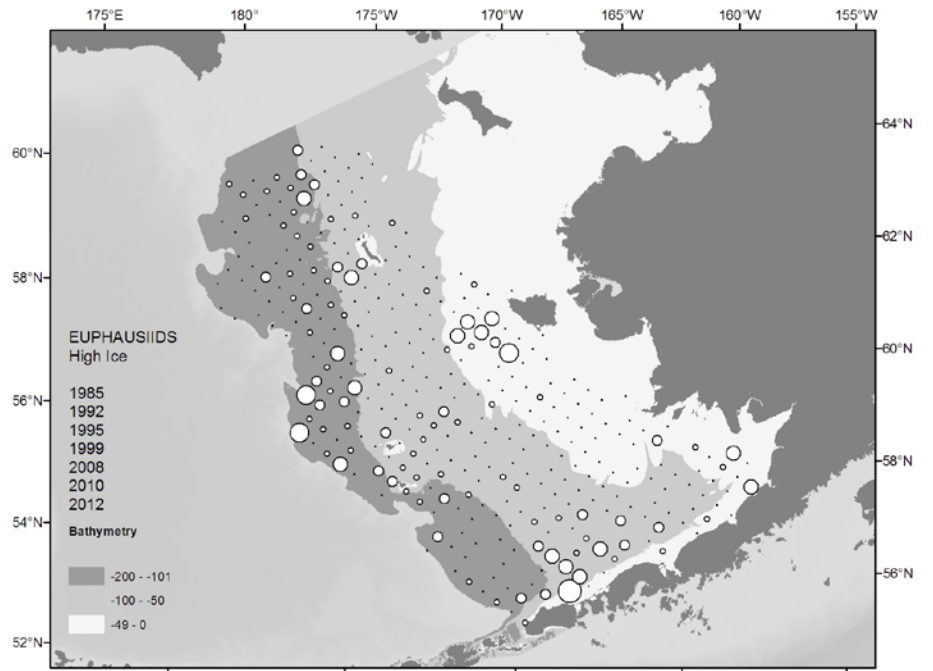


1485

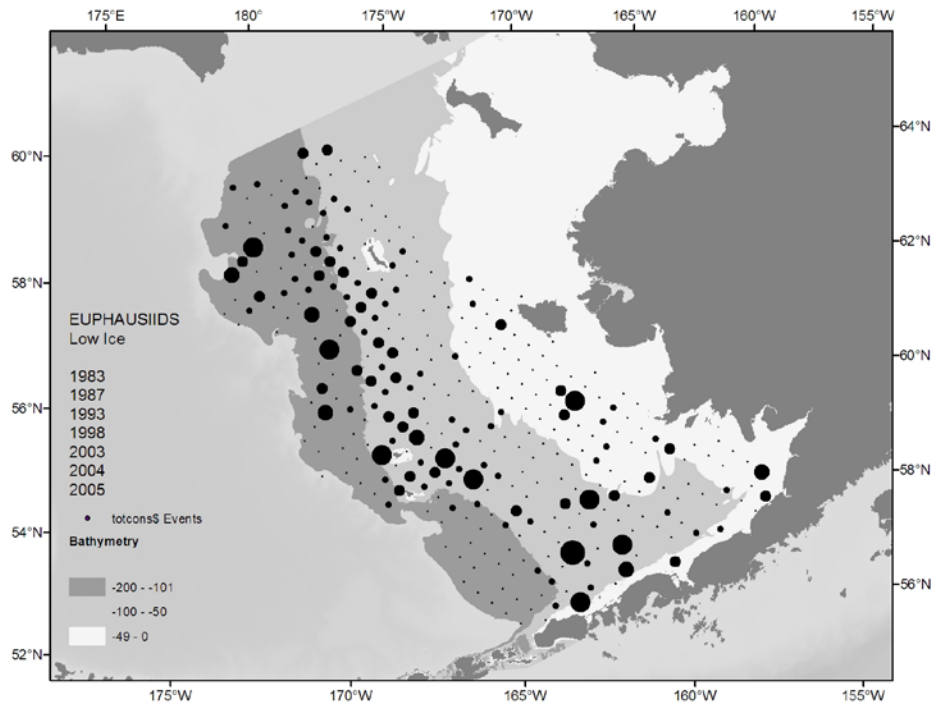
1486 Figure4.

1487

1488 Fig. 5.



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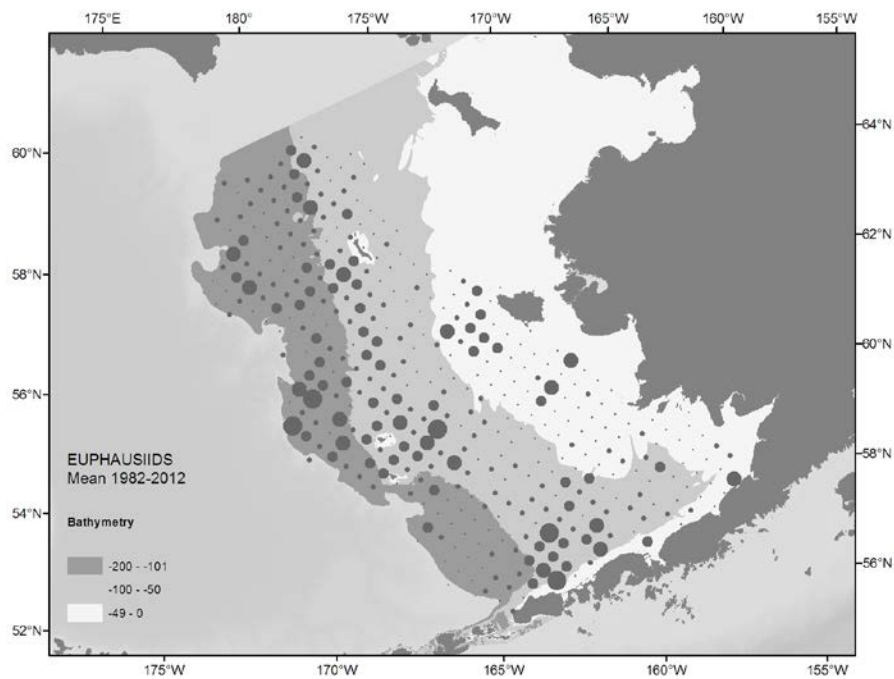


Figure 5.

Fig. 6

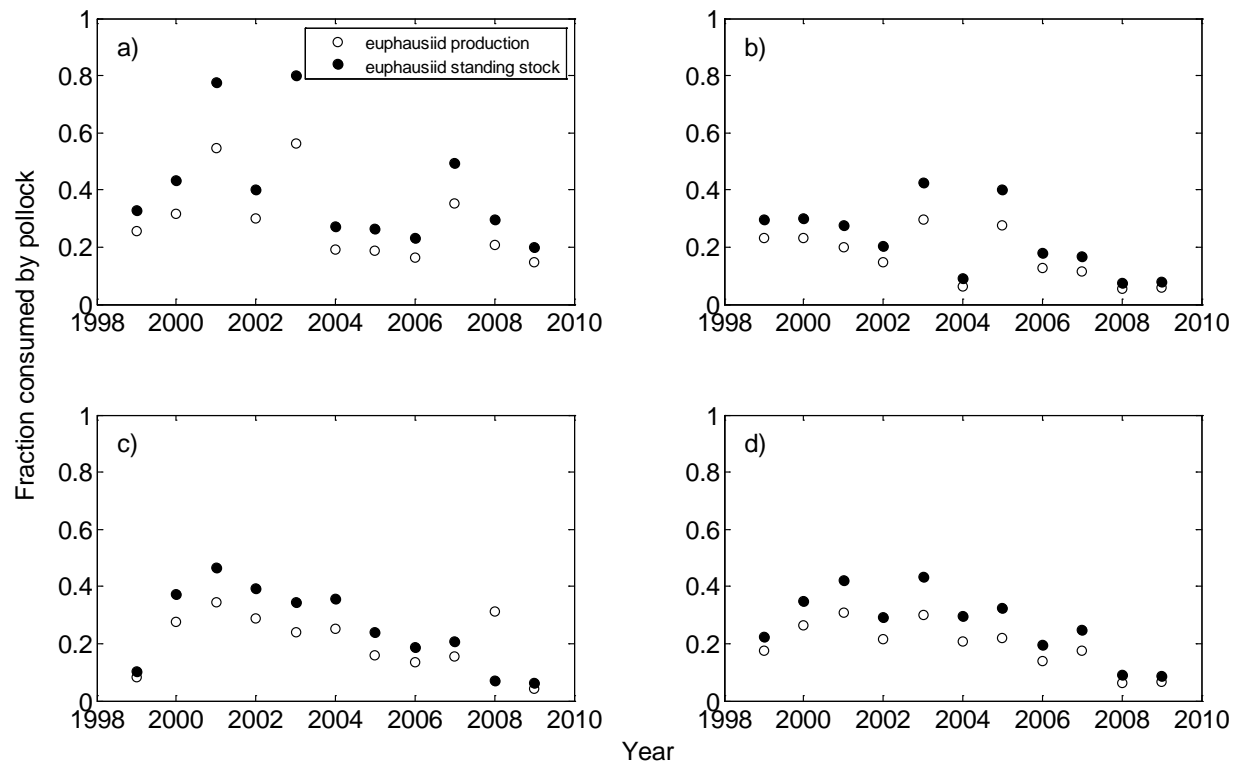


Figure 6.

Fig 7.

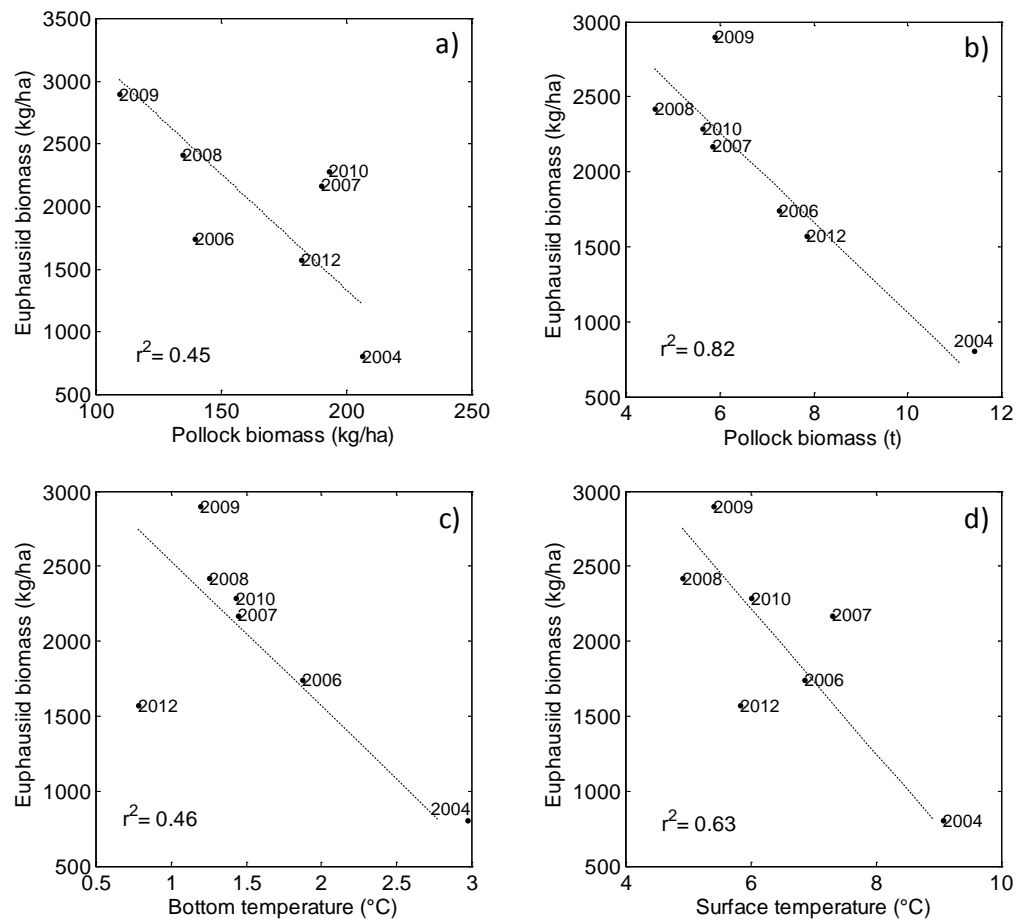
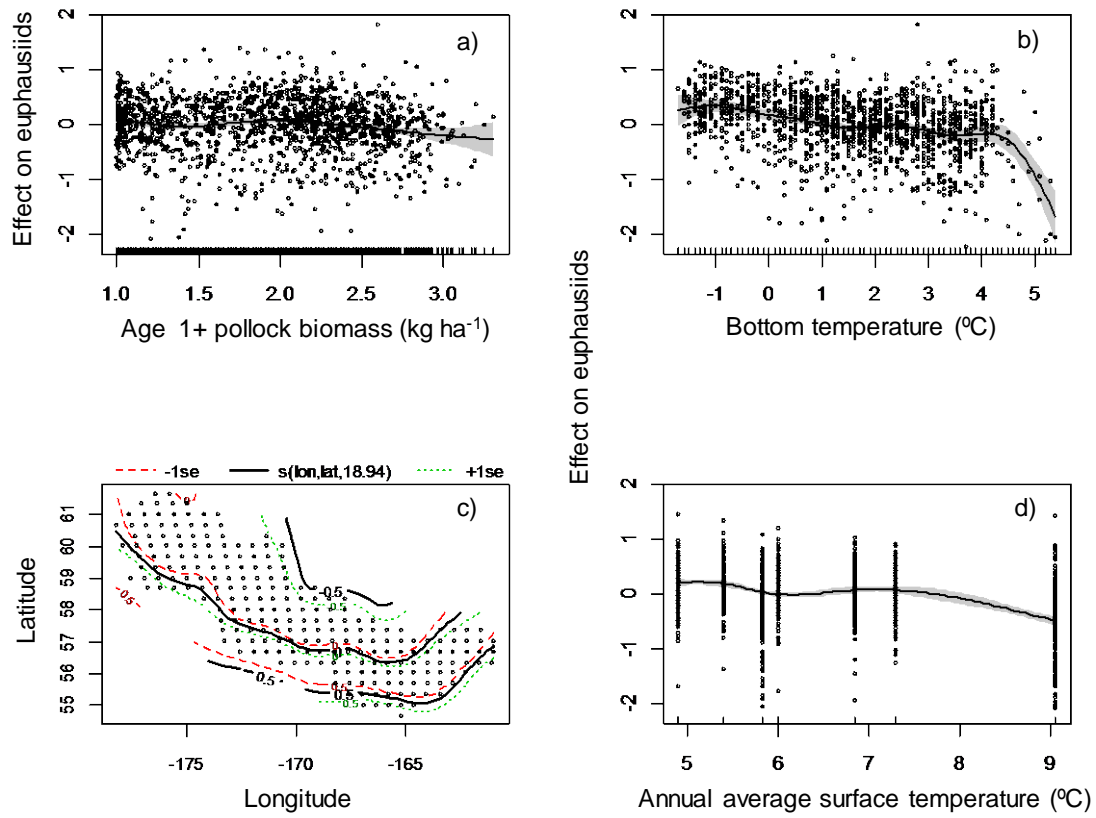


Figure 7.

1515

1516 Fig. 8

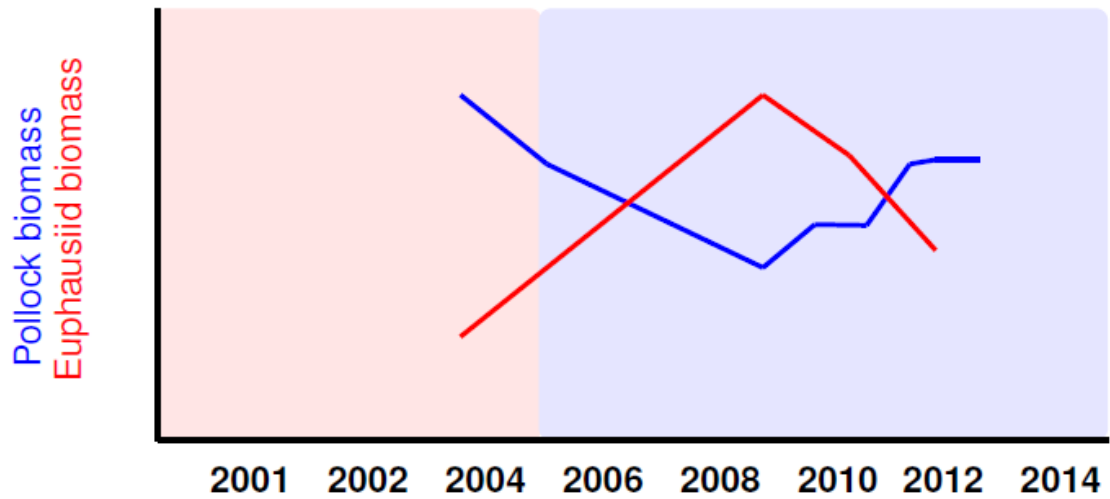


1517

1518 Figure8.

1519

Fig 9



Ice in April	No Ice	Ice	
Spring Algae	No Algae	Algae	
Control of Krill Biomass	Poor recruitment, high predation	Good feeding, low predation	Good feeding, heavy predation
Control of Pollock Abundance	Fishing removals, weak recruitment	Juvenile growth < fishery takes	Juvenile growth > fishery takes

Figure 9.

Appendix A: How many euphausiids are there (really) in the Eastern Bering Sea?¹

Euphausiids are a key zooplankton taxon in the eastern Bering Sea (and elsewhere), linking lower trophic levels to top predators. However, the absolute magnitude of the standing stock of euphausiids in the Bering Sea (principally *Thysanoessa* spp.) is not well known, and estimates made using different techniques vary widely. In this Appendix, we propose how the differences between biomass estimates from net samples and acoustic-trawl surveys can be reconciled for purposes of our analysis.

1. Motivation

Expected values of euphausiid standing stock can be calculated based on approximate values of primary production, euphausiid production, and production:biomass ratio. Annual primary production on the Bering Sea shelf is thought to average 84 -150 g C m⁻² yr⁻¹ (Lomas et al., 2012, Rho and Whitledge, 2007). Few estimates of annual production by Bering Sea euphausiids are available in the literature. An ecosystem model by Walsh and McRoy (1986) estimated 6 and 12 g C m⁻² yr⁻¹ for middle and outer shelf of the eastern Bering Sea respectively, which was about 4 - 7% of primary production estimated by the same model. Production:biomass ratios for *T. inermis* and *T. raschii* based on field observations range from 1.3 – 4.1 (Siegel, 2000). Rough computations using values of euphausiid production and the production:biomass ratio at the middle of these ranges imply euphausiid standing stocks of ca. 3 g C m⁻².

¹Excerpted from Ressler, P.H., A.I. Pinchuk, G.A. Gibson, J.D. Warren. "How Many Euphausiids are There (Really) in the Eastern Bering Sea?", poster at Bering Sea Open Science Meeting, 22-23 February 2014, Honolulu, HI. URL: http://access.afsc.noaa.gov/pubs/posters/pdfs/pRessler02_ebs-euphausiids.pdf

Though this result is highly uncertain, net capture estimates of euphausiid biomass (average 1.05 g C m^{-2} for the outer shelf, summers 2008-2010, Table 1) seem too low, while acoustic estimates (average 24.7 g C m^{-2} for outer shelf, summers 2008-2010, Table 1) seem too high.

2. Net sampling

Euphausiids are known to avoid towed samplers (Clutter and Anraku, 1968, Sameoto et al., 2000), and the magnitude of this avoidance could range from 2 to 5-fold at night and 7 to 20-fold during daytime, according to the literature. Sameoto et al. (1993) found that the use of lights on a 1 m^2 mouth area, 243 μm mesh BIONESS towed at $1.5\text{--}2.0 \text{ m s}^{-1}$ (3 - 4 knots) increased the catch of euphausiids by 10 to 20-fold during daytime and 2 to 3-fold at night (Sameoto et al., 1993). Similarly, Wiebe et al. (2013) found that lights increased euphausiid catch in tows with a 1 m^2 mouth area, 335 μm mesh MOCNESS towed at 1.0 m s^{-1} (2 knots) by 11-fold during daytime and 4.5 fold at night. Coyle and Pinchuk (2002a) inferred from acoustic backscatter data and concurrent collections with a 1 m^2 mouth area, 500 μm mesh MOCNESS towed at 1.0 m s^{-1} (2 knots) that the MOCNESS was probably underestimating euphausiid abundance by 3.3 fold during nighttime and by a larger amount during the day. Finally, Smith (1991) attributed to avoidance 7-fold higher euphausiid catch rates at night than daytime with a 1 m^2 mouth area, 149 μm mesh MOCNESS towed at 1.0 m s^{-1} (2 knots). Recognizing that estimates of euphausiid avoidance of nets are difficult to make, uncertain, and likely variable, we chose to adjust biomass in daytime net samples upward by a factor of 10,

and in nighttime net samples by a factor of 5, as plausible adjustments for net avoidance in our analysis (Table 2).

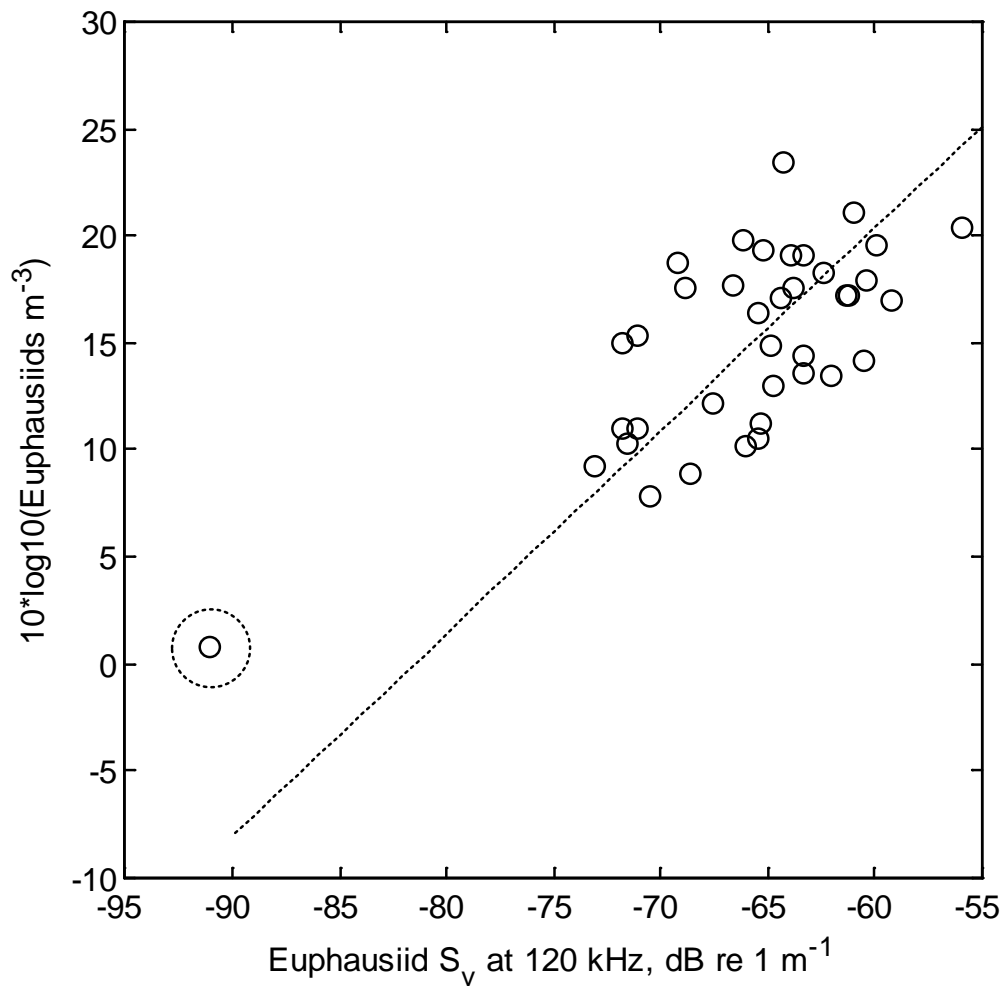
3. Acoustic-net sampling

Euphausiids dominate net catches from layers of euphausiid backscatter in the eastern Bering Sea (Ressler et al., 2012). However, uncertainty in backscatter classification and in target strength (TS, the backscatter from a single euphausiid) propagates to computations of derived density and biomass (Equation 1). TS for Bering Sea euphausiids was estimated using a physics-based scattering model (Ressler et al., 2012; Smith et al., 2010, 2013); model parameter scenarios indicated that uncertainty in these model estimates of TS could have been at least 8-10 fold (Ressler et al., 2012; Smith et al., 2010).

An alternative estimate of mean euphausiid TS can be made by regression of daytime catches from targeted 5 m² Methot trawls (Methot, 1986) towed at 1.5 m s⁻¹ (2 - 3 knots) on concurrently observed volume backscatter (S_v) layers described in Ressler et al. (2012), as in Sameoto et al. (1993). If we assume these daytime net catches should be adjusted upward by 10-fold to account for avoidance by euphausiids (avoidance is much greater during daytime; see above) and solve the regression (Fig. A.1) for x where $y = 0$ (a density of 1 animal per m³), a euphausiid TS of -81.5 dB re 1 m² is suggested, ca. 8-fold higher than the average scattering model estimate (-90.5 dB). However, this regression estimate of TS is highly uncertain due to variability in the

1593 fit: a 95% confidence interval on the intercept spans +/- 20 dB.² Estimates of the TS for
1594 a *Thysanoessa* spp. euphausiid of the average euphausiid length of about 18 mm
1595 (Ressler et al., 2012) from other studies (e.g., -80 dB, net catch- S_v regression, Sameoto
1596 et al., 1981; -88 dB, physics-based scattering model, McQuinn et al., 2013) suggest that
1597 there is a great deal of uncertainty about euphausiid TS, and neither the TS values from
1598 the physics-based model nor from the regression fit in our paper are unreasonable
1599 *prima facie*. However, given that both 1) net estimates of euphausiid biomass adjusted
1600 for the potential effects of avoidance and 2) expectations of euphausiid standing stock
1601 based on the magnitude of primary and euphausiid production are much lower than the
1602 “raw” acoustic-trawl estimates from this study (Table 1), we suggest an 8-fold reduction
1603 in acoustic estimates of euphausiid biomass is a plausible adjustment for comparative
1604 purposes in our analysis (Table 2).

² In fact, the large uncertainty in such relationships was a main motivation for the development and deployment of physics-based scattering models for zooplankton (e.g., Martin, L. V., Stanton, T. K., Wiebe, P. H., and Lynch, J. F. 1996. Acoustic classification of zooplankton. – ICES Journal of Marine Science, 53: 217–224).



1607

1608 Appendix Fig. A.1. Regression of Methot trawl net catch on euphausiid S_v , 2004-2009.

1609 The data, originally reported by Ressler et al. (2012), were corrected for two minor

1610 transcription errors and then adjusted by multiplying net catches by a factor of 10 to

1611 account for net avoidance by euphausiids during daytime. A functional regression fit

1612 (excluding the circled outlier) to the adjusted data yielded the equation $y=0.9508x+$

1613 77.4704 , $r^2=0.32$, $n=37$. Solving this equation where $y=0$ (e.g., a density of one

1614 euphausiid per m³) implies an average target strength of -81.5 dB re 1 m².