Title: Summer diet composition of walleye pollock and predator-prey relationships with copepods and euphausiids in the eastern Bering Sea, 1987-2011

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ABSTRACT – The composition of walleye pollock diets from the eastern Bering Sea continental shelf was determined from 25 years of sampling during summer surveys from 1987 through 2011. Substantial differences in the stomach contents of walleye pollock were found among the sizes and geographic strata that correspond to geographic distribution of the prey. With increasing pollock size, copepods decreased in importance in middle and outer shelf areas while mysids decreased in importance in the inner shelf. Euphausiids increased in importance with increasing pollock size in southeastern areas of the shelf, and fishes and shrimp increased in importance with increasing pollock size in northeastern areas of the middle and outer shelf. The biomass-weighted average diet composition of eastern Bering Sea pollock in each year's survey indicated perennial but variable importance of euphausiids and copepods as prey. An index of partial fullness indicated an interannual pattern of below-average consumption of copepods by the surveyed pollock from 1993 to 2004, but during this period the amount of euphausiids consumed continued to fluctuate about a mean that was similar to years surveyed before and after that period. The summer feeding success, as indicated by average stomach fullness, of intermediate sizes of pollock appears to be closely related to the consumption of copepods (especially for pollock 30-39 cm fork length (FL)) and prey other than euphausiids (especially for pollock 40-49 cm FL). Length-specific predator-prey relationships with copepods and euphausiids correspond to patterns in pollock feeding migrations. Interannual trends in the biomass of copepods in the EBS are reflected most closely in the diet of 20-29 cm FL pollock, and trends in the biomass of euphausiids in the EBS are reflected most closely in the diet of the

largest pollock (60+ cm FL). Climate-mediated changes in the zooplankton community will likely have differential impacts across the demographic spectrum of pollock in the EBS.

1. INTRODUCTION

Walleye pollock (*Gadus chalcogrammus* – Coulson et al., 2006; hereafter referred to as pollock) has a central role in the eastern Bering Sea (EBS) food web. It is a key forage species for many intermediate and upper trophic level predators and is the dominant consumer within the EBS food web (Aydin and Mueter, 2007). Understanding the physical and ecological factors that influence pollock recruitment in the EBS is crucial to the overall understanding of energy flow within the EBS ecosystem (Aydin and Mueter, 2007). Fluctuations in pollock abundance may affect the abundance of other forage species, particularly euphausiids, through top-down predation pressure (Aydin and Mueter, 2007; Ressler et al., 2012). However, from a bottom-up perspective, water temperature was found to be a better predictor of localized euphausiid abundance than pollock biomass in the EBS (Ressler et al., 2014). The interplay between bottom-up and top-down processes (Hunt et al., 2002; Hunt et al., 2011) and data on zooplankton abundance are beginning to inform the assessment and management of EBS pollock (Zador and Gaichas, 2010; Ianelli et al., 2011; Siddon et al., 2013). This paper is a contribution to the Bering Sea Integrated Ecosystem Research Program (BSIERP), where collaborative research among multiple disciplines investigates the linkages and interactions in the EBS marine environment to predict future climate impacts (Wiese et al., 2012).

While sampling of pollock stomach contents has been widely distributed over the EBS shelf during annual summer surveys since 1987 (Boldt et al., 2012;

http://www.afsc.noaa.gov/REFM/REEM/DietData/dietmap.html), a consistently calculated time series of diet composition has not been published. Pollock diet composition is known to differ with pollock length and location in the EBS (Bailey and Dunn, 1979; Dwyer et al., 1987; Mito et al., 1999; Lang et al., 2000; 2003; 2005). The length composition of the EBS pollock stock changes over time (Ianelli et al., 2011), and the geographic distribution of the EBS pollock stock during surveys is affected by interannual differences in water temperature (Francis and Bailey, 1983; Kotwicki et al., 2005) and by strong year classes (Francis and Bailey, 1983; Ianelli et al., 2001). In addition, the sampling of pollock stomachs during the surveys varies in intensity and geographic distribution among years (Fig. 6 in Boldt et al., 2012; http://www.afsc.noaa.gov/REFM/REEM/DietData/dietmap.html). Accounting for these variations to present a consistently calculated time series of diet composition could provide insight into the dynamic interaction of pollock with the zooplankton community, including euphausiids, copepods, and amphipods (Lang et al., 2000; 2003; 2005; Napp et al., 2002; Aydin and Mueter, 2007; Boldt et al., 2012) inhabiting the EBS continental shelf.

In this paper, we describe the diet of pollock in the EBS and examine the predator-prey relationships with two important groups of zooplankton, copepods and euphausiids. We use 25 years (1987 – 2011) of stomach contents data to illustrate changes in diet composition with pollock length and geographic distribution over the EBS continental shelf. We then focus on the diet composition of the pollock assessed in annual bottom trawl surveys (BTS) of the EBS shelf. Length-specific characteristics of the feeding relationship with copepods and euphausiids were examined to consider how pollock food habits might respond to changes in the zooplankton community resulting from climate change.

2. METHODS

2.1 Surveys

Data used in this investigation were collected from 1987 through 2011 during summer bottom trawl surveys of the EBS continental shelf conducted by NOAA's Alaska Fisheries Science Center (AFSC). Bottom trawl surveys were generally conducted between the last week of May and the first week of August over a standard area of the EBS continental shelf (≤200 m depth) with standard stations located over a regular 20 × 20 nmi (37 × 37 km) grid (Fig. 1). The details of the survey design, sampling gear, and sampling methods are described by Lauth (2011) and Stauffer (2004). At each station, the biomass of pollock captured by the bottom trawl was calculated and a subsample was measured for length composition. Pollock catch per unit of effort (kg/hectare) was calculated based on the area swept by the trawl. Partitioning of survey biomass into six pollock length categories, described below, used annual length-weight relationships from 1999 through 2011, but due to data limitations, for the 1987 through 1998 period, the length-weight relationship used was the average from 1999 through 2011. Seven strata, roughly corresponding to historical patterns in groundfish distribution, bathymetric features, and oceanographic domains on the EBS shelf (Stauffer, 2004), were used to capture regional variation in pollock abundance and food habits (Fig. 1). The Inner Shelf (strata A and B), Middle Shelf (strata C, D and E), and Outer Shelf (strata F and G) are divided into a Southeastern (SE) region (strata B, E, and G) and a Northwestern (NW) region (strata A, C, D, and F) by a line approximately perpendicular to the major EBS shelf bathymetry (Fig. 1).

2.2 Stomach contents

Annually, a subset of pollock was selected for stomach content analyses during the summer bottom trawl surveys of 1987 through 2011. At opportunistically selected hauls, within a multispecies sampling scheme during each survey (Table 1), stomachs were collected from a subsample (≤ 20) of pollock in the catch. The length and sex of each individual was recorded, and the stomach was fixed in a 10% buffered formalin and seawater solution. Stomach samples were collected from a wide length-range of pollock, 6-90 cm FL, and the body weights of individual pollock were estimated from length-weight regression. In the laboratory, stomach contents were removed, separated into lowest practical taxonomic prey categories, and the weight (g) of each prey category was recorded. For the present analyses, prey were consolidated into the following 10 major prey categories that were at least 2% of the diet in at least 5 of the 25 years sampled: copepods, mysids, hyperiid amphipods, gammarid amphipods, euphausiids, shrimps, chaetognaths, larvaceans, fishes, and other prey. Representative detailed prey lists for 1993 through 2001 can be found in reports by Lang et al. (2003 and 2005). Distributional, behavioral and food habits differences are known to occur with increasing pollock length (Fig. 2; Bailey et al., 1999; Lang et al., 2003; 2005; Boldt et al., 2012), therefore prey composition was aggregated for six length categories; < 20, 20-29, 30-39, 40-49, 50-59, and 60+ cm fork length (FL). The weight of the stomach contents of these pollock more than doubles, on average, with every 10 cm increase in FL (Fig. 3), so the wider the length category used to summarize the stomach contents, the less representative the aggregate information becomes for the small end of that length-range. All empty stomachs were excluded from our analyses. The taxonomic composition by weight (%W) of the pollock stomach contents from a haul was calculated for each length category of pollock. To impart greater influence to locations where pollock fed more heavily, each sampled station was weighted by the station-average stomach fullness, as a percentage of body weight, to calculate the average diet composition within each stratum in each year. The average taxonomic composition of the stomach contents of each length category of pollock in each stratum was calculated for the 25 year period. The annual average diet composition of the EBS pollock stock was calculated for 1987-2011 by weighting the six length categories in the seven strata by the BTS estimated biomass of each. Similarly, the annual average stomach fullness (%bw) was also calculated for the EBS pollock stock by weighting the six length categories in the seven strata by the BTS estimated biomass of each.

In contrast to diet composition information, a partial fullness index for a prey type provides a better indicator of the relative consumption of that prey type among predator groups over time (Fahrig et al., 1993). Partial fullness considers the amount of a prey type consumed against the size of the predator, which is essentially scaling the overall stomach fullness of a predator by the percentage of a prey type in the diet. Annual average Partial Fullness index (PF) values were calculated for the EBS pollock stock by weighting the six length categories in the seven geographic strata by the BTS estimated biomass of each. Annual average PF values were calculated for the six length categories of the EBS pollock stock by weighting the seven geographic strata by the BTS estimated biomass of each.

2.3 Copepod and Euphausiid abundance

The consumption of copepods and euphausiids by each length category of pollock were compared to a time series of copepod abundance and a time series of euphausiid abundance. Summer zooplankton samples were collected in the SE region of the EBS by the Hokkaido

University research vessel T/S *Oshoru Maru* (Napp et al., 2002; Napp and Yamaguchi, 2010). We used the time series of zooplankton biomass estimates to evaluate temporal patterns in the PF of copepods in the diet of the six length categories of pollock from the Middle and Outer SE EBS Shelf. This time series is heavily influenced by copepod biomass (Napp et al., 2002) and is used in modeling applications as a proxy for copepod biomass over time (A. Yamaguchi, pers. comm.). We weighted the estimated Middle and Outer Shelf zooplankton densities by the area of each subregion for an index of zooplankton biomass.

Euphausiid biomass estimates have become available from recent AFSC hydroacoustic surveys of the EBS shelf (2004, 2006-2010) that have partial temporal and geographical overlap with the BTS (Ressler et al., 2012). These euphausiid biomass estimates may also include some hyperiid amphipods. Hyperiid amphipods are pelagic zooplankton similar in length to euphausiids (and thus can be detected with the same acoustic frequencies), they are important in the pollock diet during this time period, and they were caught using Methot tows (a net for capturing macrozooplankton; Methot, 1986) conducted during recent hydroacoustic surveys assessing euphausiid biomass (Ressler et al., 2012), particularly in the northern part of the survey area (P.H. Ressler, pers. comm.).

2.4 Statistical Analyses

The sequence of PF values for copepods and euphausiids in the diet of the EBS pollock stock were evaluated for serial randomness using the mean square successive differences test (Zar, 1984). The annual PF indices for copepods were below the 25 year average of 0.22 for 12 consecutive years (1993-2004), so the average index was calculated and plotted for copepods and euphausiids for three time periods; 1987-1992, 1993-2004, and 2005-2011, with the middle period being 12 years of consecutive below-average PF values for copepods.

The correlation between the annual average %W of copepods and euphausiids to the annual average stomach fullness (%bw) was examined for each length category of pollock and tested against the null hypothesis that $r = 0$ after arcsin transformation of the %W data (Zar, 1984).

The correlation between the zooplankton biomass estimates for the Middle and Outer SE EBS Shelf and the PF of copepods in the diet of the six length categories of pollock from the Middle and Outer SE EBS Shelf was evaluated after log-transformation of the biomass and PF data (Zar, 1984). The correlation between the euphausiid biomass estimates and the PF of euphausiids and hyperiid amphipods in the diet of the six length categories of pollock was evaluated after log-transformation of the biomass and PF data (Zar, 1984).

3. RESULTS

The diet composition (%W) of pollock in the EBS varied by length category and by stratum (Fig. 4). Stomachs of larger pollock contained fewer copepods and/or mysids and more euphausiids, hyperiid amphipods, shrimp and/or fishes relative to smaller pollock. Length based differences in %W varied by stratum. The overall %W of copepods was greater in Outer Shelf strata (Fig. 4; F and G) while mysids were relatively more important in Inner Shelf strata (Fig. 4; A and B) for smaller pollock. Shrimp, hyperiids and fishes were generally more important components of the stomach contents in NW region (Fig. 4; A, C, D and F), and euphausiids were more important in the SE region (Fig. 4; B, E and G) for larger pollock. Predation on fishes increased with increasing pollock length, especially in the NW Outer shelf where they were the dominant prey type by %W for the largest pollock (Fig. 4; F).

The annual average diet composition of the EBS pollock stock for each of the 1987 through 2011 BTSs is shown in Table 2. Euphausiids (40%W) and copepods (27%W) were the highest percentage of the stomach contents when averaging all years, ranging annually from 23% to 65% for euphausiids and from 8% to 43% for copepods. Euphausiids ranked either first or second in overall importance in 24 out of the 25 years of our data, while copepods did so in 21 out of 25 years (Table 2). The consistent dominance of euphausiids (> 45%W) in the diet from 1994 through 2003 (except for 1999, which was an anomalously cold year; Lauth, 2011), coincides with generally lower stomach fullness values relative to earlier and later periods. Fishes was the second most important prey in 4 of the 25 years sampled, and hyperiid amphipods was not a particularly important diet component, except in 2002 and 2008-2011, but it was the most important prey in 2010 (Table 2).

Partial fullness is an indicator of the relative consumption of each prey type (Fahrig et al., 1993), and annual PF values were plotted for the five most important prey (Fig. 5). The null hypothesis that the PF values for copepods were serially random was rejected ($C = 0.49$, $P < 0.005$), but the PF values for euphausiids appear to be serially random ($C = -0.25$, $P > 0.9$). The PF averages for the three time periods (1987-1992, 1993-2004, and 2005-2011) illustrate more similarity for PF of euphausiids than for copepods, with the PF values of copepods being more similar to the PF values of euphausiids in the 1987-1992 and 2005-2011 time periods. The pattern in fishes (mostly cannibalism of juvenile pollock) is described thoroughly in Boldt et al. (2012) and is attributed to varying spatial overlap of adult and juvenile pollock.

The relationship between the annual %bw and the annual %W of copepods and of euphausiids in the diet varied by pollock length (Fig. 6). The significant positive relationship ($r = 0.44$, $P < 0.05$) between %bw and copepod %W in the diet of 30-39 cm pollock indicates interannually higher stomach fullness was related to higher relative consumption of copepods. The significant negative relationship (r = -0.46, $P < 0.05$) between %bw and euphausiid %W in the diet of 40-49 cm pollock indicates that interannually lower stomach fullness was associated with a higher relative consumption of euphausiids (and, conversely, a lower relative consumption of other prey). In other words, years with higher relative amounts of euphausiids in the diet are related to years of overall lower stomach fullness.

Interannual changes in the biomass of copepods in the SE EBS and the biomass of euphausiids over the EBS shelf were tracked by the PF values in the diets of different sizes of pollock. Correlation between the estimated EBS zooplankton (mostly copepods) biomass and the PF values of copepods was significant (r = 0.57, $P < 0.005$) for the 20-29 cm FL pollock in the SE region (Fig. 7). Correlation between the increase in estimated EBS euphausiid biomass and the PF values of euphausiids was significant (r = 0.89, $P = 0.02$) for the largest length category of pollock in this short time series (Fig. 8).

4. DISCUSSION

Variations in the observed diet reflect the spatial and temporal variation in prey distribution and abundance, as well as the interannual variations in pollock distribution and demography. Substantial differences in the pollock diet were found among the sizes and geographic strata examined, and the relative importance of major prey categories varied interannually in the diet of the surveyed EBS pollock. The effects of interannual and geographic variability in the intensity of stomach sampling were removed as much as practical by summarizing diet information by distinct predator length categories and geographic strata, then weighting each length-stratum by the surveyed pollock biomass in each. This standardized, consistent representation of the main prey types of EBS pollock caught by the annual summer BTS is concurrent with other biological and physical information collected during this survey (e.g. – Buckley et al., 2009; Zador and Gaichas, 2010; Boldt et al., 2012), and more consistently represents the importance of each prey type to the surveyed EBS pollock than other published values. Consequently, the diet information presented here will be biased toward larger, more benthic individuals from the EBS pollock stock because this bias is inherent to the BTS (Kotwicki et al., 2005). When diet information from the midwater component of the EBS pollock stock, as assessed by the AFSC hydroacoustic survey, is incorporated, copepods increase and euphausiids decrease in relative importance in the summer diet (Buckley et al., in prep.).

4.1 Ontogenetic and geographic variation in the pollock diet

The long-term average diet of pollock sampled during summer BTSs of the EBS differed among the pollock length categories and major geographical strata. The patterns we found in ontogenetic and geographic variation in pollock diets are generally in agreement with other studies. For example, Dwyer et al. (1987) show a shift, with increasing pollock length, in the dominant prey (%W), from copepods, to euphausiids, then to cannibalized pollock in the NW region, and a dietary increase in euphausiids in the SE region. In this study, the 25-year aggregate diet shows similar patterns, but we also illustrate differences among the depth zones. The importance of fish (which were primarily cannibalized pollock; Boldt et al., 2012) increased the most with predator length in the NW Outer Shelf (Fig. 4; F), and mysids rather than copepods were eaten on the Inner Shelf (Fig. 4; A and B). Mysids are known to be an important component of the macrozooplankton community in shallower waters of the SE and NW regions of the EBS continental shelf (Coyle and Pinchuk, 2002; De Robertis and Cokelet, 2012). Euphausiids were generally more important in the diet of pollock in the SE than the NW region

(Fig. 4) and this corresponds to the distribution of euphausiid biomass being higher over the SE than the NW region of the EBS shelf (Ressler et al., 2012).

The length-specific relationships between stomach fullness and prey composition were in accord with length-specific migratory behavior and prey distribution. All the pollock diet data used in this study were collected during the EBS BTS which occurs during a portion of the summer feeding migration (Kotwicki et al., 2005). This migration moves away from spawning areas, mostly near the outer SE continental shelf, in a generally northerly and northwesterly direction (Kotwicki et al., 2005; De Robertis and Cokelet, 2012). The feeding migration of intermediate sizes of pollock (30-50 cm FL) was found to have greater amplitude than smaller and larger pollock over the EBS shelf (Kotwicki et al., 2005). Consequently, these fish would be migrating away from areas of high euphausiid abundance in the SE region (Ressler et al., 2012) and toward areas of possibly higher copepod abundance in the NW region (Kotwicki et al., 2005). In contrast, few larger pollock (>50 cm FL) undergo a feeding migration (Kotwicki et al., 2005), and may thus remain in areas of higher euphausiid abundance (Ressler et al., 2012) during the summer.

These length-specific dietary and migratory patterns, may also be related to ontogenetic changes in gill raker spacing. An allometric increase in gill raker spacing with fish size is a common feature among zooplanktivores, including rainbow trout (*Oncorhynchus mykiss*), Pacific sardine (*Sardinops sagax*) and northern anchovy (*Engaulis mordax*) (Budy et al., 2005; Rykaczewski, 2009). Generally, the closer the gill raker spacing, the smaller the prey that can be retained by the zooplanktivore, especially during filter feeding (Budy et al., 2005; Rykaczewski, 2009). The observed changes in the composition of the stomach contents with size, the relationship between copepod %W and stomach fullness, and the amplitude of summer feeding migrations by EBS pollock, suggests that the gill raker spacing of larger pollock may contribute to a reduction in the efficiency of retaining large copepods, and we hypothesize this may begin when pollock are near 45-50 cm FL. A description of the allometry of gill raker spacing in EBS pollock would provide a better understanding of the predatory relationship of pollock with the zooplankton community in the EBS.

4.2 Copepods and euphausiids as prey of pollock

Over the 25 year period examined, euphausiids and copepods were the most important prey of the EBS pollock stock sampled by the BTS. However, patterns in the data indicate that pollock's predator-prey relationship with euphausiids (Hunt et al., this volume) differs from that with copepods and is very size dependent. During a period from the mid-1990s to the mid-2000s, euphausiids were the dominant zooplankton component in the diet of the EBS pollock stock, but annual PF values suggest this may result from lower copepod consumption rather than higher euphausiid consumption. Related to this, the average stomach fullness each year of intermediate sizes of pollock was higher when the proportion of copepods was higher or when the proportion of euphausiids was lower in the diet.

If average stomach fullness can be used as a proxy for feeding success, then copepod consumption seems strongly related to feeding success for intermediate lengths of pollock. Stomach fullness is influenced by the frequency and intensity of foraging and the rate of digestion and evacuation of the stomach contents. Complete stomach evacuation may take several days for EBS pollock (Dwyer et al., 1987), so stomach samples may contain prey from multiple days of feeding, albeit at various stages of digestion. Each year, stomach samples are collected throughout daylight hours, and any small bias this may cause relative to diel feeding periodicity would be consistent among years. The interannual trend in the relative composition of euphausiids and copepods in pollock diets appears to be driven largely by the consumption of copepods. The %bw each year tended to be higher when the proportion of copepods was higher in diets of 30-39 cm FL pollock. This suggests that these pollock generally feed most successfully in years of higher copepod production or availability. From the late 1990's to the late 2000's, copepod biomass over the Middle and Outer EBS shelf dropped to very low levels then rebounded (Napp and Yamaguchi, 2010; Stabeno et al., 2012) and the copepod PF values of 20-29 cm FL pollock followed this pattern. Given these length-specific relationships in the dietary importance of copepods to pollock, the extended period of euphausiid dominance in the diet from 1994 to 2003, as indicated by the %W composition, seems to be influenced more by lower availability of copepods than by exceptionally high availability of euphausiids, as indicated by the annual PF values.

On the other hand, euphausiids may provide a more consistent food source than other potential prey for the EBS pollock stock. The long-term average euphausiid PF values remained relatively consistent through periods of higher and lower copepod PF values over the 25-year period. Although euphausiids were one of the most important prey every year, stomach fullness tended to be lower when euphausiids comprised a higher portion of the diet for intermediate lengths (40-49 cm FL) of pollock. For these pollock, euphausiids became more important in the annual average diet when feeding success (based on stomach fullness) was the lowest. These interannual patterns appear similar to the role of euphausiids as a more consistent, baseline food source in seasons when other prey becomes less available (Dwyer et al., 1987; Mito et al., 1999; Aydin and Mueter, 2007). However, the largest pollock had euphausiid PF values that tracked the increasing EBS euphausiid biomass in the mid- to late-2000's (Ressler et al., 2012) suggesting that pollock ≥ 60 cm FL have a much closer feeding relationship with euphausiids than other sizes of pollock.

The estimation of diet composition without appropriate weighting of distinct length and geographic segments may lead to biased conclusions regarding predation pressure on euphausiids and copepods by the EBS pollock stock. Our results indicate that recent estimates of the impact the pollock stock might have on euphausiid biomass in the EBS (Ressler et al., 2012) should be adjusted downward, and conversely, the predation pressure imposed on EBS copepod biomass during the summer by the pollock stock may be greater and more variable than is generally appreciated. The values used for the euphausiid fraction of the diet (37-70 %W from Lang et al., 2005), when predation pressure on euphausiids was estimated (Ressler et al., 2012), may be too high to accurately represent the diet of the EBS pollock stock, especially when the stock biomass is dominated by younger fish (Ianelli et al., 2011). We found a lower fraction of euphausiids in the diet (29-55 %W) for the same period, 1997-2001, which occurred during a longer period of generally higher proportions of euphausiids in the pollock diet. During the years of the predation pressure calculations reported by Ressler et al. (2012) (2004, 2006-2010), we found even lower values of 24-40 %W euphausiids in the pollock diet. Our annual summer diet composition estimates for EBS pollock differ from those of Lang et al. (2003, 2005) because our samples were collected only during the EBS BTS (largely in June and July), while they included all samples collected in May through September from a variety of surveys and fisheries operations, and their weighting of samples was different from ours. Interannual differences in pollock predation pressure on the copepod biomass in the EBS may be greater than indicated solely by the interannual changes in our estimates of copepod %W because the sizes of pollock that consume a high percentage of copepods (Fig. 4) have a higher estimated summer daily ration than larger pollock (Buckley and Livingston, 1996). In addition, the catchability of these sizes of pollock by the BTS is lower than that of the larger sizes of pollock (Kotwicki et al., 2005), so the predation impact of very large year classes of pollock, when they are young, is not fully incorporated by our size-specific BTS biomass weightings. Spatially explicit and size-specific models can incorporate variations in year class strength, water temperature and consumption rates by pollock to assess predation pressure and the extent of top-down pressure on euphausiids and copepods in the EBS (Ortiz et al., this volume).

4.3 Diet of pollock in relation to climate change

Interannual variation in the diet of EBS pollock seems to reflect some of the changes in the zooplankton community structure mediated by the recent changes in the EBS environment. Prior to the early 2000s, interannual variability in spring sea-ice extent, summer bottom temperatures, and summer zooplankton biomass was typical (Napp et al., 2002; Lauth, 2011; Stabeno et al., 2012; Eisner et al., 2014), but a series of warm years in the early 2000s followed by a series of cold years in the late 2000s resulted in distinct differences in zooplankton biomass and community composition between these two periods (Ressler et al., 2012; Stabeno et al., 2012; Pinchuk et al., 2013; Eisner et al., 2014). Warm years were characterized by low zooplankton biomass, especially a decrease in larger copepod species and euphausiids, and the following colder years were characterized by increasing zooplankton biomass, particulary larger copepod species, euphausiids and hyperiid amphipods (Ressler et al., 2012; Stabeno et al., 2012; Pinchuk et al., 2013; Eisner et al., 2014; Hunt et al., this volume). During the warmer years, copepod PF values in the diet of smaller and intermediate sized pollock in the SE region of the EBS appear to trend downward with the biomass of zooplankton, but subsequent increases in PF values are extremely variable relative to the changes in zooplankton biomass as determined by net samples

(Fig. 7). During the colder years, euphausiid PF values in the diet of the largest pollock in the EBS appear to trend upward with the biomass of euphausiids (Fig. 8). The rapid increase in the population of the hyperiid amphipod, *Themisto libellula*, during the colder years (Volkov, 2012; Pinchuk et al., 2013) was also reflected in the diet of the EBS pollock stock. Hyperiid amphipods were not important in the diet of EBS pollock in most years, but their importance in the diet increased from low levels in 2007 to become the dominant prey in 2010 (Table 2; Fig. 5). The majority of these amphipods were likely *T. libellula* based on the locations and water temperatures where they were consumed (Wing, 1976; Dalpadado et al., 2001). Based on their decrease in the pollock diet in 2011, a precipitous decline in the abundance of hyperiid amphipods in the EBS survey area may have occurred when bottom temperatures returned to average.

4.4 Pollock as samplers of zooplankton

The ability of marine predators to integrate characteristics of prey populations over time and space may be better than conventional sampling methods (Fahrig et al., 1993; Ainley et al., 1996; Boldt et al., 2012). At large spatial or temporal scales, the opportunistic component of pollock feeding, within a suite of acceptable prey, can provide insight into the variation of the prey types in the environment (Boldt et al., 2012; Yamamura et al., 2013). Although prey selectivity by pollock has been identified (Lang et al., 2000), it was determined by comparison of the prey consumed by pollock and prey caught by nets, both of which are selective processes. Zooplankton sampling gear is prone to avoidance behavior by active prey types (Wiebe et al., 1982) or extrusion through the mesh of smaller prey types (Lang et al., 2000), and the timing and scaling of the sampling effort and the ability of the sampling gear to catch prey types with different patterns of dispersion (Underwood et al., 2004), relative to a predator's "sampling" capability, influence the conclusions about prey selectivity by a predator.   Marine resource surveys also have some element of selectivity (Kotwicki et al., 2005), but with consistent bias over time, a standardized survey provides a relative index for monitoring trends and is valuable to stock assessments (e.g. – Ianelli et al., 2011).

The utility of using stomach contents of EBS pollock to detect changes in the abundance of zooplankton appears promising, especially when specific length categories, having positive predator-prey relationships with the target prey, are considered. Successfully detecting changes in abundance requires use of a sampling tool that is sensitive to, and positively correlated to, changes in abundance. For euphausiids, our results indicate that the largest pollock (60+ cm FL) would be better suited than other sizes for this purpose due to their diet positively tracking increases in euphausiid biomass (Fig. 8). For copepods, our results indicate that 20-29 cm FL pollock may be better suited than other sizes to detect changes in copepod abundance because their consumption of copepods correlates with changes in copepod abundance in the SEBS shelf (Fig. 7). When the entire EBS shelf is considered, 30-39 cm FL pollock may also be useful in tracking copepod abundance because higher proportions of copepods in the diet are related to successful feeding (Fig. 6). Analyses of length-specific pollock feeding responses to conditions within subregions of the EBS shelf (Ortiz et al., 2012; Baker and Hollowed, 2014) may differ from the results we found for the EBS shelf as a whole (see also Hunt et al., this volume).

To the extent that understanding linkages between pollock and the zooplankton community in the EBS is a priority, modifications to stomach content analyses methods and zooplankton surveys should be incorporated into future research. Historically, the sampling of stomach contents in the EBS has largely been directed toward assessing predation mortality on early life stages of commercially important species and improving our understanding of energy flow through the ecosystem, thus the emphasis has not been on parsing the zooplankton prey beyond broad taxonomic levels in most years. Increasing the standard taxonomic resolution of the stomach contents of pollock would increase the clarity of the connections with the temporally and geographically dynamic zooplankton community in the EBS. The potential costs of implementing this, including potentially reducing the number of samples from pollock and/or other species, would need to be considered. Recent zooplankton surveys (Eisner et al., 2014) are geographically more extensive than in the past (Napp et al., 2002), however, the NW Outer Shelf remains virtually unsampled, and this stratum generally has very high pollock biomass during the summer (Ressler et al., 2012). In addition, the temporal mismatch between groundfish surveys (conducted mostly in June and July; Lauth, 2011) and zooplankton surveys (conducted from mid August to early October; Eisner et al., 2014) may hinder achieving strong conclusions about the dynamics of the predator-prey relationships during the pollock feeding migration.

4.5 Conclusions

Substantial differences in the stomach contents of walleye pollock, averaged from 25 years of sampling during the AFSC BTS, were observed among pollock length categories and among geographic strata of the EBS. These patterns are consistent with length-specific patterns in the summer feeding migration. The biomass-weighted average diet composition of the EBS pollock stock, as assessed by the BTS, indicated the perennial but variable importance of euphausiids and copepods over the 25-year period. However, the predator-prey relationship of pollock with euphausiids and copepods differs, and the summer feeding success of intermediate lengths of pollock appears to be related to the consumption of copepods (30-39 cm FL) and prey that are not euphausiids (40-49 cm FL). The summer diet of EBS pollock reflects climate-mediated changes in the zooplankton community, but different sizes of pollock reflect these changes to differing degrees. Comparisons to time series of copepods and euphausiids indicated that the diet of 20-29 cm FL pollock tracks copepod abundance and the diet of 60+ cm FL pollock may track euphausiid abundance most closely. Given the size-specific differences in predator-prey relationships of pollock with euphausiids and copepods, alterations in the zooplankton community that result from climate change will likely have differential impacts across the demographic spectrum of pollock in the EBS.

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Figures:

Fig. 1. Chart of the eastern Bering Sea continental shelf indicating the major strata (A – G) sampled annually by the Alaska Fisheries Science Center's bottom trawl survey and a typical hydroacoustic survey track-line.

Fig. 2. Spatial distribution of pollock by length category in the 1999 bottom trawl survey relative to bottom temperature during this was a very cold year.

Fig. 3. Weight of the stomach contents by length of pollock. The horizontal marker indicates the average weight of the stomach contents for each length indicated and the vertical bar represents the range of the second and third quartiles of the stomach contents weight with empty stomachs excluded.

Fig 4. Gravimetric composition (%W) of the stomach contents by pollock length categories (cm FL, below column) in each major stratum (A – G) of the eastern Bering Sea bottom trawl surveys, 1987-2011. The number of years each length category was sampled in each stratum is shown above each column.

Fig. 5. An index of partial fullness of major components in the diet of eastern Bering Sea pollock from 1987 through 2011. The average index for copepods (Avg cop) and euphausiids (Avg euph) are indicated for three periods; 1987-1992, 1993-2004, and 2005-2011.

Fig. 6. The trend in the average annual weight composition (%W) of copepods (a) and euphausiids (b) in the diet relative to the average annual stomach fullness (%bw) of each length category of pollock sampled by the eastern Bering Sea (EBS) bottom trawl survey, 1987-2011. Correlations that are significantly different from zero are indicated by an asterisk (* $P < 0.05$).

Fig. 7. Time series of zooplankton biomass from the Middle and Outer shelf of the southeastern Bering Sea (SEBS) shelf and the Partial Fullness (PF) values of copepods in the diets of five length categories of pollock from the Middle and Outer shelf of the southeastern Bering Sea. The six time series are shown relative to their average value to indicate the relative change over time. Correlations between the zooplankton biomass and the copepod PF values of each length category of pollock are presented (**$P < 0.005$), see Methods.

Fig. 8. Time series of euphausiid biomass from the hydroacoustic survey (Ressler et al., 2012) and the Partial Fullness (PF) values of euphausiids and hyperiid amphipods combined in the diets of six length categories of pollock from the bottom trawl survey. The seven time series are shown relative to their average values to indicate the relative change over time. Correlations that are significantly different from zero are indicated (*$P = 0.02$).

Tables:

Table 1. The number of hauls from which pollock stomach samples were collected by year of the eastern Bering Sea bottom trawl surveys.

Table 2. The annual average diet composition (%W) and fullness (%bw) of pollock sampled during eastern Bering Sea (EBS) bottom trawl surveys (BTS). Annual averages are weighted by biomass of six length categories in seven strata described in the Methods. The two highest composition prey each year are in **bold** text.

Table 1.

Survey Year	Number of Hauls
1987	74
1988	63
1989	178
1990	198
1991	173
1992	163
1993	191
1994	191
1995	183
1996	162
1997	169
1998	140
1999	163
2000	174
2001	160
2002	173
2003	167
2004	175
2005	109
2006	114
2007	178
2008	185
2009	163
2010	167
2011	176

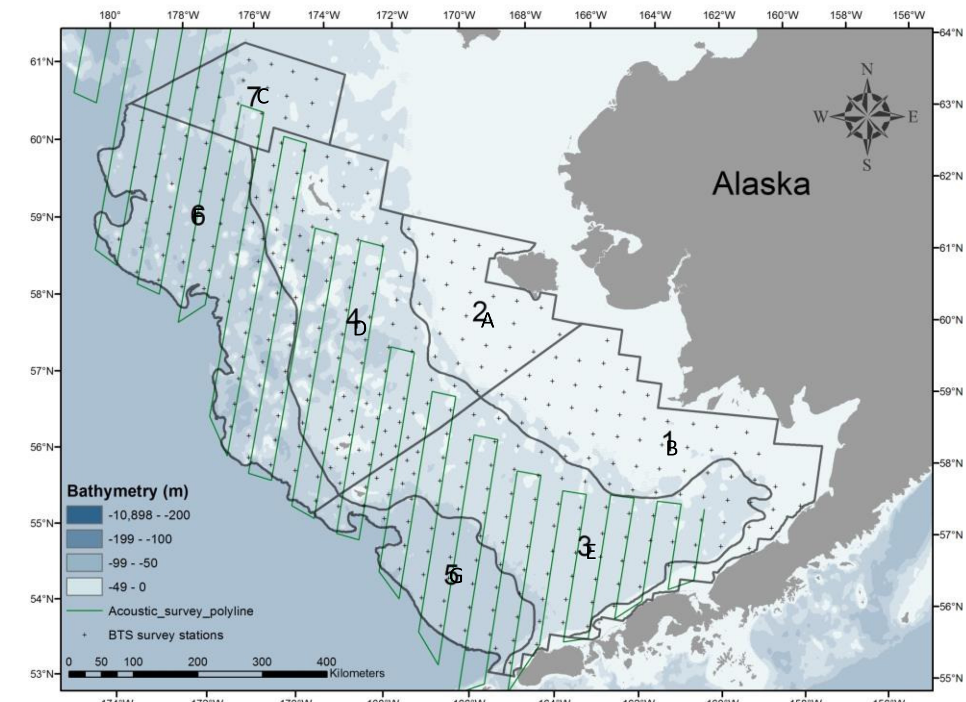
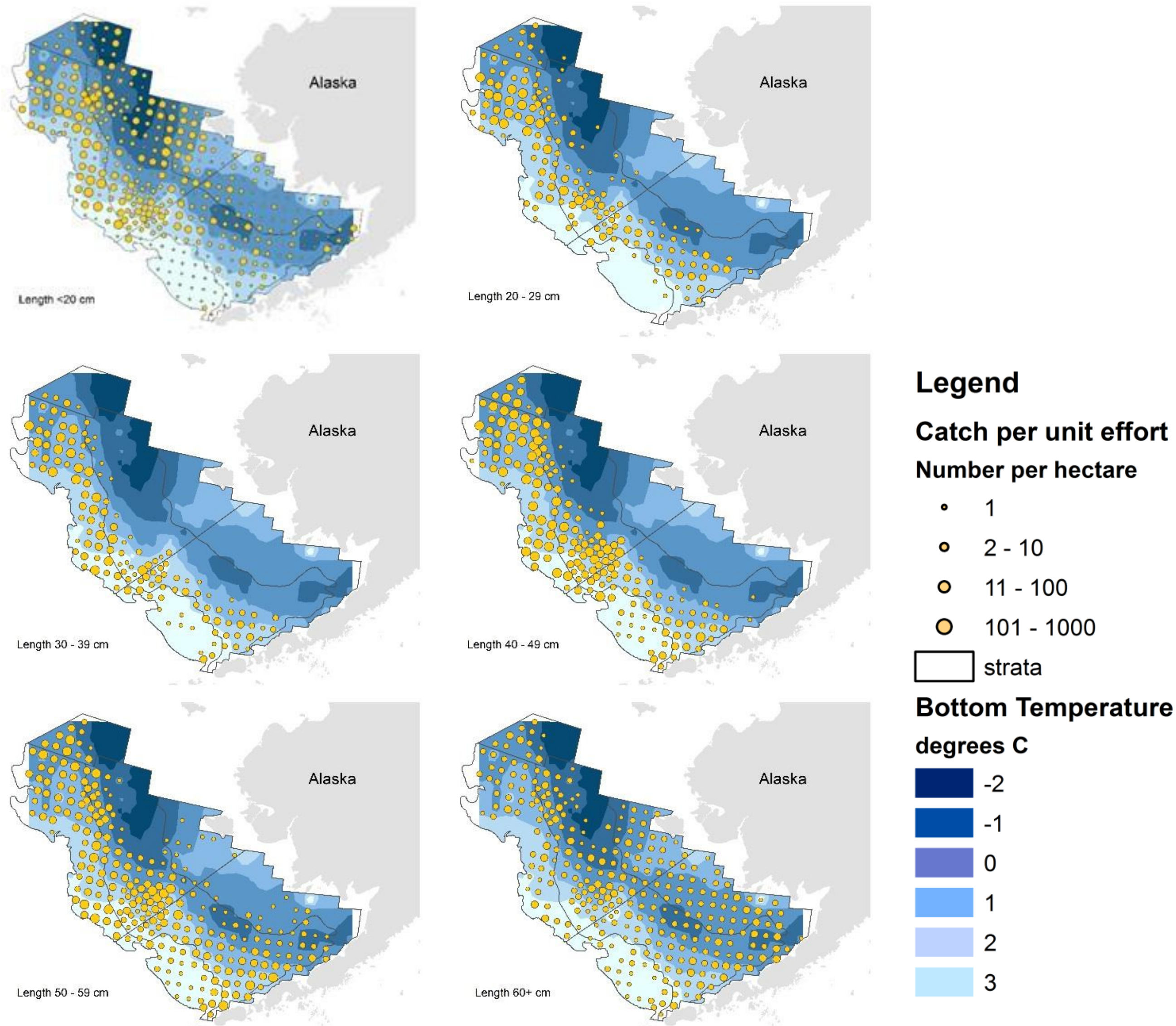

Alaska
N
W
E
S
7C
6
4D
2A
1B
3E
5G
Bathymetry (m)
-10,898 - -200
-199 - -100
-99 - -50
-49 - 0
Acoustic_survey_polyline
BTS survey stations
0 50 100 200 300 400
Kilometers
180°
178°W
176°W
174°W
172°W
170°W
168°W
166°W
164°W
162°W
160°W
158°W
156°W
61°N
60°N
59°N
58°N
57°N
56°N
55°N
54°N
53°N
64°N
63°N
62°N
61°N
60°N
59°N
58°N
57°N
56°N
55°N

Fig. 1.



Alaska
Length <20 cm
Alaska
Length 20 - 29 cm
Alaska
Length 30 - 39 cm
Alaska
Length 40 - 49 cm
Alaska
Length 50 - 59 cm
Alaska
Length 60+ cm
Legend
Catch per unit effort
Number per hectare
1
2 - 10
11 - 100
101 - 1000
strata
Bottom Temperature
degrees C
-2
-1
0
1
2
3

Fig. 2.

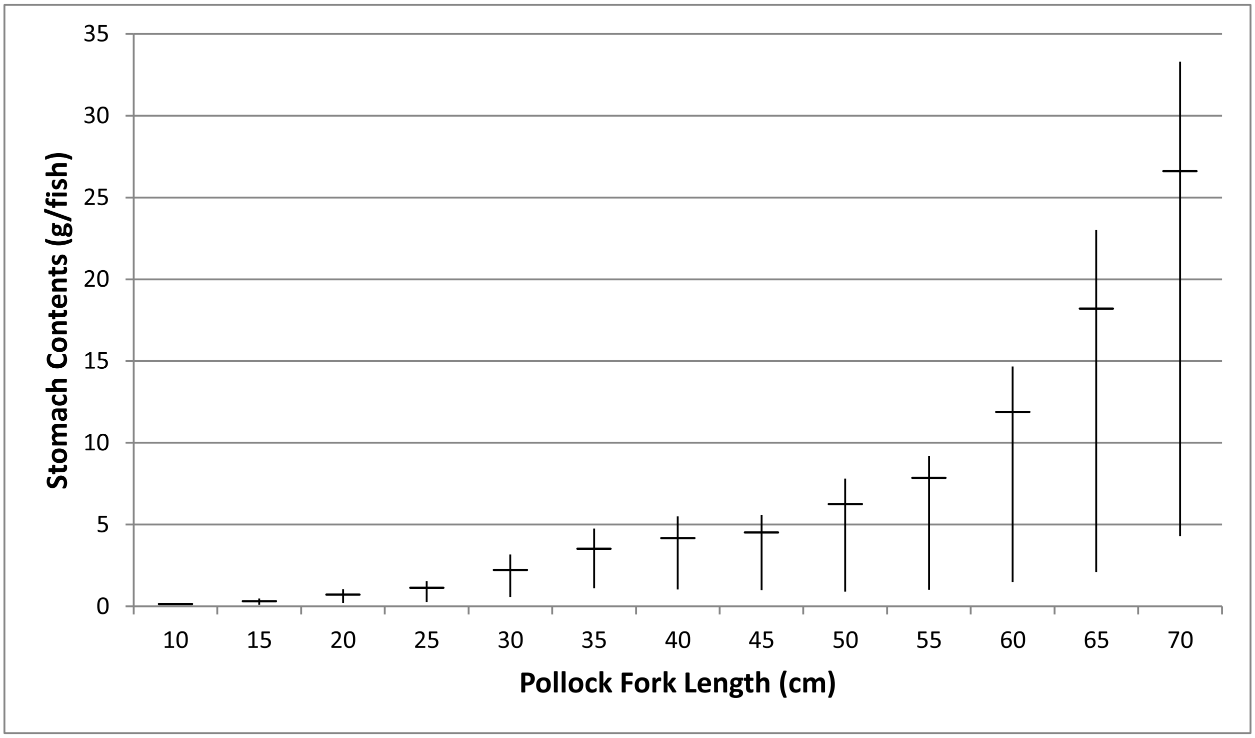
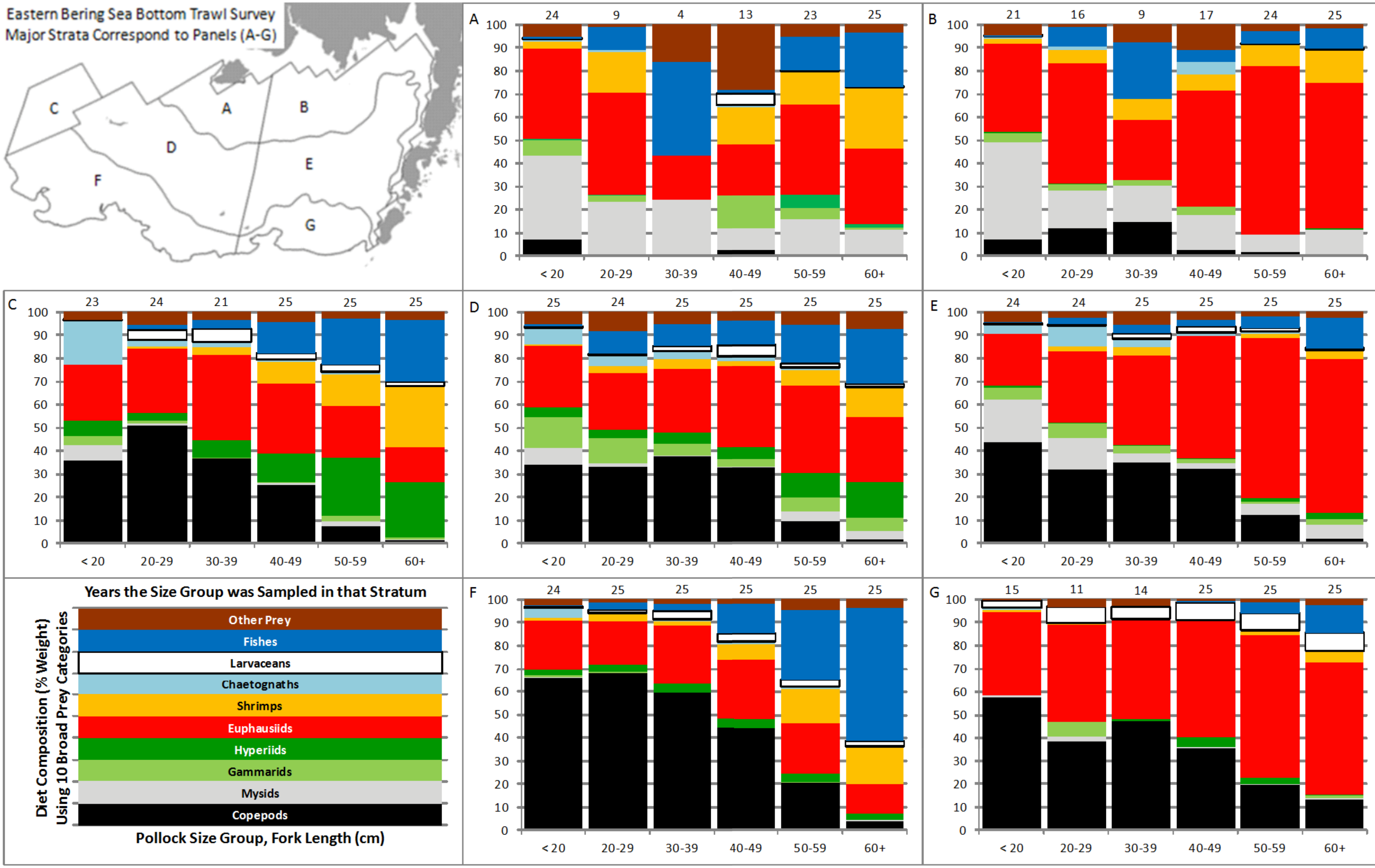

Stomach Contents (g/fish)
0
5
10
15
20
25
30
35
10
15
20
25
30
35
40
45
50
55
60
65
70
Pollock Fork Length (cm)

Fig. 3

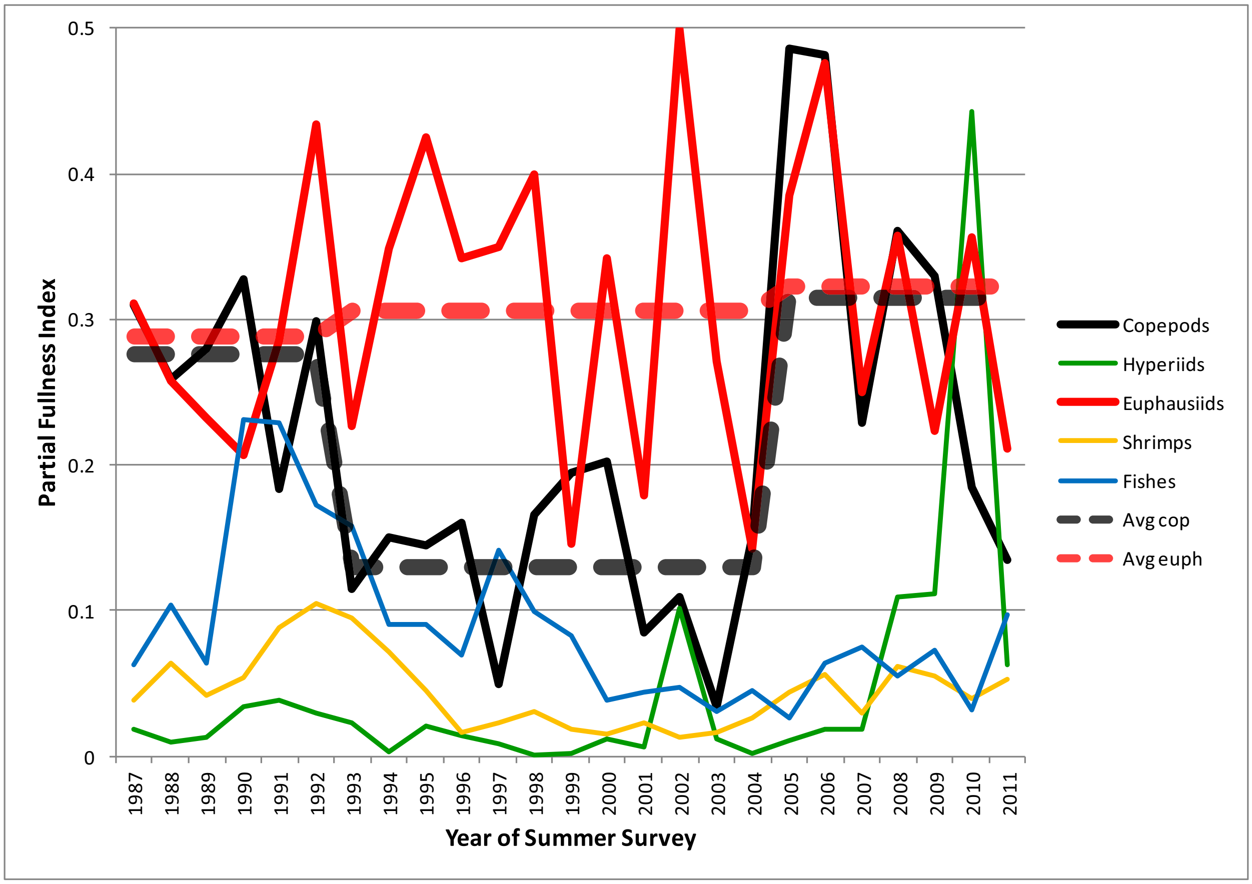


Eastern Bering Sea Bottom Trawl Survey
Major Strata Correspond to Panels (A-G)
A
B
C
D
E
F
G
Inner Shelf
Middle Shelf
Outer Shelf
Years the Size Group was Sampled in that Stratum
Other Prey
Fishes
Larvaceans
Chaetognaths
Shrimps
Euphausiids
Hyperiids
Gammarids
Mysids
Copepods
Diet Composition (% Weight)
Using 10 Broad Prey Categories
Pollock Size Group, Fork Length (cm)
< 20
20-29
30-39
40-49
50-59
60+

Fig. 4.

Table 2.

Year	Average weight composition (%W) of 10 prey categories in pollock stomach contents by EBS BTS year:										Average fullness:
Year	Copepods	Mysids	Gammariids	Hyperiids	Euphausiids	Shrimps	Chaetognaths	Larvaceans	Fishes	Other	(%bw)
1987	**38.73**	0.13	0.71	2.33	**38.85**	4.80	0.74	1.03	7.88	4.80	0.801
1988	**33.85**	0.97	3.02	1.25	**33.80**	8.40	1.24	0.98	13.64	2.85	0.764
1989	**37.71**	0.80	1.92	1.77	**31.32**	5.57	0.62	2.72	8.60	8.97	0.743
1990	**36.29**	1.10	1.08	3.80	22.90	5.93	1.51	0.00	**25.64**	1.75	0.903
1991	20.38	0.43	1.31	4.27	**31.67**	9.84	0.25	2.64	**25.47**	3.74	0.901
1992	**26.49**	1.53	0.52	2.64	**38.47**	9.33	2.13	0.50	15.32	3.07	1.127
1993	16.82	1.19	2.01	3.35	**33.35**	13.97	1.15	1.27	**23.23**	3.66	0.681
1994	**20.71**	1.31	1.95	0.37	**47.96**	9.94	0.12	3.62	12.42	1.59	0.727
1995	**17.41**	1.30	2.03	2.51	**50.91**	5.36	1.71	4.96	10.89	2.92	0.835
1996	**24.32**	4.38	1.70	2.20	**52.06**	2.42	0.05	1.34	10.63	0.90	0.658
1997	7.88	0.78	0.73	1.27	**54.87**	3.55	0.54	6.34	**22.18**	1.86	0.636
1998	**22.94**	0.27	0.33	0.10	**55.33**	4.33	0.41	1.11	13.79	1.39	0.723
1999	**39.23**	2.41	0.39	0.38	**29.42**	3.81	0.24	2.58	16.77	4.77	0.496
2000	**30.03**	1.30	4.23	1.75	**50.78**	2.25	0.41	0.90	5.71	2.64	0.672
2001	**22.99**	1.16	1.88	1.65	**48.53**	6.16	0.00	1.03	11.99	4.62	0.368
2002	**12.23**	3.14	3.38	11.34	**55.66**	1.46	0.83	1.60	5.22	5.14	0.898
2003	**8.22**	0.34	0.99	2.74	**64.95**	3.87	2.81	1.26	7.39	7.43	0.418
2004	**33.66**	5.24	1.15	0.53	**31.88**	5.97	3.44	4.21	10.18	3.74	0.447
2005	**42.68**	2.56	1.41	0.92	**33.82**	3.87	2.62	3.33	2.36	6.43	1.139
2006	**40.37**	2.47	1.12	1.52	**39.92**	4.76	0.33	2.51	5.33	1.67	1.191
2007	**32.43**	0.35	0.56	2.70	**35.39**	4.16	0.72	11.72	10.57	1.40	0.705
2008	**34.46**	1.58	0.96	10.44	**34.12**	5.88	1.82	4.96	5.29	0.49	1.047
2009	**35.05**	3.61	0.20	11.83	**23.80**	5.82	0.62	10.52	7.80	0.75	0.940
2010	16.54	0.75	0.23	**39.70**	**31.94**	3.60	2.75	0.05	2.85	1.59	1.115
2011	**19.56**	10.98	1.01	9.15	**30.59**	7.66	0.93	4.11	14.14	1.87	0.690
Average	**26.84**	2.00	1.39	4.82	**40.09**	5.71	1.12	3.01	11.81	3.20	0.785



Partial Fullness Index
0.5
0.4
0.3
0.2
0.1
0
1987
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
Year of Summer Survey
Copepods
Hyperiids
Euphausiids
Shrimps
Fishes
Avg cop
Avg euph

Fig. 5.

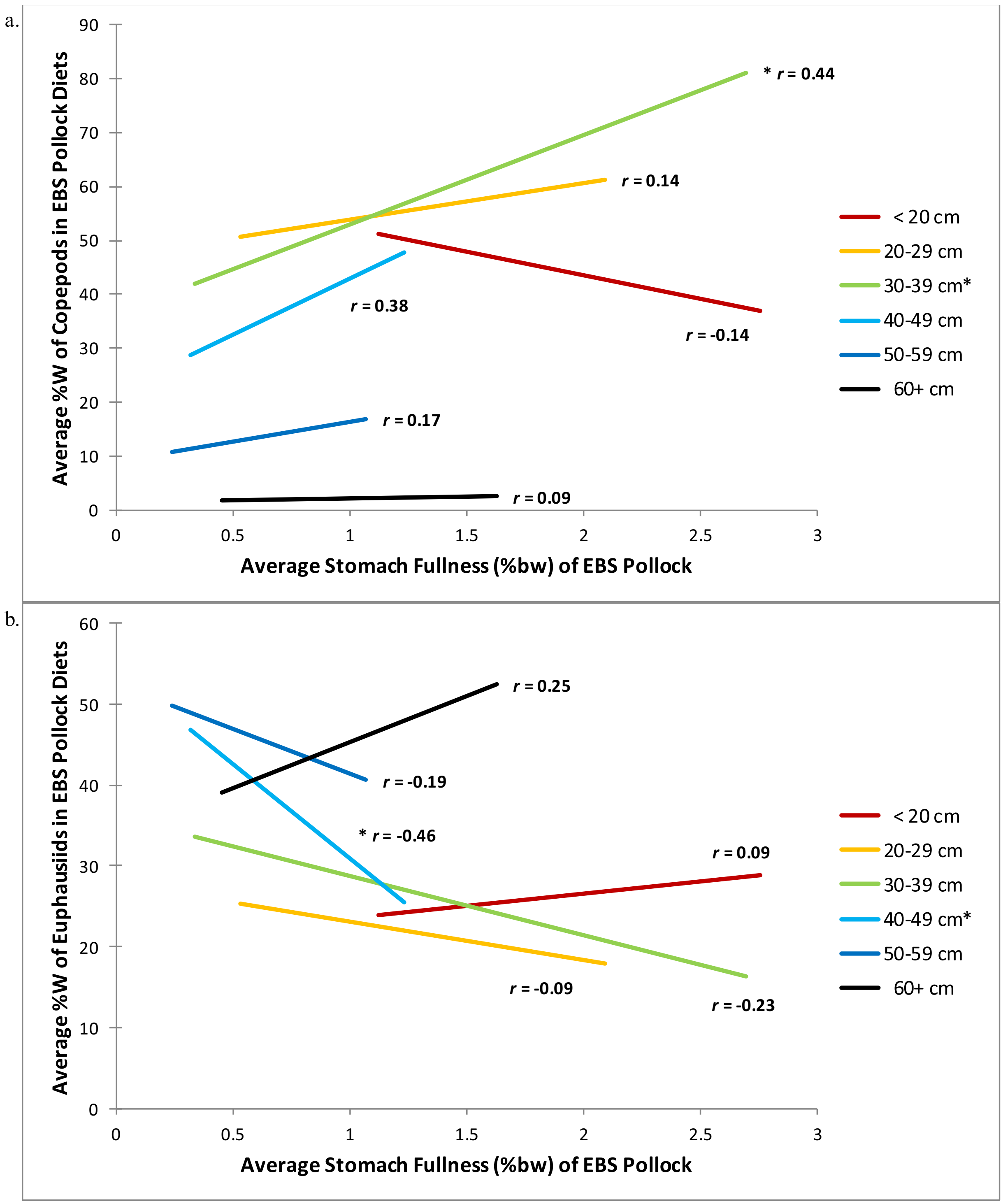

a.
Average %W of Copepods in EBS Pollock Diets
Average Stomach Fullness (%bw) of EBS Pollock
* r = 0.44
r = 0.14
r = 0.38
r = -0.14
r = 0.17
r = 0.09
< 20 cm
20-29 cm
30-39 cm*
40-49 cm
50-59 cm
60+ cm
b.
Average %W of Euphausids in EBS Pollock Diets
Average Stomach Fullness (%bw) of EBS Pollock
r = 0.25
r = -0.19
* r = -0.46
r = 0.09
r = -0.09
r = -0.23
< 20 cm
20-29 cm
30-39 cm
40-49 cm*
50-59 cm
60+ cm

Fig. 6.

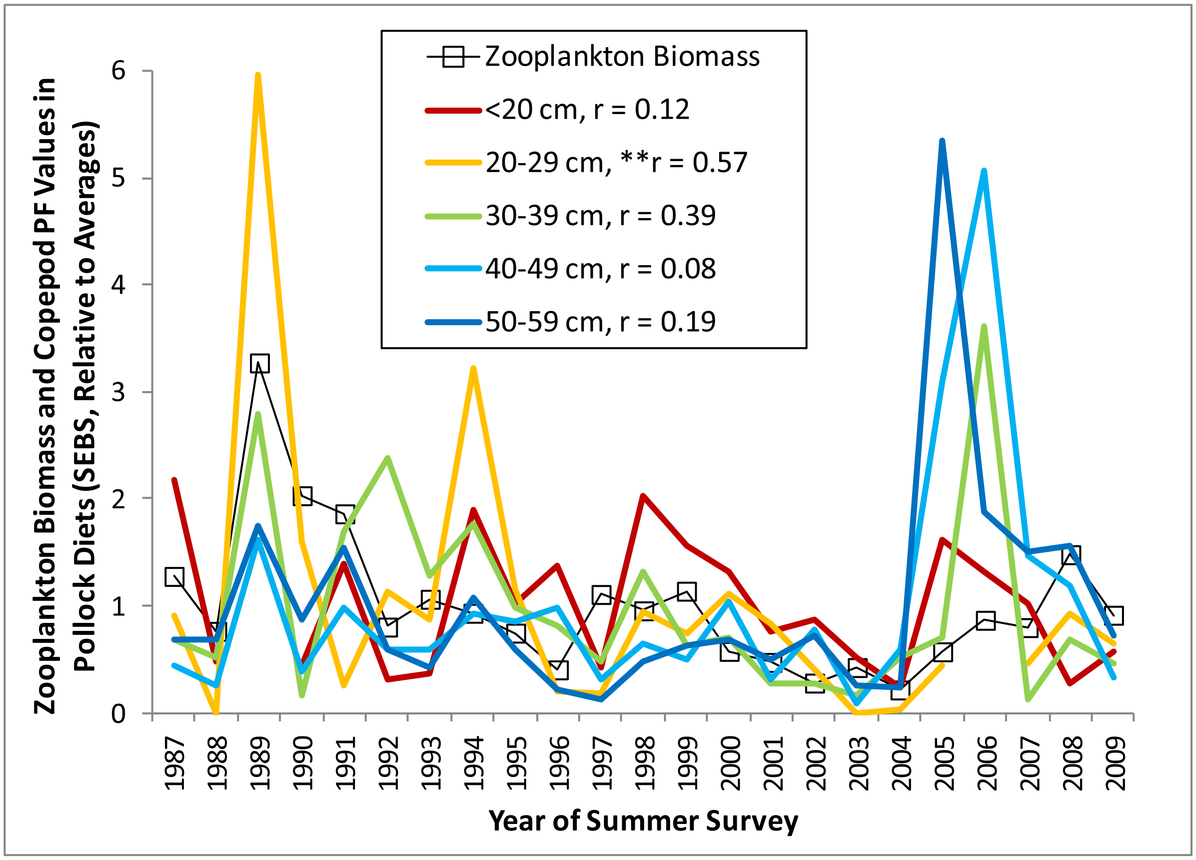
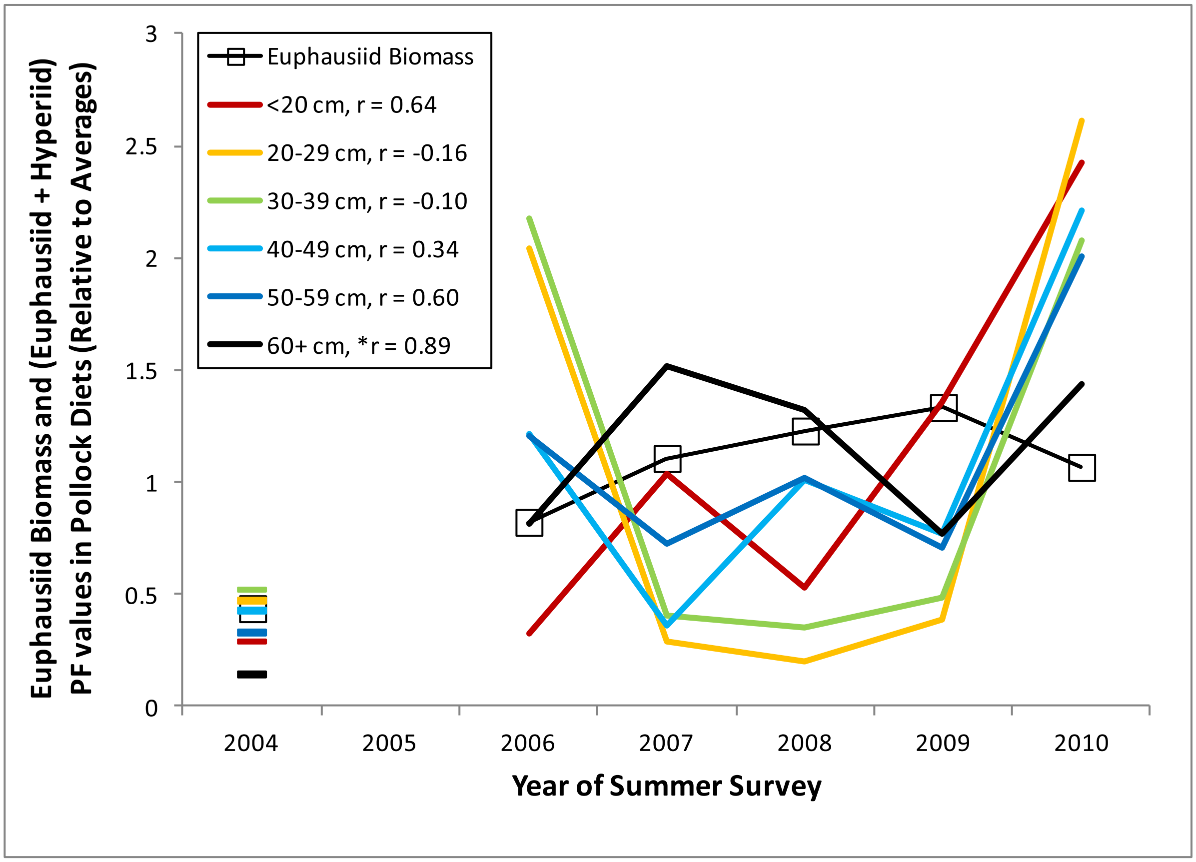

Zooplankton Biomass
<20 cm, r = 0.12
20-29 cm, **r = 0.57
30-39 cm, r = 0.39
40-49 cm, r = 0.08
50-59 cm, r = 0.19
Zooplankton Biomass and Copepod PF Values in Pollock Diets (SEBS, Relative to Averages)
0
1
2
3
4
5
6
1987
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
Year of Summer Survey

Fig. 7.



Euphausiid Biomass
<20 cm, r = 0.64
20-29 cm, r = -0.16
30-39 cm, r = -0.10
40-49 cm, r = 0.34
50-59 cm, r = 0.60
60+ cm, *r = 0.89
Euphausiid Biomass and (Euphausiid + Hyperiid) PF values in Pollock Diets (Relative to Averages)
Year of Summer Survey
3
2.5
2
1.5
1
0.5
0
2004
2005
2006
2007
2008
2009
2010

Fig. 8.