

The spatial distribution of euphausiids and walleye pollock in the eastern Bering Sea does not imply top-down control by predation

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ABSTRACT: Although euphausiids of the genus *Thysanoessa* ('krill') are a key zooplankton taxon in the Bering Sea ecosystem, the processes controlling variation in the standing stock of these animals are not well understood. Both forcing by temperature ('bottom-up') and predation ('top-down') have been proposed. If strong top-down forcing were present, a negative relationship would be expected between the standing stock of euphausiids and that of walleye pollock *Gadus chalcogrammus*, their single most important predator in the Bering Sea. We developed multiple regression models using survey data collected over several years to test the hypothesis of a negative relationship between local (mesoscale) densities of these animals. We used the models to evaluate the relative importance of pollock biomass and water temperature in predicting euphausiid biomass, and found that temperature was a far better predictor, a result that is not consistent with dominant top-down control of euphausiids by pollock predation.

KEY WORDS: Alaska · Bering Sea · Walleye pollock · *Theragra chalcogramma* · Euphausiids · *Thysanoessa* · *Gadus chalcogrammus* · Acoustics · Top-down · Bottom-up · GAM

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INTRODUCTION

Euphausiids are a key group of zooplankton in the eastern Bering Sea shelf ecosystem. The dominant euphausiid species are *Thysanoessa raschii*, found principally on the middle continental shelf (<100 m bottom depth), and *T. inermis*, found more commonly on the outer shelf (100 to 200 m bottom depth) (Vidal & Smith 1986, Smith 1991). Both species reproduce on the shelf in April and May (Smith 1991), and can be found there throughout the year (De Robertis & Cokelet 2012). Euphausiids form an important trophic link between phytoplankton and microzooplankton and animals at upper trophic levels (Aydin & Mueter 2007), including walleye pollock *Gadus chalcogrammus* (formerly known as *Theragra chalcogramma*; Page et al. 2013), which supports one of the world's largest commercial fisheries (FAO 2012). Walleye pollock (hereafter 'pollock') domi-

nates the fish assemblage of the eastern Bering Sea shelf, spawning in late winter and early spring on the outer shelf and moving inshore and north to feed on the middle and outer shelf during summer (Kotwicki et al. 2005).

Sea temperature and ice cover play a key role in the annual cycle of phytoplankton, zooplankton, and fish production in this system (Hunt et al. 2002, Stabeno et al. 2007, 2012, Sigler et al. 2014). In particular, Baier & Napp (2003) found that *Calanus* spp. recruitment was better in cold, icy years with an earlier spring phytoplankton bloom, possibly due to favorable feeding conditions and reduced predation pressure for the critical copepodite stage at ice retreat and onset of the spring bloom. The broad notion that cold conditions are favorable for recruitment and survival has been extended to euphausiids via the following possible mechanisms: better feeding conditions associated with the ice cover in spring-

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time, increased and sustained phytoplankton food production in colder, less-stratified summers, and reduced metabolic demands overall due to lower water temperatures (Coyle et al. 2008, 2011, Pinchuk & Coyle 2008, Hunt et al. 2011). Temperature and ice cover have also been linked to the distribution and abundance of walleye pollock (Swartzman et al. 1994, Wyllie-Echeverria & Wooster 1998, Kotwicki et al. 2005, De Robertis & Cokelet 2012, Kotwicki & Lauth 2013). From 2001 to 2005, conditions on the Bering Sea shelf were warm, euphausiid abundance was low, and pollock recruitment was poor (Ianelli et al. 2012); a series of cool years followed, characterized by increases in copepods and euphausiids and a rebound of the pollock stock after a nadir sometime between 2007 and 2009 (Ressler et al. 2012, Stabeno et al. 2012). Such observations led to the hypotheses that warm conditions and poor zooplankton prey availability between 2001 and 2005 may have reduced the recruitment and survival of young pollock (Coyle et al. 2011, Hunt et al. 2011, Stabeno et al. 2012), and that, as the biomass of the adult pollock stock subsequently declined, the coincident increase of euphausiid biomass could have been due in part to a significant release of pollock predation pressure (Ressler et al. 2012).

However, a complete understanding of the mechanisms driving these patterns has been elusive. Conceptual models of the interplay of predation pressure ('top-down') and environmental drivers ('bottom-up') on euphausiids in the eastern Bering Sea have been largely limited to categorical (e.g. warm vs. cold, high vs. low) comparisons, mostly relying on the synthesis of disparate types of field observations (Coyle et al. 2011, Hunt et al. 2011, Stabeno et al. 2012) or the results of mass-balance modeling (Springer 1992, Aydin & Mueter 2007). The recent availability of high-resolution surveys of euphausiids and pollock conducted over multiple years (2004 to 2012) and covering most of the continental shelf (Ressler et al. 2012) offers a new opportunity for an examination of the hypothesis that pollock predation is a dominant control of the standing stock of euphausiids on the Bering Sea shelf.

We developed multiple regression models to evaluate the relative importance of pollock predation and temperature in predicting euphausiid density. In these models, water temperature serves as a proxy for 'bottom-up' forcing of euphausiid biomass by environmental conditions, and pollock biomass as a proxy for 'top-down' predation by the single largest consumer of euphausiids in this ecosystem. A multiple regression model framework allows the power of

all explanatory variables to be competed simultaneously. The expectation in the case of strong top-down control by predation in our models is clear: all other factors being equal, pollock biomass should be the best predictor of euphausiid density, and the relationship between pollock and euphausiid biomass should be negative. Rejection of this hypothesis would be interpreted as strong evidence against top-down control.

MATERIALS AND METHODS

Pollock biomass

Pollock biomass data analyzed here came from 2 types of surveys of the Bering Sea shelf conducted during the summers of 2004, and 2006 through 2010. An annual bottom trawl survey (Lauth 2011) collected observations of the number of demersal pollock caught per area swept by a bottom trawl with a head-rope height of approximately 3 m at fixed stations spaced at a distance of 37 km (20 nautical miles, nmi). The density of pollock was converted to biomass per area at length using a length-weight regression. Water temperature (°C) at each trawl location was measured with a Seabird SBE-39 temperature-depth sensor mounted on the trawl. Mid-water pollock in the remainder of the water column was observed by an annual or biennial acoustic-trawl survey (Honkalehto et al. 2012), which estimates biomass density at length in 926 m (0.5 nmi) intervals along north-south survey transects spaced at an east-west distance of 37 km (20 nmi), using acoustic backscatter at 38 kHz, length and species composition from midwater trawl catches, a target strength model (Traynor 1996), and a length-weight regression. The acoustic estimates were averaged in 37×37 km (20×20 nmi) blocks around each bottom trawl survey station, and then the acoustic and bottom trawl estimates of pollock biomass density (kg ha^{-1}) were added to yield a combined estimate of pollock biomass density throughout the water column, as described by Ressler et al. (2012) (Fig. 1; data from 2007 are shown as an example). Both surveys are assumed to be quasi-synoptic east to west scans of the summertime distribution of pollock on the shelf.

Euphausiid biomass

Euphausiid biomass was estimated using acoustic and zooplankton trawl data from the acoustic-trawl

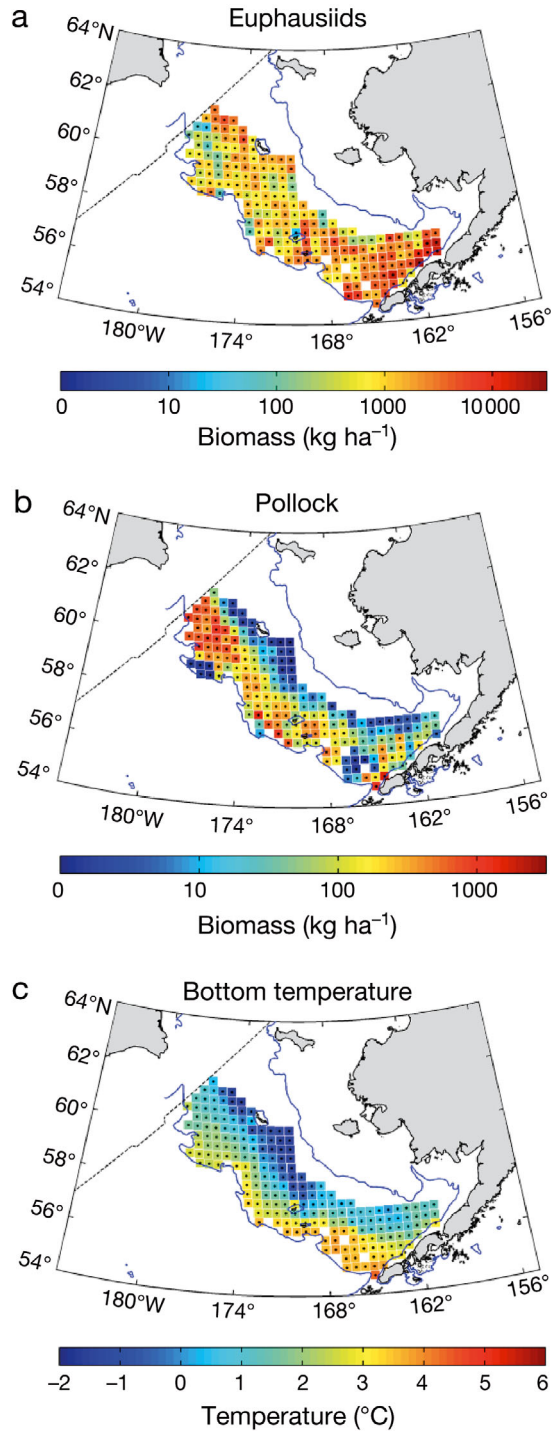


Fig. 1. Examples of survey data sets from summer 2007. Blocks with black dots in the center represent 37×37 km (20×20 nmi) averages around each bottom trawl survey station. Panels show (a) euphausiid biomass from the acoustic-trawl survey, (b) sum of Age 1+ pollock biomass from both surveys, (c) water temperature at the bottom measured during the bottom trawl survey. The 50 and 200 m isobaths are shown as blue line contours. The boundary between the USA and Russian exclusive economic zones is shown as a diagonal dashed line across the top left corner in each panel

surveys of pollock described above (see Ressler et al. 2012 for complete details). Briefly, acoustic backscatter at 120 kHz throughout the water column was classified by analyzing the frequency response measured at 18, 38, 120, and 200 kHz (De Robertis et al. 2010), converted from backscatter to biomass at length using length and species composition from Methot trawl samples (Methot 1986), a target strength model (Smith et al. 2013), and a length–weight regression (Harvey et al. 2012). Euphausiid biomass was vertically integrated to within 0.5 m of the acoustically-detected seafloor and spatially averaged in the same manner as the acoustic-trawl pollock survey biomass estimates to produce density estimates (kg ha^{-1}) in the same 37×37 km blocks as the pollock biomass data (Fig. 1). No estimates of euphausiid biomass are available for the so-called ‘acoustic deadzone’ (Ona & Mitson 1996) that occurs very close to the seafloor, but unlike for pollock (Kotwicki et al. 2013), limited net sampling of euphausiids in the study area using a Tucker trawl modified with runners for epibenthic deployment suggests that a relatively small fraction of the euphausiid density in the entire water column is located there (mean 5.4% within 2 m of the seafloor, SD = 8.3, $n = 6$; P. H. Ressler unpubl. data).

Model fitting

Data from 6 surveys with between 195 and 216 stations per survey were analyzed. Only stations where data for all variables were measured were included in the analysis. This excluded inshore stations sampled only by the bottom trawl survey, where no estimates of midwater pollock and euphausiid biomass were available. Survey data show that relatively little pollock biomass is found in this inshore region (Fig. 1; Ressler et al. 2012, Kotwicki & Lauth 2013), but some unknown amount of euphausiid biomass exists there (Smith 1991, Coyle & Pinchuk 2002); our study is necessarily limited to the area covered by both surveys.

Generalized additive models (GAMs) were fit to the data using the ‘mgcv’ package (version 1.7-13; Wood 2006) in R (version 2.15.0; R Development Core Team 2012). These models assume that effects of the predictors are additive, and use smooth functions (penalized regression splines; Wood & Augustin 2002) to model the effect of each term on the response variable. The full model had the following form:

$$\begin{aligned} \log_{10}(\text{euph} + 10) = & s[\log_{10}(\text{pk} + 10)] \\ & + s(\text{bot_temp}) + s(\text{ann_surf_temp}) \\ & + s(\text{lon}, \text{lat}) + s[\log_{10}(\text{pk} + 10), \text{bot_temp}] + e \end{aligned} \quad (1)$$

where $s(x)$ indicates a smooth of the effect of each covariate, euph = euphausiid biomass (kg ha^{-1}), pk = pollock biomass (kg ha^{-1}), bot_temp = bottom temperature ($^{\circ}\text{C}$), ann_surf_temp = the annual average surface temperature ($^{\circ}\text{C}$), lon = longitude, lat = latitude, and e indicates independently and identically distributed normal residuals. Both bottom temperature and annual average surface temperature were included in the model because they appeared to have separate, significant effects on euphausiid density, and are only weakly correlated spatially ($R^2 = 0.11$). Summer bottom temperatures are closely related to the spatial extent of ice cover in the previous winter, and they changed little over the course of the summer while the survey was conducted, while surface temperatures changed substantially during the survey due to seasonal warming and wind mixing after ice retreat (Stabeno et al. 2007, Lauth 2011). The geographic term $s(\text{lon}, \text{lat})$ was included to model any large-scale spatial trend that was present and not attributable to the other covariates we included (Wood & Augustin 2002); essentially, this controls for the average spatial distribution over all years in the data set. We considered all possible combinations of latitude, longitude, and depth when deciding how to specify the geographic term in our models, choosing to use only one pair of these variables since knowing latitude and longitude will specify the value of depth. We chose $s(\text{lon}, \text{lat})$ as it was the most intuitive and provided the best model performance. Finally, since pollock are thought to avoid the coldest bottom temperatures on the Bering Sea shelf in summer (Swartzman et al. 1994, Wyllie-Echeverria & Wooster 1998, Kotwicki et al. 2005, De Robertis & Cokelet 2012), and because consumption of euphausiids by pollock could increase with temperature due to higher metabolic demands (e.g. Dwyer et al. 1987), an interaction between the effects of bottom temperature and pollock in these models might be expected. We examined this interaction by including a bivariate smooth of pollock biomass and bottom temperature as a term in the full model.

Backward variable selection was performed by fitting the full model, and then dropping terms one at a time if several criteria were met: a nonsignificant F -test for the model term, estimated degrees of freedom equal to 1 with 95% confidence intervals of the partial fit including zero throughout the range of the predictor, and an increase in Akaike's information

criterion (AIC) and the generalized cross-validation (GCV) score for the model (Wood & Augustin 2002). The model in which all terms were significant by these measures was retained as the best model. Fits were evaluated by examining plots of model residuals and partial residuals for each covariate to determine whether distributional assumptions had been met, as well as for indications of autocorrelation. We also tested for spatial autocorrelation in model residuals using variography. Transformation of euphausiid biomass data was required to achieve approximately normally distributed model residuals. After trying several different data transformations, we selected a logarithmic transformation and the addition of a constant as it provided satisfactory residual plots and intuitive scaling of the partial plot axes. We applied the same transformation to the pollock biomass data to keep both biomass series in the same units; transformation of this covariate also slightly improved model fit based on the AIC score.

Prediction of out-of-sample surveys

Since: (a) GAMs are very flexible and capable of fitting many types of relationships, (b) it is likely that the stations in these data sets are not completely independent, and (c) most terms in Eq. (1) were retained in the best model, we suspected that overfitting could have occurred. We further supposed that additional out-of-sample prediction (beyond the cross-validation that is normally part of fitting GAM models; Wood 2006) would allow us to evaluate the relative importance of the predictors we retained and judge how robust the model predictions were to out-of-sample data. Jensen et al. (2005) approached this problem by fitting GAM models to single years of a data set and then evaluating out-of-sample model prediction of the remaining years. Loots et al. (2010) fit a GAM to half of a spatial fisheries time series and used the other half of the data set for cross-validation. We used a method analogous to the latter, in which we iteratively fit Eq. (1) to 5 of the 6 surveys in our data set, leaving 1 survey out in turn for prediction, and then computed the mean-squared prediction error as a measure of a model's ability to predict the remaining out-of-sample survey data set. Mean-squared prediction error (mspe) was computed for each of several selected models as follows:

$$\text{mspe}_j = \text{Sum}_{n,i} [(\text{predicted } \text{euph}_{ij} - \text{observed } \text{euph}_{ij})^2] / n_j \quad (2)$$

where mspe_j is the mean-squared prediction error for

survey j , predicted $euph_{ij}$ is the euphausiid density predicted by the model for station i of survey j , observed $euph_{ij}$ is the euphausiid density from the survey at the same station, n is the number of stations in survey j , and $\text{Sum}_{n,i}$ is the sum over all $i = n_j$ stations in survey j .

Relative importance of bottom temperature and pollock

To further examine the importance of temperature and pollock to model predictions of euphausiid density, we used the GAM in Eq. (1) to make sets of predictions for 2 contrasting survey years and for a 'base case' of average temperature and average pollock biomass, as follows:

P1: average temperature, average pollock biomass (base case)

P2: temperature in the coldest year (2009), average pollock biomass

P3: temperature in the warmest year (2004), average pollock biomass

P4: average temperature, pollock biomass in year with most pollock (2004)

P5: average temperature, pollock biomass in year with least pollock (2009)

Bottom temperatures and pollock biomass for these predictions were either the average at each station for all years, or the value at each station in one of the contrasting years (2004 or 2009). Average surface temperatures were either the average value for all stations in all years, or the average value for all stations in one of the contrasting years. The spatial term $s(lon, lat)$ was the same for all prediction data sets. We used these sets of predictions to draw contrasts between the predicted change in euphausiid density due to the effect of temperature and of pollock biomass relative to the base case predictions, as follows:

C1: relative effect of temperature, $(P2 - P3) / P1 \times 100$

C2: relative effect of pollock biomass, $(P5 - P4) / P1 \times 100$

In each case, predicted euphausiid biomass in 2004 is subtracted from predicted biomass in 2009 and divided by predicted euphausiid biomass in the base case. These contrasts were drawn using back-transformed data, and only the 183 stations sampled in both 2009 and 2004 (the years used for the warm/cold high pollock/low pollock contrasts) were included in this exercise.

RESULTS

Euphausiids, pollock, and temperature

Annual averages of euphausiid biomass varied inversely with average pollock biomass ($R^2 = 0.43$), average bottom temperature ($R^2 = 0.94$), and average surface temperature ($R^2 = 0.81$) (Fig. 2). Euphausiids were found throughout the surveyed area in all years, with patchy regions of high density, especially in the southeastern part of the shelf (Fig. 1; Ressler et al. 2012). Pollock biomass was typically concentrated between ca. 75 and 200 m bottom depth, and in the northwestern portion of the continental shelf. Shelf-wide patterns in bottom temperature data are dominated by the cold pool ($<2^\circ\text{C}$; Wyllie-Echeverria & Wooster 1998, Stabeno et al. 2007), with coldest temperatures inshore and to the north; the warmest part of the shelf was usually near the shelf break in the southeast (Fig. 1). As noted in the Methods, summer surface temperatures (not shown) are dominated by seasonal warming and wind mixing; since the survey progressed from east to west in June and July, surface temperatures were always warmest in the westernmost part of the surveyed area (cf. Lauth 2011).

Model results

The best model included all terms except for the interaction of bottom temperature and pollock,

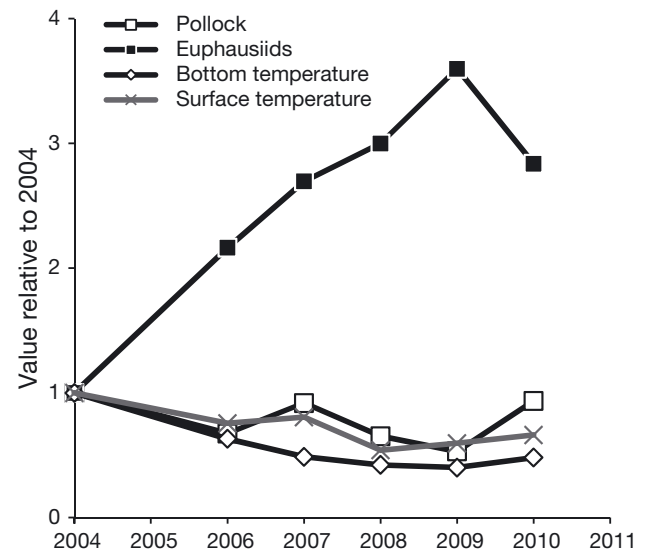


Fig. 2. Interannual pattern in average pollock biomass (kg ha^{-1}), euphausiid biomass (kg ha^{-1}), bottom temperature ($^\circ\text{C}$), and sea surface temperature ($^\circ\text{C}$). Value for each series is shown relative to the value in 2004

Table 1. Model statistics for several generalized additive models (GAMs) based on Eq (1). AIC = Akaike's information criterion; na = not applicable; edf = estimated degrees of freedom

Model	Pollock biomass		Bottom temperature		Longitude × Latitude		Annual average surface temperature		Deviance explained (%)	AIC
	edf	F	edf	F	edf	F	edf	F		
Best model	4.05	3.59	8.43	17.16	22.86	10.25	3.63	27.32	47.0	1618.94
No pollock		na	8.37	16.61	23.34	11.37	3.57	25.80	46.1	1631.90
No annual average surface temperature	4.14	2.45	7.63	62.50	23.95	22.02	na	na	42.5	1712.56
No bottom temperature	3.86	3.41		na	22.29	5.65	3.89	118.51	40.1	1752.12
Environmental terms only	3.96	8.77	8.62	4.43		na	3.86	99.20	34.2	1839.37
Geographic terms only		na		na	21.00	4.98		na	10.7	2220.69

which was not significant. In the best model, the remaining terms were statistically significant, AIC was minimized, and deviance explained (47.0%) was highest (Table 1). Model residuals were approximately normal and showed no evidence of spatial autocorrelation or patterns. A strong negative effect of bottom temperature and a moderate negative effect of annual average surface temperature were indicated (Fig. 3), while the effect of pollock was relatively flat in comparison. There was a significant geographic trend in the data over all years: the $s(lat, lon)$ term was positive in the southeast part of the continental shelf, and negative inshore and to the west. Compared to the best model, a model without the pollock term had only a slightly smaller value for deviance explained (-0.9%) and slightly larger AIC score (Table 1). Larger increases in AIC and reductions in deviance explained were observed when either bottom temperature (-6.9% deviance explained) or surface temperature (-4.5% deviance explained) terms were dropped from the best model. Both environmental and geographic covariates contributed substantially to model fit: a model using only the environmental covariates (pollock biomass and bottom temperature) explained 34.2% of the deviance in euphausiid biomass, while a model using only the geographic term had even less explanatory power (10.7%). Both environment-only and geographic-only models had inferior AIC and residual structure compared to the selected model (Table 1). Finally, it is important to note that more than half of the variability in log-transformed euphausiid biomass remained unexplained by the best model.

Prediction of out-of-sample surveys

When 5 model variants of the best model derived from model selection using Eq. (1) were iteratively fit using 5 of 6 survey years (leaving 1 survey year out in turn for cross-validation), the full model had the lowest AIC and highest deviance explained on average (Table 2), as would be expected from the results of backward variable selection using Eq. (1). In terms of out-of sample prediction, the full model also had the lowest mspe on average. The mspe decreased when annual average surface temperature was dropped from the model, and was slightly smaller when pollock was dropped from the model, but the largest changes occurred when either $s(bot_temp)$ or $s(lon, lat)$ were dropped. The mspe of a model with only bottom temperature and spatial location differed by

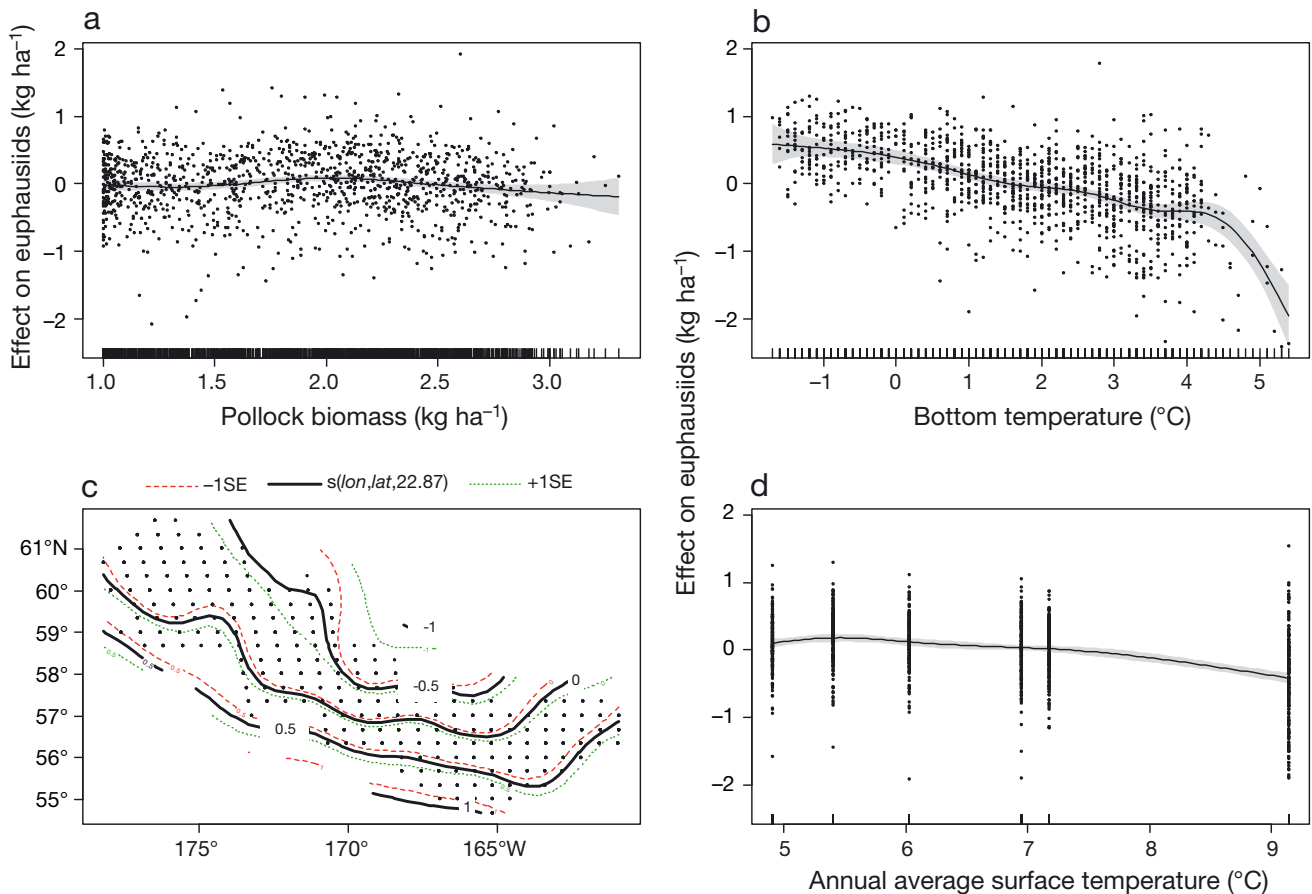


Fig. 3. Effect of each term in the best generalized additive model (GAM) of euphausiid biomass density (kg ha^{-1}). Covariates shown by each panel are as follows: (a) Age 1+ pollock biomass, (b) bottom temperature, (c) latitude and longitude, and (d) annual average surface temperature. Note that the units of pollock and euphausiid biomass have undergone a $\log_{10}(x + 10)$ transformation. In each panel, the points on the plots are residuals from the full model without the effect of the covariate on the x-axis, and the solid lines are smooth functions indicating the modeled effect of that covariate on predicted euphausiid density. In panels (a), (b), and (d), the shading denotes a 95 % confidence interval around the fit; in panel (c), green dotted lines indicate +1 SE and red dotted lines indicate -1 SE

Table 2. Leave-one-out cross validation for several selected models. Darker shades of gray indicate poorer performance on each model statistic. AIC = Akaike's information criterion; mspe = mean squared prediction error

Model	Average AIC	Average deviance explained	Average mspe	Average % increase in mspe from full model
Full model $\log_{10}(\text{euph} + 10) \sim s[\log_{10}(\text{pk} + 10)] + s(\text{bot_temp}) + s(\text{ann_surf_temp}) + s(\text{lon}, \text{lat})$	1336.43	45.38	0.30	0.00
No annual average surface temperature $\log_{10}(\text{euph} + 10) \sim s[\log_{10}(\text{pk} + 10)] + s(\text{bot_temp}) + s(\text{lon}, \text{lat})$	1402.54	41.58	0.31	5.35
No annual average surface temperature or pollock $\log_{10}(\text{euph} + 10) \sim s(\text{bot_temp}) + s(\text{lon}, \text{lat})$	1407.74	40.85	0.31	5.34
Geographic terms only $\log_{10}(\text{euph} + 10) \sim s(\text{lon}, \text{lat})$	1801.45	12.01	0.42	41.12
Environmental terms only $\log_{10}(\text{euph} + 10) \sim s[\log_{10}(\text{pk} + 10)] + s(\text{bot_temp}) + s(\text{ann_surf_temp})$	1521.95	31.75	0.52	74.47

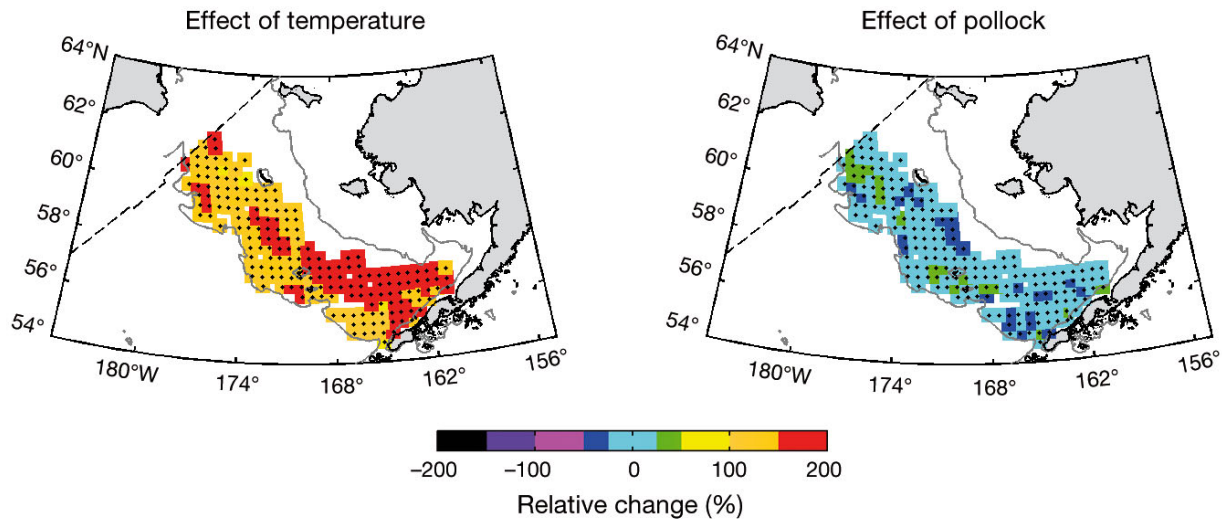


Fig. 4. Comparison of the relative effect of pollock and temperature on euphausiid density. The left panel shows the relative change in predicted euphausiid density due to the temperature change from the warmest year (2004) to the coldest year (2009) given the average effect of pollock. The red and orange colors indicate the relatively large increases in euphausiid biomass at each station attributed to temperature in the model as temperatures cooled between 2004 and 2009. The right panel shows the relative change in predicted euphausiid density due to the change in pollock biomass from the year with the least pollock (2009) to the year with the most pollock (2004) given the average effect of temperature. The blue and green colors indicate the relatively small change in euphausiid biomass at each station attributed to pollock biomass in the model

only about 5% on average from that of the full model. Eliminating the pollock term from the model (although it was statistically significant) appeared to have only a marginal effect on predictive power.

Relative effect of temperature and pollock

Compared to 'base case' model predictions made using average temperature and average pollock biomass, the change in predicted euphausiid density from 2004 to 2009 was greatest when temperature was varied (Fig. 4). Under our hypothesis, a positive value would be expected for each contrast (euphausiid biomass peaked in 2009, coinciding with both the coldest temperatures and lowest pollock biomass); if top-down control by pollock predation dominated variability in euphausiid biomass, the effect of pollock biomass on predicted euphausiid density should be largest. On average, the relative change in predicted euphausiid density at each station given temperatures in the coldest year (2009) and the warmest year (2004) with average pollock biomass was 160.53% (min. 51.45, max. 363.78). The relative change in predicted euphausiid density from given pollock biomass in 2009 and 2004 with average temperatures was close to zero and slightly negative on average (mean -3.02% , min. -49.85 , max. 44.70).

DISCUSSION

The results presented here are not consistent with dominant top-down control of euphausiids by pollock predation on the eastern Bering Sea shelf. We hypothesized that if predation by pollock were the dominant factor affecting the standing stock of euphausiids on the eastern Bering Sea shelf, we would have observed a strong, negative spatial relationship between local densities of pollock and euphausiids. Instead, while pollock biomass was a statistically significant model covariate, there was only a modest reduction in explanatory power when the pollock term was dropped from our GAMs (Table 1). Further, the effect of pollock on euphausiid biomass was rather flat and not strongly negative (Fig. 3). The effects of temperature were much stronger, a robust observation that held true during both stepwise model selection (Table 1) and leave-one-out cross validation (Table 2). When model predictions based on the temperature and pollock biomass extremes in the data set (2004: warm, high pollock; 2009: cold, low pollock) were compared with euphausiid biomass predicted under average conditions, the change in euphausiid biomass indicated by the range of temperatures in this data set was much larger than for observed changes in pollock biomass (Fig. 4).

Effect of temperature

The effect of temperature on euphausiid biomass appeared relatively strong and negative in all of the GAMs (Fig. 3b), which is consistent with the negative correlation of interannual shelf-wide averages (Fig. 2) of euphausiid biomass and temperature. Bottom temperature was also the most important single covariate in predictions of out-of-sample data (Table 2). Annual average surface temperature also had an independent, negative effect on euphausiid biomass in these models. Water temperature on the Bering Sea shelf is uniform and well-mixed from surface to bottom in winter; but after ice retreat in spring, seasonal warming of surface waters occurs over the course of the summer while bottom temperatures remain cold, reflecting the extent of winter ice cover (Stabeno et al. 2007). The negative effects of both surface and bottom temperatures in the models (the warmer the temperature, the lower the euphausiid biomass) are consistent with the idea that warmer conditions with reduced ice cover, early ice retreat, greater spring and summer insolation, and reduced wind mixing leading to smaller 'cold pools' and warmer, stratified surface temperatures in summer are somehow unfavorable for euphausiids.

De Robertis & Cokelet (2012) reported that the effect of bottom temperature on the spatial distribution of acoustic backscatter from zooplankton (principally euphausiids) on the Bering Sea shelf during spring and summer of 2007 and 2008 was weaker than the effect on the spatial distribution of fish backscatter (principally pollock), but they did note that on average, euphausiids were found in somewhat colder water temperatures than pollock. This is consistent with the negative effect of temperature on euphausiid biomass observed here. However, the temperatures on the Bering Sea shelf are not near physiological (Pinchuk & Hopcroft 2006) or distributional (Brinton et al. 2000) limits for these euphausiid species, and a negative association of biomass and temperature for these species is not universally found (Zhukova et al. 2009, Dalpadado et al. 2012). Potential mechanisms underlying positive 'bottom-up' forcing of euphausiid standing stocks during the recent cold, icy conditions on the Bering Sea have been proposed, including increased and sustained new production in summertime due to reduced stratification, favorable timing and composition of phytoplankton blooms associated with sea ice, and release from metabolically demanding warm temperature conditions (Pinchuk & Coyle 2008, Coyle et al. 2008, Hunt et al. 2011, Coyle et al. 2011). How-

ever, more recent studies have suggested that annual primary production is not significantly different between 'warm' and 'cold' years (Brown & Arrigo 2013, C. L. Liu et al. unpubl. data), and that colder summers are not necessarily less stratified (Ladd & Stabeno 2012), but also that euphausiids may preferentially use and benefit from increased availability of ice-associated algal production in cold years (E. J. Lessard pers. comm.). The question of whether any of these mechanisms explain the pattern of increased euphausiid abundance in the summers of cold years (and decreased abundance in warm years) remains unresolved.

Effect of pollock biomass

Pollock biomass had a relatively flat effect on euphausiid density in our models; being slightly positive at low pollock densities and slightly negative at high pollock densities (Fig. 3a). A consistently strong, negative effect of pollock biomass on euphausiid density was not observed; rather, it was weak and variable compared with the effect of temperature (Fig. 4, Table 1). There was no apparent interaction between the effects of temperature and pollock on euphausiid density, supporting the assumption of additive model effects. If the effect of pollock in the model had been temperature dependent, this could have produced a spatially variable predator-prey response in the model (*sensu* Ciannelli et al. 2008, Windle et al. 2012), but we found no evidence for this. Overall, inclusion of pollock terms lent a statistically significant amount of predictive power to the model, but particularly when compared to the impact of bottom temperature and spatial location (Tables 1 & 2, Figs. 3 & 4), the predictive power of pollock biomass in the GAM was weak.

We did not observe the negative association between pollock and euphausiid biomass that we expected, based on previous comparisons of pollock and euphausiid standing stocks showing that annual predation could be significant (Ressler et al. 2012), and previous studies suggesting tight coupling between zooplankton and higher trophic levels (Springer 1992, Aydin & Mueter 2007) in the Bering Sea. Though top-down control of zooplankton by fish predation has been shown in closed freshwater systems (Brooks & Dodson 1965, Gliwicz 1986, Carpenter & Kitchell 1993), clear demonstrations of this in marine systems are rare (but see Dalpadado & Skjoldal 1996, Worm & Myers 2003, Stige et al. 2014). The scale of analysis can change the sign of apparent

correlation between predator and prey: for example, a positive correlation between predator and prey could occur at a large scale since both species occupy the same habitat, while a negative correlation due to predator avoidance or local depletion of prey might only appear at a much finer scale (Rose & Leggett 1990, Ciannelli et al. 2008, Windle et al. 2012). Though the local resolution of our data set was a mesoscale station spacing of 37 km (20 nmi), we interpret the stronger association of euphausiid density with temperature than with pollock density at both the shelf-wide (Fig. 2) and local scale (Fig. 3) as inconsistent with strong top-down predation pressure. The present study demonstrates that negative associations of pollock and euphausiid standing stock (Ressler et al. 2012) appear much weaker when included with other potential covariates in a multiple regression model.

Effect of spatial location

Spatial location lent a significant amount of predictive power to the models. Though the environmental covariates are clearly more important in the models, the spatial term $s(lon, lat)$ was able to explain 10 to 12% of the deviance in euphausiid biomass on its own, and models that included the spatial term had better predictive power than those including only environmental covariates (Tables 1 & 2). Accounting for large-scale trends when fitting regression models to spatial data has been recommended to avoid incorrectly attributing that trend to other model covariates (Legendre 1993), and a geographic term is often included in spatial regression models of fisheries data (Swartzman et al. 1992, Wood & Augustin 2002, Mueter & Litzow 2008, Planque et al. 2011). However, the ecological interpretation of this term can be problematic (Wood 2006): for example, the spatial trend is present in all years of this data set, and it is not clear what environmental or life history processes could have produced this pattern in euphausiid biomass, or how long the pattern has persisted (nor is it possible to examine these questions with the data set in hand). Thus, the effect of $s(lon, lat)$ is probably best interpreted as a proxy for spatial processes unresolved by the other covariates in these models.

Weaknesses of the method and data set

GAMs are vulnerable to overfitting and non-independence of observations, which could lead to

overestimation of precision and a bias toward more complex models (e.g. Jensen et al. 2005, Loots et al. 2010). We addressed this by comparing traditional model selection with leave-one-out cross validation of out-of-sample survey data sets. This approach showed that the conclusions drawn about the relative predictive importance of pollock and bottom temperature from traditional model selection were robust. It is also important to note that the shape of the smooths for each covariate (Fig. 3) remained consistent when a year of observations was left out of the model; i.e. no single year in the data set drove these results. Secondly, our analysis was limited to summers between 2004 and 2010, and we do not know for certain whether the relationships modeled in our study are representative of all conditions in the eastern Bering Sea. The string of very warm years in the early 2000s followed by cold years from 2007 to 2010 is an unusual pattern in environmental conditions in this region (Hunt et al. 2011, Stabeno et al. 2012), but it is not statistically unexpected given historical variability (Overland et al. 2012). Similarly, the standing stock of Bering Sea pollock was lower during our study period than peak biomass values in the mid-1980s and late 1990s, and was very low from 2007 to 2010, but was not without precedent (Ianelli et al. 2012). Finally, our hypothesis regarding control of euphausiid standing stock by pollock predation relies on a spatial comparison of biomass, rather than of production rates. However, given the difficulty of obtaining robust production estimates for euphausiids and pollock at the spatial resolution of our data sets, we think our approach is a reasonable one.

CONCLUSIONS

The amount of euphausiid biomass consumed annually by walleye pollock is substantial, and we cannot categorically exclude predation as one of several possibly important factors affecting the standing stock of euphausiids on the Bering Sea shelf. However, the effect of pollock predation does not appear predominant. Despite negative interannual and spatial relationships between pollock and euphausiid biomass, the effect of pollock on euphausiid density was weak when competed with other covariates in a multiple regression model.

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