Developing an acoustic survey of euphausiids to understand trophic interactions in the Bering Sea ecosystem

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A B S T R A C T

Euphausiids (principally Thysanoessa spp.) are a key group of organisms in the Bering Sea ecosystem, linking production at lower trophic levels to top predators and important commercial fish stocks such as walleye pollock (Theragra chalcogramma). Here, we combine multifrequency acoustic survey methods, physics-based models of euphausiid backscatter, and net sampling to provide a means of monitoring the status and trends of euphausiid standing stock biomass on the Bering Sea shelf. Observations made using this approach during six summers (2004 and 2006–2010) indicate that standing stocks of euphausiids and pollock were inversely correlated over time as well as in space across the continental shelf. First-order calculations show that when pollock abundance was at its peak during these years, the pollock stock could have consumed 10–87% of the euphausiid standing stock between May and September. We hypothesize that predation by pollock is a significant top-down control on euphausiid standing stock in this system.

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1. Introduction

Euphausiids (Family Euphausiidae) or ‘krill’ play a key role in the Bering Sea ecosystem. Euphausiids are important prey for many species, forming an important node in the food web and a major pathway for transfer of energy from primary production to higher trophic levels (Aydin and Mueter, 2007). They are also one of the most important prey items for walleye pollock (Theragra chalcogramma, hereafter ‘pollock’; Brodeur et al., 2002; Lang et al., 2000, 2005), which supports one of the largest single-species fisheries in the world and the largest fishery by volume in the United States (FAO, 2009; NMFS, 2010). The principal euphausiid species on the Bering Sea shelf are Thysanoessa inermis and T. raschii; the typical length of adult animals in midsummer is ca. 18–19 mm (Coyle, 2000; Coyle and Pinchuk, 2002; Smith, 1991; Stockwell et al., 2001). Thysanoessa inermis begins to spawn in April and is more common on the outer shelf (100–200 m bottom depth), while T. raschii begins to spawn in May and is the dominant euphausiid further inshore; each species is thought to spawn once per year (Dalpadado and Skjoldal, 1996; Pinchuk and Hopcroft, 2006; Smith, 1991). There is some recent evidence that the abundance of euphausiids on the Bering Sea shelf is greater in years with cold, icy springs and cold summers versus years with warmer conditions (Coyle et al., 2008, 2011; Hunt et al., 2011). Despite their great importance in the Bering Sea ecosystem, however, knowledge of the stock size and factors controlling the population dynamics of euphausiids in the Bering Sea remains limited. For example, the net sampling methods used in existing long-running time series of Bering Sea zooplankton abundance are better suited to capturing smaller zooplankton taxa (such as copepods; Napp et al., 2002) than the larger euphausiids. Time series observations of the abundance and distribution of euphausiids would fill a gap in what is known about this important group of animals in the Bering Sea, benefiting both resource management and our understanding of trophic interactions and ecosystem function.

Seminal observations by Balls (1948) and Sund (1935) in the first half of the 20th century showed that ship-based acoustic echosounders could detect fish schools, and since that time there has been substantial development of acoustic equipment and methods to estimate the abundance of both fishes (Simmonds and Maclellan, 2005) and zooplankton including euphausiids (Foote and Stanton, 2000; Holliday and Pieper, 1995; Sameoto, 1980). Acoustic methods have been applied to studies of euphausiid distribution in the Bering Sea (Coyle, 2000; Coyle and Pinchuk, 2002; Swartzman et al., 2002) as well as in other locations (Brierley et al., 1997; Lawson et al., 2008; Ressler et al., 2005; Simard and Lavoie, 1999; Stevick et al., 2008; Warren and Demer, 2010),

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but the application of these methods to routinely monitor euphausiid stocks has been uncommon due to the limited availability and complexity of the necessary data. The major exceptions are surveys of Antarctic krill, *Euphausia superba*, for which acoustic-trawl surveys are the method of choice (Brierley et al., 1997; Hewitt and Demer, 2000; Hewitt et al., 2004; Reiss et al., 2008). In the Bering Sea, the large-bodied crustacean zooplankton assemblage is dominated by euphausiids (Vidal and Smith, 1986), and multifrequency acoustic data are available from existing resource monitoring surveys (Honkalehto et al., 2010). Recent work on multifrequency classification and ground-truth identification of target species (De Robertis et al., 2010), and new area- and species-specific work on modeling acoustic backscatter from euphausiids (Smith, 2010; Smith et al., 2010), have made the application of acoustic techniques to monitoring this euphausiid standing stock feasible. This study demonstrates that acoustic methods are a suitable means of monitoring euphausiid standing stock and distribution on the Bering Sea shelf. These standing stock estimates, along with recent pollock survey results, allow us to draw some first-order inferences about the predation impact of pollock on euphausiids and the potential for top-down control of the euphausiid standing stock by predation.

2. Material and methods

2.1. Survey data sets

Acoustic backscatter and net capture data for midwater pollock and euphausiid distribution and abundance were collected during summertime acoustic-trawl surveys conducted by scientists from NOAA’s Alaska Fisheries Science Center (NOAA-AFSC) aboard NOAA Ships *Oscar Dyson* or *Miller Freeman* using standard acoustic survey methods (Simmonds and Maclennan, 2005). Honkalehto et al. (2002, 2010) provide more details on the routine methods used for estimation of midwater pollock biomass; only an overview, with additional details pertinent to the estimation of euphausiid biomass (which has not been a routine survey product), is given here. The surveys consisted of acoustic backscatter measurements averaged into 0.5 nmi (0.926 km) elementary distance sampling units (EDSUs) along north–south oriented transects spaced 20 nmi (37 km) apart (Fig. 1). Acoustically detected aggregations were opportunistically sampled with large midwater and bottom trawls to verify size and species composition of acoustic targets. The survey speed of the vessel averaged approximately 12 nmi h⁻¹ (6 m s⁻¹). Operations were conducted during daylight hours only. The echosounder used was a Simrad¹ EK500 or a Simrad EK60 operating at frequencies including 18, 38, 70, 120, and 200 kHz, at a ping interval of 1 s⁻¹, and calibrated using a standard target (Foote et al., 1987). Midwater pollock biomass was estimated from 16 m below the sea surface to 3 m above the seafloor. In some years, areas of both the U.S. and Russian exclusive economic zones (EEZs) were surveyed, but we present results only for the U.S. EEZ.

Observations of demersal pollock distribution and abundance were obtained from bottom trawl surveys on the Bering Sea shelf conducted by NOAA-AFSC using chartered fishing vessels. The bottom trawl survey was also conducted only during daylight hours. Area-swept pollock density estimates of pollock within approximately 3 m of the seafloor were made at standard stations located nearby to the acoustic survey transects and spaced at a distance of 20 nmi (37 km; Fig. 1; see Lauth, 2010 for details). The bottom trawl survey covered most of the U.S. EEZ sampled by the midwater acoustic survey, as well as areas further inshore where most or all of the pollock stock is found very close to the bottom (Honkalehto et al., 2002; Kotwicki et al., 2005). Both midwater and bottom trawl surveys were conducted from early June to early August in 2004 and 2006–2010.

2.2. Classification of euphausiid backscatter

Euphausiid backscatter was identified by comparing the observed backscatter frequency response at 18, 38, 120, and 200 kHz from acoustic survey transects to a reference data set obtained from trawl-verified measurements of frequency response collected between 2004 and 2007 using the method of De Robertis et al. (2010), who present the details of this classification method as well as a rigorous evaluation of its application to classification of backscatter from pollock. Echoview software (Myriax Pty, Hobart, Australia) and custom Matlab (The Mathworks, Natick, MA) routines were used for this work. Briefly, volume backscattering strength ($S_v$, dB re 1 m⁻¹; see MacLennan et al., 2002 for a review of acoustic terminology) was averaged over 5 ping (horizontal) by 5 m (vertical) cells, and then all pairwise differences between $S_v$ at different frequencies were computed for each of these cells. The absolute value of the mean normal deviate (Z-score) over all frequency pairs for each 5 ping by 5 m cell was computed relative to the expected pairwise frequency differences for each of several taxonomic groups (including euphausiids; see Table 2 in De Robertis et al., 2010). This mean Z-score indicates how well the observed frequency response matches the expectation for the various taxa and can be used to classify each cell; for example, a mean Z-score of 2 relative to the expectation for euphausiid frequency response ($Z_{euph} = 2$) indicates that the observed frequency response of $S_v$ in that cell is within approximately two standard deviations of the mean frequency response for euphausiids in the reference set.

The signal-to-noise ratio (SNR) of the $S_v$ in each cell was evaluated before multifrequency classification occurred, following De Robertis and Higginbottom (2007). SNR is range- and frequency-dependent. In practice, $S_v$ at 38 kHz has a SNR of $\geq 10$ dB up to a range of 500 m or more. $S_v$ at 120 and 200 kHz exhibit a significant reduction in SNR at ranges $\geq 200$ m. At 18 kHz, transducer ringing generated noise that decayed rapidly with depth, but which sometimes dominated the received signal.

¹ Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.
Two potential biases in the euphausiid backscatter data set were examined in greater detail. Walleye pollock are relatively strong acoustic targets (ca. $10^5$ times stronger scattering per individual than euphausiids, e.g., Demer and Conti, 2005; Traynor, 1996) with a relatively flat $S_o$ response at the frequencies in use here (De Robertis et al., 2010). Backscatter from pollock and euphausiids located in the same cubic meter of water will typically be dominated in terms of frequency response by scattering from the pollock, which could lead to underestimates of euphausiid densities (Coyle and Pinchuk, 2002). In practice, the size of this bias depends on the vertical and horizontal overlap of pollock and euphausiids during the daytime acoustic surveys. To examine the significance of this potential bias in our data, we computed a correction factor by using the ‘background’ euphausiid $S_o$ surrounding detected pollock schools to estimate the $S_o$ of euphausiids that might be within the area encompassed by those schools but obscured by scattering from the pollock. Vertical bins (5 nmi (9.26 km) by 20 m) were used for this local average of euphausiid backscatter in these cells. The $S_o$ of all cells where $SNR > 10 \text{ dB, } Z_{\text{euph}} \leq 2$, and $Z_{\text{euph}}$ was the minimum $Z$-score for any other class in the analysis was classified as euphausiid backscatter (Fig. 2). The four known classes of acoustic targets included were pollock, euphausiids, jellyfish, and myctophids; discrimination power for euphausiids is likely to be high given the difference in frequency responses among these classes (cf. De Robertis et al., 2010). In cells meeting these criteria, $S_o$ at 120 kHz above a $-80 \text{ dB integration threshold}$ was then integrated into $0.5 \text{ nmi (0.926 km)} \times 20 \text{ m}$ bins between depths of $20 \text{ m}$ from the sea surface and $0.5 \text{ m}$ above the seafloor to a maximum range of $500 \text{ m}$. These larger bins were required to have a mean $Z_{\text{euph}}$ of $\leq 1.5$ before being subjected to further processing and analysis. The nested approach of thresholding $Z_{\text{euph}}$ at the scale of both the 5 ping by $5 \text{ m}$ and $0.5 \text{ nmi by 20 m}$ scales has the effect of classifying marginal analysis cells (i.e., $1.5 < 1.5 < Z_{\text{euph}} < 2 < 2$) as consistent with euphausiids only when the surrounding cells are more consistent with the expectation for euphausiids (cf. De Robertis et al., 2010).

2.3. Corrections for overlap with pollock and diel period

Two potential biases in the euphausiid backscatter data set were examined in greater detail. Walleye pollock are relatively strong acoustic targets (ca. $10^5$ times stronger scattering per individual than euphausiids, e.g., Demer and Conti, 2005; Traynor, 1996) with a relatively flat $S_o$ response at the frequencies in use here (De Robertis et al., 2010). Backscatter from pollock and euphausiids located in the same cubic meter of water will typically be dominated in terms of frequency response by scattering from the pollock, which could lead to underestimates of euphausiid densities (Coyle and Pinchuk, 2002). In practice, the size of this bias depends on the vertical and horizontal overlap of pollock and euphausiids during the daytime acoustic surveys. To examine the significance of this potential bias in our data, we computed a correction factor by using the ‘background’ euphausiid $S_o$ surrounding detected pollock schools to estimate the $S_o$ of euphausiids that might be within the area encompassed by those schools but obscured by scattering from the pollock. Vertical bins (5 nmi (9.26 km) by 20 m) were used for this local average of euphausiid backscatter (Fig. 2). The four known classes of acoustic targets included were pollock, euphausiids, jellyfish, and myctophids; discrimination power for euphausiids is likely to be high given the difference in frequency responses among these classes (cf. De Robertis et al., 2010).
euphausiid backscatter. The cumulative impact of this correction was small on a survey-wide basis, ranging from an 0.5% to 4.2% increase in mean euphausiid backscatter (averaging 1.4%) for all surveys. The data presented in this paper include this correction.

The second potential bias is related to the vertical distribution of euphausiids. As noted, the acoustic pollock survey transects were sampled almost entirely during daytime hours (Honkalehto et al., 2010), but for logistical reasons, small portions of the transects were sampled near dusk, and occasionally even at night. Euphausiids in the Bering Sea and elsewhere exhibit a regular diel vertical migration to near-surface waters each night (Mauchline, 1980), eventually moving above where they can be detected by vessel-mounted transducers. After examining the ratio of euphausiid backscatter integrated over the water column (s_m, m^2 nmi^-2) to daytime mean backscatter as a function of time of day, we suspected that some measurements of euphausiid density were biased low (Fig. 3); pollock backscatter data did not exhibit this pattern (not shown). Therefore, we corrected the euphausiid data set for this diel bias by removing data collected after sunset and before sunrise from further analysis. As with the correction for pollock overlap with euphausiids, on a survey-wide basis the magnitude of this bias was extremely small, ranging from an 0.8% to 3.6% increase in mean euphausiid backscatter (averaging 2.0%) over successive surveys.

2.4. Quality control and verification of acoustic backscatter classification

The average, backscatter-weighted Z_euph computed over all EDSUs for each survey transect (De Robertis et al., 2010) was used to measure how well observed data classified as euphausiids compared to the reference data set. Since the reference set is a fixed and separate data set, it can be used to evaluate relative quality and internal consistency of euphausiid backscatter classifications in the data analyzed here.

Backscatter layers identified as being composed of euphausiids were also sampled to verify species composition and obtain length–frequency information with targeted tows using a rigid frame Methot trawl with a 5 m^2 mouth area, 2 mm x 3 mm mesh in the body of the net, and 1 mm mesh in the codend (Methot, 1986). Tows were made at a nominal vessel speed of 3 nmi h^-1 in the body of the net, and 1 mm mesh in the codend (Methot, 1986). Tows were made at a nominal vessel speed of 3 nmi h^-1 in the body of the net, and 1 mm mesh in the codend (Methot, 1986). Euphausiid lengths were measured from the curve of the carapace behind the telson as given by Shaw et al., 2006). Euphausiid density was estimated using the volume of water filtered by the net as computed from flowmeter measurements and mouth area dimensions, and counts of euphausiids in the preserved samples. These net capture estimates of euphausiid numerical density were compared with S_v from euphausiids measured in the path of each Methot trawl deployment between 2004 and 2009, accounting for the mouth area of the net and the setback between acoustic transducers and the net frame (Zhou et al., 1994). Samples from summer 2010 are not included as they have yet to be enumerated.

2.5. Target strength model and biomass computation

The acoustic scattering from an individual organism can be expressed as a backscattering cross-section (\(\sigma_{bs}\), m^2) or its logarithmic counterpart, target strength (TS = 10 \times \log_{10}(\sigma_{bs})) dB re 1 m^2). This quantity is fundamental to estimation of number of targets from S_v measurements. When a single organism type dominates the acoustic scattering in a volume, number of targets in the volume can be calculated using the equation

\[ N = \frac{S_v}{\sigma_{bs}} \]  

where N is the number of organisms per unit volume (m^-3), S_v is the volume backscattering coefficient (S_v = 10^{S_v/10}, m^-1), and \(\sigma_{bs}\) (m^2) is the average backscattering cross-section weighted by the distribution of organism lengths.

Currently, the most common way to estimate euphausiid \(\sigma_{bs}\) is via a physics-based scattering model (Conti and Demer, 2006; McGehee et al., 1998; Reiss et al., 2008; Stanton and Chu, 2000). For the analysis presented here, a distorted wave Born approximation (DWBA) model (Lawson et al., 2006; McGehee et al., 1998; Stanton and Chu, 2000) is employed. The parameterization and use of the DWBA model for Bering Sea euphausiids is described in detail by Smith et al. (2010) and Smith (2010). Briefly, the euphausiid is modeled as a fluid-filled cylindrical shape described by key parameters including length, width, sound speed and density, and orientation with respect to the impinging acoustic wave.

There were not enough data in every survey year to fully parameterize the DWBA model: there were relatively few Methot tows in 2004 and 2006, width, sound speed, and density measurements were only available for 2008 specimens, and no measurements of in situ euphausiid orientation were made. The Methot catch data that are available from 2004 to 2009 indicate that euphausiid length and species composition were very consistent among years: offshore of 100 m bottom depth, species composition was dominated by T. inermis (56% by number) with mean length 19.3 mm (SD 1.5, n=38 tows, unimodal length distribution), while inshore T. raschii were more common (75% by number) with mean length 18.3 mm (SD 2.3, n=21 tows, unimodal length distribution). Given the limited information available, we used the DWBA model to estimate \(\sigma_{bs}\) at 120 kHz in 1 mm length bins between 8 and 28 mm for the average length distribution in two strata, inshore and offshore of the 100 m isobath. For DWBA model runs, our euphausiid lengths were converted to CCAMLR (Convention on the Conservation of Antarctic Marine Living Resources) 'standard krill lengths' (anterior of eye to posterior of telson; Demer and Conti, 2005; McGehee et al., 1998) using a regression obtained using 2008 measurements (standard krill length = 1.07 x euphausiid length - 0.1041, \(r^2=0.96, n=231\)); estimates of numbers and density are subsequently reported in terms of euphausiid length. Widths were computed from a regression of standard krill length on width (width = 0.0024 x standard krill length)^2.3679, \(r^2=0.61, n=412\)) and average values for sound speed and density contrast with seawater (both obtained from euphausiid specimens measured in 2008; Smith et al., 2010) were used to parameterize DWBA model runs for both strata in all survey years. Smith et al. (2010) did not observe differences in sound speed and density contrast across species, so the same values for these model parameters were used for all euphausiids. However, species composition of Methot catches was used to apportion numbers of euphausiids among species and to convert numbers of animals to biomass when species specific information was available. Likely distributions of in situ euphausiid orientation were obtained from the literature (Conti and Demer, 2006; Kristensen and Dalen, 1986; Lawson et al., 2006). To express possible uncertainty in DWBA model estimates of \(\sigma_{bs}\) and resulting computations of numbers and biomass, we implemented three \(\sigma_{bs}\) scenarios that encompass likely values of the least well-constrained model parameters, material properties (combined effects of sound speed and density contrast with seawater) and in situ orientation. Model parameterization is summarized in Table 1.
The number of euphausiids at length in each 0.5 nmi (0.926 km) × 20 m cell in all survey data sets was computed for each species using the equation
\[ N_j = (s_A \times 0.5 \times 20)/(\pi s_\text{bs} \times 4\pi P_j) \]
where \( N_j \) is number of euphausiids at length \( i \) and species \( j \), \( s_A \) is euphausiid backscatter density per unit area at 120 kHz (m\(^2\) nmi\(^{-2}\)) in each cell, 0.5 nmi and 20 m are constants needed to expand the cell \( s_A \) to the area comprising the length of the EDSU and halfway to the adjoining survey transect on either side, \( 4\pi \) converts backscattering cross-section \( \pi s_\text{bs} \) to spherical scattering cross-section \( \pi s_\text{bs} \) (see MacLennan et al., 2002), and \( P_j \) is the proportion of euphausiids at length \( i \) and species \( j \) in Methot net tow catches. \( P_j \) differed by onshore and offshore strata, but was constant within each stratum over all years. \( s_\text{bs} \) varied for each of the three DWBA model scenarios; within each of these scenarios, it also differed by onshore and offshore strata, but was constant within each stratum in a DWBA model scenario over all years.

Biomass at length was computed from numbers using a length-wet weight regression determined in a study of euphausiid proximate composition (Harvey et al., 2012); we report biomass here in terms of the wet weight of euphausiids, but in principle other currencies such as carbon, lipid, or energy content given by Harvey et al. could be used, as well. When species-specific information on biomass conversion was available (for T. inermis, T. raschii, and T. longipes), it was used to compute biomass of the proportion of animals from each of those species in the Methot net catches. For other species, a length-wet weight regression using average parameters of the equations for other species was employed. The biomass calculation from estimated numbers of animals can be summarized in the following equation
\[ B_j = N_j P_j W_{ij} \]
where \( B_j \) is biomass of species \( j \) at length \( i \), \( P_j \) is proportion of euphausiids in species \( j \) from Methot net catches, and \( W_{ij} \) is the wet weight of a euphausiid of length \( i \) and species \( j \) computed from length-wet weight regressions given in Harvey et al. (2012). \( P_j \) differed between onshore and offshore strata, but was constant within each stratum over all years. The length-wet weight regression used for \( W_{ij} \) is based upon specimens collected from 2008 to 2010. Both euphausiid numbers and biomass were summed across length, species, and strata in each year to compute a survey total for each quantity. Sampling variability in these survey totals was estimated using a 1-D geostatistical method (Petitgas, 1993), the same technique used for acoustic-trawl pollock survey data.

2.6. Spatial and temporal patterns in euphausiid and pollock biomass

Acoustic and bottom trawl surveys detect different portions of the pollock stock. Bottom trawls capture only near-bottom pollock, while acoustic surveys cannot detect pollock in very close proximity to the seafloor (within about 1.5 m in this case; cf. Oma and Mitson, 1996). Thus, neither survey alone provides a complete picture of pollock abundance and distribution, and both are treated as separate relative indices for stock assessment purposes, rather than as absolute estimates (Ianelli et al., 2010). Similarly, acoustic surveys cannot detect euphausiids located very close to the seafloor, but limited net sampling in the study area using a Tucker trawl modified with runners for epibenthic sampling suggests that a relatively small fraction of euphausiid biomass is located there; estimates of integrated euphausiid density within 2 m of the seafloor from these samples averaged only 5.4% of integrated water column density (SD = 8.3, n = 6; Ressler, P.H., NOAA-Alaska Fisheries Science Center, unpublished data). In order to evaluate both spatial and temporal patterns of pollock (predator) relative to that of euphausiids (prey) in this study, we made the necessary assumptions that acoustic and bottom trawl survey biomass results sum to the total amount of midwater and demersal pollock throughout the water column, and that the acoustic survey detects the total amount of euphausiid biomass in the water column.

We used both bottom trawl and acoustic survey time series to evaluate temporal patterns in the standing stocks of pollock and euphausiids and the potential for their interaction in the U.S. EEZ from 2004 to 2010. The demersal pollock survey does not produce euphausiid biomass estimates, but we assumed that the temporal pattern of euphausiid biomass in the acoustic survey area reflects the shelf-wide temporal pattern in euphausiid standing stock. For spatial comparison of pollock and euphausiids, vertically integrated midwater pollock biomass density estimated by the acoustic survey (kg ha\(^{-1}\)) was averaged in 20 nmi × 20 nmi (37 km × 37 km or 1.4 × 10\(^{5}\) ha) blocks surrounding each demersal survey station, while bottom trawl catch per unit effort at each station was used to compute average pollock density in these same blocks (kg ha\(^{-1}\)). The two survey estimates were summed in each block. In the shallow areas (bottom depth <50 m) surveyed only by the bottom trawl survey where pollock is mostly or entirely demersal, we assume that the bottom trawl survey detects all pollock. Euphausiid biomass was similarly vertically integrated and block-averaged. Spatial distributions of pollock and euphausiids were compared using contoured surfaces of these block-averaged data. The covariance of pollock and euphausiid density at each block was computed over the 6 year time series for the area sampled by both surveys.
2.7. Estimation of predation impact by pollock on euphausiids

The approximate predation impact by pollock on euphausiids was estimated by taking the sum total of pollock and euphausiid biomass in each survey year only in the area sampled by both the acoustic and bottom trawl pollock surveys in each year (since euphausiid estimates are not made by the bottom trawl survey), and making some simplifying assumptions about the rate of pollock consumption, using the equation

\[ C_d = B_p R_B F_e \]

where \( C_d \) is the biomass of euphausiids consumed per day by pollock (kg d^{-1}), \( B_p \) is the sum of pollock standing stock biomass from acoustic and demersal surveys (kg) in the area covered by both surveys, \( R_B \) is the fraction of body weight in prey that pollock consumes per day (0.02; K. Aydin and T. Buckley, personal communication; Springer, 1992) for a population currently dominated by younger fish (Ianelli et al., 2010), and \( F_e \) is the fraction of pollock diet consisting of euphausiids between May and September (mean 0.53, range 0.37–0.70, for the years 1997–2001; Lang et al., 2005). The daily rate of pollock consumption of euphausiids relative to the standing stock of euphausiids can then be calculated \((C_d / B_e, \text{ d}^{-1})\), where standing euphausiid biomass \( B_e \) is the acoustic survey estimate of euphausiid biomass \( B_e \) summed over all lengths and species. This rate can be multiplied by the number of days over which feeding takes place to estimate the fraction of euphausiid standing stock consumed by the pollock standing stock over that time period. Standing stock estimates for both pollock and euphausiids come from surveys conducted from early June to early August during the summer northward and shoreward ‘feeding migration’ by pollock (Kotwicki et al., 2005). The pollock food habits data reported by Lang et al. (2005) were based on samples collected between May and September. Therefore, the computation of euphausiid consumption by pollock relative to the size of the euphausiid standing stock \( C \) was based on the May–September time period (5 months or ca. 150 day) in each survey year:

\[ C = (C_d / B_e) \times 150 \text{d} \]

3. Results

3.1. Quality control and verification of acoustic backscatter classification

Over all survey years, \( Z_{euph} \) for acoustic survey transects averaged 0.91 (SD 0.16) (Fig. 4), indicating that backscatter classified as euphausiids closely matched the reference frequency response reported by De Robertis et al. (2010). The performance of the method appears relatively consistent, although \( Z_{euph} \) in 2004 was noticeably higher than the mean of other survey years (by ca. 0.2 SD). We do not know the reason for this difference, but backscatter classified as euphausiids in that year nevertheless had a frequency response that was on average within 1.15 (SD 0.10) standard deviations of the reference set. There was no spatial pattern in \( Z_{euph} \) among transects (not shown), indicating spatial as well as temporal consistency of classification. This level of classification performance is comparable to that shown by De Robertis et al. (2010) for Bering Sea pollock using the same acoustic data set.

Since Methot samples collected between 2004 and 2007 were used to develop the frequency classification reference set (De Robertis et al., 2010), only Methot tow catches collected in 2008 and 2009 \((n=38)\) were used here to verify classification of euphausiid backscatter, providing an out-of-sample comparison. The proportion of catch comprising euphausiids and large copepods in these Methot samples averaged 0.94 (SD 0.06) by number. Other organisms such as chaetognaths, small gelatinous zooplankton, and amphipods (listed in order of their relative abundance in the samples) were not encountered consistently in these Methot tow catches, and represented a negligible fraction on average (0.06 by number) of the total catch. Of the euphausiid and copepod portion, euphausiids averaged 0.85 (SD 0.16) by number and 0.98 (SD 0.04) on a biomass basis (Fig. 5A). The biomass of euphausiids and copepods were estimated using published length-weight regressions (Harvey et al., 2012; Kobari et al., 2003) and observed lengths; in 2008 and 2009, the average length of euphausiids was 18.6 mm (SD 2.1), and the average copepod length was 7.7 mm (SD 0.9). Small organisms with lengths less than about 10 mm are probably underestimated by the Methot trawl. However, the relatively high densities of euphausiids, their larger size and biomass per individual relative to the next most common organism in the catches (copepods), and their exponentially stronger \( p_{w} \) compared to the largest copepods (one 18 mm euphausiid as modeled here is likely a 10^2-fold stronger acoustic target than a Neocalanus sp. copepod 8 mm in body length; Matsuura et al., 2009) support the contention that most backscatter in these layers is dominated by scattering from euphausiids.

Based on Eq. (1) and its underlying assumptions, we expected a positive and directly proportional relationship between euphausiid \( S_e \) at 120 kHz and the density of euphausiids captured by the Methot trawl, though we anticipated that the relationship would have a significant amount of scatter. As is often done in such cases (e.g., Warren and Wiebe, 2008), logarithmic forms of these quantities were used to improve the homogeneity of variance and linearity of the data set before statistical evaluation; we used \( S_e \) and \( 10 \times \log_{10} (\text{euphausiids m}^{-3}) \) and expected a slope of approximately 1 (Fig. 5B). The observed correlation was positive and statistically significant \((r^2=0.49, p<0.001, n=38)\). A functional regression (Ricker, 1973) of log-transformed euphausiid density on \( S_e \) was also performed, and approximate 95% confidence bounds on the slope of this regression \( (t_{0.05/2}=2.03, \text{ slope}=0.78 \pm 0.21, \text{ df}=36) \) narrowly failed to include 1. When a single, highly influential datum obtained from a Methot tow on a relatively weak and patchy euphausiid layer (Fig. 5B) was excluded and the correlation and regression were recomputed, the correlation coefficient was reduced but remained significant \((r^2=0.32, p<0.001, n=37)\) and the slope value changed to 0.97, indicating the 10th, 25th, 50th (median), 75th, and 90th percentiles of the observations.

Fig. 4. Boxplots of transect mean \( Z_{euph} \), for each survey year, indicating the 10th, 25th, 50th (median), 75th, and 90th percentiles of the observations.
with the hypothesized slope of 1 well within the recomputed 95% confidence bounds \((t_{0.05/2} = 2.03, \text{slope} = 0.97 \pm 0.32, \text{df} = 35)\). These results are consistent with the contention that despite substantial variance in the relationship, volume backscattering attributed to euphausiids is directly proportional to euphausiid density in Methot trawl catches, particularly since factors such as variation in euphausiid size, material properties and orientation, and variable catchability of euphausiids by the Methot trawl are not accounted for.

3.2. Target strength model and biomass computation

DWBA model runs indicated that euphausiid TS varies by a factor of \(40 \text{ dB} \) across the range of euphausiid lengths observed in Methot tows 2004–2010. The DWBA model was parameterized as described in Table 1. The three curves indicate high (dark dotted line), medium (dark solid line), and low (light dotted line) \(\sigma_{bs}\) scenarios.

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lengths were not very different between these areas. We will interpret results from the medium \(\sigma_{bs}\) scenario, which we consider the most reasonable estimate, but will occasionally refer to high and low \(\sigma_{bs}\) scenarios in discussion of possible bias in biomass results (note that the highest \(\sigma_{bs}\) scenario will produce the lowest estimate of euphausiid biomass; see Eq. (1)). Uncertainty due to sampling variability (error bars in Fig. 7) is much smaller than potential bias due to \(\sigma_{bs}\).

3.3. Spatial and temporal patterns in euphausiid and pollock biomass

Euphausiid biomass (kg) summed across length, species, and stratum in each survey year increased more than 3-fold between 2004 and 2009, before decreasing by approximately 20% in summer
2010 (Fig. 7). The sum of pollock biomass in both acoustic and bottom trawl surveys declined by ca. 50% between 2004 and 2009, before nearly doubling from 2009 to 2010. Pollock and euphausiid survey time series were inversely correlated ($r^2 = 0.54$). The pollock stock assessment time series (Fig. 7) is an estimate of biomass for ages 1–7 in January using a mean annual weight at age, and incorporates data from both surveys as well as fishery landings and fishery observer data, while both acoustic and bottom trawl pollock surveys take place in summer and each has a different age- and size-selectivity. Thus, the survey and model time series are not expected to show identical patterns (Ianelli et al., 2001, 2010). Nevertheless, the general temporal patterns in both survey data and model results are the same: pollock biomass declined while euphausiid standing stock increased, and when pollock biomass rebounded to near 2004 levels by 2010, euphausiid standing stock dropped.

Euphausiids were present throughout the acoustic survey area (Fig. 8), but their biomass density was usually highest in the southeastern portion of the shelf. Both acoustic and bottom trawl surveys showed that pollock biomass density was usually highest in the northwestern part of the shelf. Pollock biomass appeared to have a negative spatial relationship with euphausiid biomass. By comparing the covariance at each station between euphausiid biomass and pollock biomass for six annual summer surveys between 2004 and 2010 (Fig. 9), it is apparent that there are large areas of negative covariance between euphausiids and pollock, though this is not true in every location. Overall, biomasses of predator and prey appear to have a negative relationship in both space and time.

3.4. Estimation of predation impact by pollock on euphausiids

Although we were not able to compare production rates of pollock and euphausiids to evaluate predation impact, biomass comparisons are probably reasonable since both species have only a single generation per year (Ianelli et al., 2010; Smith, 1991), and the survey biomass estimates are done in summer after both species have reproduced. Calculations using Eqs. (4) and (5) indicated that the fraction of euphausiid standing stock consumed by pollock between May and September varied from a high of 0.38 (in 2004) to a low of 0.06 (in 2009), using the medium $\sigma_{bs}$ scenario for euphausiid biomass; corresponding ranges for high and low $\sigma_{bs}$ scenarios, respectively, were 0.87–0.14 and 0.10–0.02 (Table 2). Despite the large range in uncertainty, these estimates indicate that feeding by a single important predator population between May and September (5 months) could have consumed a measurable and substantial fraction of the euphausiid standing stock.

4. Discussion

4.1. Acoustic estimates of euphausiid biomass on the Bering Sea shelf

The acoustic estimates of euphausiid distribution and biomass presented here are an important new source of information about the distribution, abundance, and role of these animals in the Bering Sea ecosystem, augmenting the relatively small body of work that already exists on this topic (Coyle and Pinchuk, 2002; Coyle et al., 2008; Smith, 1991; Swartzman et al., 2002). In terms of scope and potential for long term monitoring of this key ecosystem component, no comparable time series exists for the Bering Sea, and the observations are derived from existing monitoring surveys for pollock at a relatively modest additional cost of ship and sample processing time. These data are beginning to inform pollock stock assessment and management (Ianelli et al., 2010; Zador and Gaichas, 2010) and contribute to an improved understanding of patterns in pollock recruitment (Hunt et al., 2011).

4.2. Top-down control of euphausiids (prey) by pollock (predator)

Although top-down control of crustacean zooplankton by fish in lakes is well-documented (e.g., Brooks and Dodson, 1965; Carpenter and Kitchell, 1993; Gliwicz, 1986), the relative importance of fish predation for controlling crustacean zooplankton populations in marine systems remains an open question (Dalpadado and Skjoldal, 1996; Mullin and Conversi, 1988; Reid et al., 2000; Robinson, 2000; Stevick et al., 2008; Wilson et al., 2009; Worm and Myers, 2003). In the Bering Sea, it has been proposed that bottom-up forcing through climate, spring water temperatures, and sea ice are an important control on large
copepods (Baier and Napp, 2003; Coyle et al., 2011) and perhaps euphausiids (Coyle et al., 2008, 2011; Hunt et al., 2008) — cold, icy springs are thought to be favorable, though the mechanism has not been demonstrated. The time period of 2004–2010 is particularly interesting in terms of bottom-up forcing of euphausiids by ocean conditions. 2004 was a relatively warm year (Stabeno et al., 2012) in which the summertime Bering Sea shelf was relatively depauperate of euphausiids and large copepods (Coyle et al., 2008; Hunt et al., 2008). In contrast, very cold conditions have prevailed since 2006 (Stabeno et al., 2012), and increases in the abundance of both large copepods and euphausiids during that time have been documented (this study; Coyle et al., 2011; Hunt et al., 2011). These observations are consistent with bottom-up forcing of large crustacean zooplankton stocks and favorable conditions for large copepods and euphausiids in cold years. However, the decrease of euphausiid biomass in 2010, another cold, icy spring in the Bering Sea, does not fit this pattern.

We show that in addition to variation in spring ice cover and water temperatures, another important factor changed over the 2004–2010 time period: the standing stock of pollock. Pollock is an enormous predatory force in the Bering Sea (Aydin and Mueter, 2007; Springer, 1992). Its recruitment may also be tied to cold, icy conditions like those experienced in recent springs and summers (Hunt et al., 2011). The increase of euphausiid biomass coincided with decreasing predation as pollock standing stock declined after 2004. Though it is not conclusive, following Dalpadado and Skjoldal (1996) and Worm and Myers (2003) we contend that such a pattern is consistent with the hypothesis of top-down control through predation (Aydin and Mueter, 2007; Smith, 1991; Springer, 1992). In particular, the 2010 observations support the notion that top-down forcing is important in spite of potentially

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**Table 2**

Estimation of predation impact on euphausiids by pollock. Table parameters are as follows: $B_p$ is the biomass of pollock in the area covered by both surveys, $R_d$ is the fraction of body weight in prey that pollock consumes per day, $F_e$ is the fraction of euphausiids in pollock diet, $C_d$ is the biomass of euphausiids consumed per day by pollock, $B_e$ is the survey estimate of euphausiid biomass, and $C$ is the fraction of euphausiid standing stock consumed by pollock from May to September (150 d).

<table>
<thead>
<tr>
<th></th>
<th>2004</th>
<th>2006</th>
<th>2007</th>
<th>2008</th>
<th>2009</th>
<th>2010</th>
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</thead>
<tbody>
<tr>
<td>$B_p$</td>
<td>$6.5 \times 10^9$</td>
<td>$4.3 \times 10^9$</td>
<td>$5.8 \times 10^9$</td>
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<td>0.02</td>
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<tr>
<td>$F_e$</td>
<td>0.53</td>
<td>0.53</td>
<td>0.53</td>
<td>0.53</td>
<td>0.53</td>
<td>0.53</td>
</tr>
<tr>
<td>$C_d$</td>
<td>$6.9 \times 10^7$</td>
<td>$4.6 \times 10^7$</td>
<td>$6.2 \times 10^7$</td>
<td>$4.1 \times 10^7$</td>
<td>$3.3 \times 10^7$</td>
<td>$6.0 \times 10^7$</td>
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<tr>
<td>$B_{e, low}$</td>
<td>$1.2 \times 10^{10}$</td>
<td>$2.2 \times 10^{10}$</td>
<td>$3.0 \times 10^{10}$</td>
<td>$3.3 \times 10^{10}$</td>
<td>$3.6 \times 10^{10}$</td>
<td>$2.9 \times 10^{10}$</td>
</tr>
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<td>$B_{e, med}$</td>
<td>$2.7 \times 10^{10}$</td>
<td>$5.1 \times 10^{10}$</td>
<td>$6.8 \times 10^{10}$</td>
<td>$7.6 \times 10^{10}$</td>
<td>$8.2 \times 10^{10}$</td>
<td>$6.6 \times 10^{10}$</td>
</tr>
<tr>
<td>$B_{e, high}$</td>
<td>$1.1 \times 10^{11}$</td>
<td>$2.0 \times 10^{11}$</td>
<td>$2.7 \times 10^{11}$</td>
<td>$3.0 \times 10^{11}$</td>
<td>$3.3 \times 10^{11}$</td>
<td>$2.6 \times 10^{11}$</td>
</tr>
<tr>
<td>$C_{low}$</td>
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<td>0.31</td>
<td>0.19</td>
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<td>0.31</td>
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<tr>
<td>$C_{med}$</td>
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<td>0.08</td>
<td>0.06</td>
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<tr>
<td>$C_{high}$</td>
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<td>0.03</td>
<td>0.02</td>
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</tr>
</tbody>
</table>

*a All biomass values are in kg wet weight.

*b Low, med, and high euphausiid biomass estimates ($B_{e}$) and corresponding fractions consumed by pollock relative to euphausiid standing stock ($C$) correspond to high, medium, and low $\sigma_{so}$ scenarios, respectively. See Eq. (1).
favorable ocean conditions for euphausiids: as the pollock stock climbed again in 2010 toward stock levels observed in the early 2000s, its predatory influence increased proportionately, which could explain the drop in euphausiid standing stock in 2010 despite continued cold conditions. The negative spatial association between euphausiid and pollock standing stocks would also be consistent with top-down forcing due to fish predation (Genin et al., 1988; Koslow, 1981); certainly, current hypotheses of direct bottom-up forcing of euphausiids in the Bering Sea do not offer an easy explanation for these spatial patterns.

The summer surveys described here are two-month snapshots that may confound spatial and temporal variability, but they do take place at a consistent point in the year, subsequent to reproduction of euphausiids and inshore movement by pollock for feeding (Smith, 1991; Kotwicki et al., 2005). Our euphausiid length data do not suggest that some of our surveys were ‘early’ or ‘late’ in terms of euphausiid reproduction. It is possible that bottom-up effects (forcing of pollock distribution by physical environmental conditions) could influence top-down processes (predation impact on euphausiids by pollock). Changes in pollock distribution during non-summer months are not completely understood, but migration and movement of pollock throughout the year appears to be limited by physical conditions such as water temperature and sea ice (De Roberts and Cokelet, 2012; Kotwicki et al., 2005) which could mediate the impact of pollock predation upon euphausiids by changing the temporal and spatial overlap of predator and prey.

The calculations presented here suggest that particularly at high stock levels, predation by pollock is large enough to make a substantial impact, though it is not clear whether this alone could control the standing stock of euphausiids. Many other animals prey upon euphausiids as well (Aydin and Mueter, 2007), and pollock feed on euphausiids throughout most of the year, not just from May through September (Dwyer et al., 1987; Smith, 1981), so Eq. (5) is probably a conservative estimate of the total amount of euphausiid standing stock removed annually. At the same time, some unknown amount of euphausiid biomass is inshore of our area of comparison (Coyle and Pinchuk, 2002), while the pollock biomass on the inner shelf appears to be relatively small (Fig. 8). If the amount of euphausiid biomass on the inner shelf is very large compared to the standing stock estimated here, it would reduce the apparent impact of pollock predation in our calculations. It is worth noting that ecosystem modeling has independently suggested the possibility of top-down control of zooplankton by pollock predation in the Bering Sea (Aydin and Mueter, 2007; Springer, 1992). Springer (1992) claimed very close coupling between pollock and zooplankton; his estimate of annual zooplankton consumption by pollock was 1.7 × 10¹² g C yr⁻¹, which is of the same order of magnitude as our acoustic euphausiid standing stock estimates for the entire acoustic survey area expressed in terms of carbon (1.1 × 10¹³ g C, using the med σbs scenario).

Order of magnitude (or greater) discrepancies between acoustic and net capture estimates of euphausiid density are the rule in the literature (Coyle, 2000; Coyle and Pinchuk, 2002; Warren and Wiebe, 2008), and our data are no exception. The mean density of euphausiids in our acoustic data set was about 30 m⁻³ using the med σbs scenario, while our Methot net capture density estimates averaged about 4 m⁻³; a euphausiid biomass estimate derived from any net capture data set would almost certainly be much lower than what we estimated acoustically. This discrepancy could be explained by a systematic low bias to modeled TS estimates (which inflates acoustic estimates of euphausiid density); though such models have been experimentally validated (Demer and Conti, 2003; McGehee et al., 1998), considerable uncertainty in model predictions still exists because of the difficulty in correctly parameterizing the models in terms of material properties and orientation to reproduce in situ TS (Chu et al., 2000; Smith et al., 2010; Stanton and Chu, 2000). Net avoidance by euphausiids could also explain the discrepancy between net capture and acoustic estimates of density (Coyle, 2000; Everson and Bone, 1986; Smith, 1991; Wiebe et al., 1982). The size of this effect is difficult to measure directly (Clutter and Anraku, 1968); however, artificial lights have been shown to increase net estimates of euphausiid density by a factor of 2–20 fold, implying that the effect of avoidance could be of that magnitude (Sameoto et al., 1993; Wiebe et al., 2004). We currently lack the data to make a conclusive determination of the source of this discrepancy, but additional measurements of the material properties of euphausiids, their in situ orientation during surveys, and further experimental validation of the application of TS model estimates would help answer this question. Until more is known, acoustic and net capture estimates might be considered upper and lower bounds on euphausiid density, respectively (Warren and Wiebe, 2008).

The conclusions drawn here are necessarily tentative, given the simplified nature of the calculations (for example, variation in pollock diet within years, among years, and among predator size groups was not specifically accounted for) and the potentially wide uncertainty in euphausiid standing stock estimates. Yet, the calculations illustrate that the impact of pollock predation on euphausiid biomass could be substantial and explain in part the negative association between pollock and euphausiid biomass that was observed spatially as well as among survey years. More detailed pollock diet data collected concurrently with the acoustic observations of euphausiid prey, as well as extensive observations of physical environmental conditions in the Bering Sea, is becoming available through research conducted as part of the BEST-BSIERP Ecosystem Partnership (http://bsierp.nprb.org/). These new observations will allow a better examination of both interannual and spatial variation in pollock predation rates in comparison to the available euphausiid prey field, and further evaluation of the interplay of predation and oceanographic conditions in controlling euphausiid standing stock.

5. Conclusions

Acoustic estimates of summertime euphausiid standing stock on the Bering Sea shelf derived from regular resource assessment surveys represent a valuable new source of information for fisheries and ecosystem management. Results show that euphausiid biomass increased between 2004 and 2009 while the pollock stock declined after a series of years with poor recruitment. Pollock and euphausiid time series appear closely coupled, however; as pollock biomass climbed again toward 2004 stock levels in 2010, euphausiid biomass dropped by about 20%. Calculations of the approximate predation impact by pollock on euphausiids suggest this top-down effect could be significant, particularly when pollock biomass is high. While cold, icky springs and cool summers also coincided with the period of increasing euphausiid standing stock, the negative association between pollock and euphausiid biomass in both space and time is more consistent with ‘top-down’ than ‘bottom-up’ control. Physical environmental conditions probably still play a role in this trophic interaction, perhaps by mediating overlap between predator and prey throughout the year.

Acknowledgments

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