



Feeding ecology of age-0 walleye pollock (*Gadus chalcogrammus*) and Pacific cod (*Gadus macrocephalus*) in the southeastern Bering Sea

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ABSTRACT

Walleye pollock (*Gadus chalcogrammus*) and Pacific cod (*Gadus macrocephalus*) are of particular economic and ecological importance in the southeastern Bering Sea. The spatial and temporal overlap of early life stages of both species may explain their strongly correlated recruitment trends. Pelagic larvae and juveniles were collected during four research cruises in May, July and September of 2008, an exceptionally cold year, and their stomach contents were examined. Feeding success and diet composition of walleye pollock and Pacific cod were consistently different in spring, summer, and fall. Pacific cod larvae and juveniles always consumed larger and progressively fewer prey items per stomach than walleye pollock; this difference was particularly pronounced in the fall. Our data suggest that co-occurring early life stages of walleye pollock and Pacific cod were dividing prey resources rather than competing for them, at least during the exceptionally cold conditions in 2008 in the southeastern Bering Sea.

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1. Introduction

Walleye pollock (*Gadus chalcogrammus*), hereafter called pollock, and Pacific cod (*Gadus macrocephalus*) are two of the largest and most valuable fisheries in the Bering Sea, with an annual harvest of 0.48–1.40 million metric tons (lanelli et al., 2011) for pollock in the southeastern Bering Sea (SEBS) and 120,000–183,000 metric tons for Pacific cod in the eastern Bering Sea over the past decade (Thompson et al., 2011). These species are of ecological importance within the SEBS ecosystem (Aydin and Mueter, 2007), where they serve as prey for seabirds (Decker and Hunt, 1996), marine mammals (Sinclair et al., 1994) and other fishes, including older age-classes of pollock (Bailey, 1989). Both species are predatory, pollock consumes a variety of forage fishes (Coyle et al., 2011), while Pacific cod consume large amounts of commercially targeted crab species (Livingston, 1989; Urban, 2012). Thus, pollock and Pacific cod play a central role in the food web of the SEBS. A better understanding of the ecology of these two species and their interactions with different ecosystem components would enhance

our ability to successfully model these populations via changing prey and prey quality as they are mediated by changing climatic conditions.

In the SEBS, pollock and Pacific cod exhibit similarities in early life history patterns, spatial distribution, and subsequent recruitment success (Bacheler et al., 2010; Duffy-Anderson et al., 2006; Hurst et al., 2012; Matarese et al., 2003; Mueter et al., 2011). Both species spawn from January to April (Bacheler et al., 2010; Shimada and Kimura, 1994) in relatively deep waters over the continental shelf, along the Alaska Peninsula, and near the Pribilof Islands (Bacheler et al., 2010; Fritz et al., 1993). Pollock eggs tend to be slightly positively buoyant and pelagic, while Pacific cod eggs tend to be negatively buoyant and demersal (Dunn and Materese, 1987). Post-hatch, both species rise to the epi-pelagic layer and share a similar horizontal distribution (Duffy-Anderson et al., 2006; Matarese et al., 2003). Specifically, both species have larval abundance maxima in the SEBS along the Alaska Peninsula and Aleutian Islands, particularly in and around Unimak Pass, as well as north of the Pribilof Islands (Matarese et al., 2003). During late spring and early summer, pelagic larvae and juveniles are concentrated in the upper mixed layer (10–40 m). By the fall, juvenile pollock disperse throughout the water column at standard lengths (SL) > 40 mm, while Pacific cod juveniles begin to settle out to a demersal lifestyle earlier in the year at > 35 mm SL (Bailey, 1989; Blackburn and Jackson, 1982; Ciannelli et al., 1998; Dunn and Materese, 1987; Nishiyama et al., 1986; Rugen and Materese, 1988).

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Due to the spatial and temporal overlap of early pelagic life stages, and because of similarities in body size and shape, it is reasonable to assume that pollock and Pacific cod exploit similar prey resources, resulting in potential dietary overlap and the possibility for competition. Numerous studies have been conducted on the diet of larval and juvenile pollock in the SEBS, most of these diet studies focused either on larval fish in spring (Hillgruber et al., 1995; Nishiyama et al., 1986; Porter et al., 2005) or on juvenile stages later in the fall (Brodeur et al., 2000; Coyle et al., 2008, 2011; Moss et al., 2009; Schabetsberger et al., 2000, 2003). Published information regarding feeding success and dietary patterns of age-0 Pacific cod in the SEBS is limited, and is only available for juveniles later in their first year (Lee, 1985). Knowledge of early life stage feeding patterns in both species is of importance to better understand recruitment success, particularly in light of changing environmental conditions in the Arctic and sub-Arctic (Hunt et al., 2011).

The SEBS experiences oscillating temperature ranges (Mueter and Litzow, 2008; Overland and Stabeno, 2004) marked by variable sea ice conditions (i.e., extent, thickness, and time of retreat), water temperature, and stratification in this region (Stabeno et al., 2012). These changes in the physical environment influence the timing, duration, and magnitude of the spring bloom, as well as recruitment success, growth, and nutritional condition of the zooplankton community (Hunt and Stabeno, 2002; Hunt et al., 2002, 2011; Walsh and McRoy, 1986); which in turn affects larval and juvenile pollock and Pacific cod relying on the zooplankton community for prey (Coyle et al., 2011; Hunt et al., 2011; Moss et al., 2009). Seasonal sampling for this study was conducted in 2008, a year characterized by heavy sea ice cover, late ice retreat, and cold temperatures (Stabeno et al., 2012). The overall goal of this study was to examine and compare feeding success and dietary composition of both pollock and Pacific cod during their first year, and during cold conditions in the SEBS. The underlying hypothesis was that larvae and juveniles of these two species, which share ecological preferences, may feed on similar prey items and during cold conditions may both primarily consume large prey taxa (*Calanus marshallae*/*glacialis*, hereafter referred to as *Calanus* spp. and juvenile *Thysanoessa* spp.) which in turn may contribute to coincident strong cohorts. To test this hypothesis we

- 1) compared patterns of dietary composition of larvae and juveniles of these two gadoid species, and
- 2) compared measures of feeding success and dietary composition from the exceptionally cold growing season in 2008 to previous studies to evaluate environmental effects on recruitment potential.

2. Methods

2.1. Sample collection

This study was based on samples of early life history stages of pollock and Pacific cod that were acquired opportunistically from multiple projects (Table 1). The goal of sample acquisition was to obtain a good seasonal coverage of age-0 larval and juvenile stages of

both species. Early life stages were obtained from sampling efforts in spring (May), summer (July), and fall (September) of 2008.

In spring of 2008, pre-flexion larvae were collected by the Alaska Fisheries Science Center, National Marine Fisheries Service participating in the Bering Sea Project (AFSC, NMFS; Fig. 1A). Fish larvae were collected with oblique 60 cm diameter Bongo tows (Table 1). Sampling was conducted 24 h a day; however, only two stations included in this study were sampled after dusk. After retrieval of the sampling gear, all fish larvae were removed from the codend and preserved in 5% buffered formalin-seawater solution. Six pollock and 8 Pacific cod larvae in these collections still retained a yolk-sac and were therefore considered to be not yet

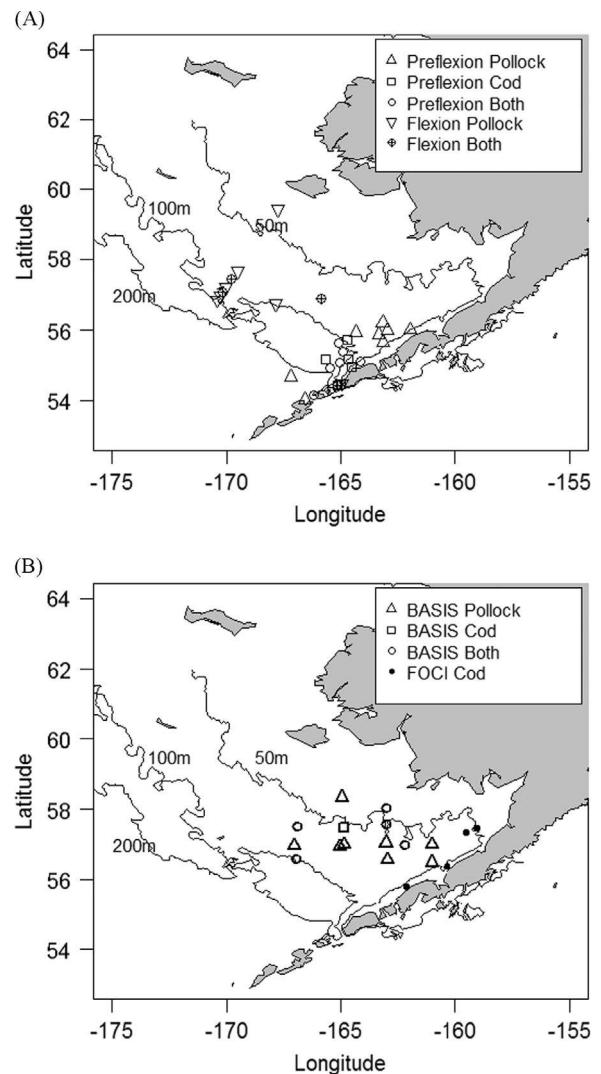


Fig. 1. Sampling sites for walleye pollock and Pacific cod used in this study. (A) Spring and mid-summer samples and (B) fall samples. See Table 1 for cruise details.

Table 1

Sample size (N) of walleye pollock and Pacific cod collected in 2008 by season (spring, summer, and fall), agency and/or project, sample gear, and mesh size. FOCI: Fisheries Oceanography Coordinated Investigations; NOAA AFSC: National Oceanic and Atmospheric Administration, Alaska Fisheries Science Center; BEST/BSIERP SFOS: Bering Ecosystem Studies/Bering Sea Integrated Ecosystem Research Project, School of Fisheries and Ocean Sciences; BASIS: Bering-Aleutian Salmon International Survey.

| Season | Project/Agency | Gear | Mesh | Sample date range | Number of hauls (# of hauls with both pollock and cod) | Walleye pollock, N (size range, mm) | Pacific cod, N (size range, mm) |
|--------|------------------|------------|-------------|-------------------|---|--|------------------------------------|
| Spring | FOCI, NOAA AFSC | Bongo | 500 μ m | May 12–28 | 21 (7) | 17 (3.2–7.4) | 17 (3.0–7.6) |
| Summer | BEST-BSIERP SFOS | MOCNESS | 500 μ m | July 3–31 | 11 (4) | 11 (4.4–22) | 4 (9.1–16.4) |
| Fall | BASIS, NOAA AFSC | Rope Trawl | 120 mm | September 9–27 | 14 (5) | 13 (36.2–88) | 6 (52.8–87) |
| Fall | FOCI, NOAA AFSC | Beam Trawl | 7.0 mm | September 10–20 | 4 (0) | – | 4 (65–87.2) |

actively feeding. Consequently, these fish were excluded from all subsequent calculations of feeding success and diet composition.

In the summer of 2008, samples of pelagic flexion larvae were obtained by the University of Alaska Fairbanks, School of Fisheries and Ocean Sciences (UAF, SFOS) during a cooperative research cruise conducted as part of the Bering Ecosystem Study, National Science Foundation (BEST, NSF) and the Bering Sea Project, North Pacific Research Board (BSIERP, NPRB; Fig. 1A). Ichthyoplankton was collected using a 1 m² Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS; Wiebe et al., 1976). The oblique MOCNESS tows provided depth-stratified samples in 20 m increments from a depth of 100 m, or near the bottom, to the surface. Sampling was conducted 24 h a day; however, no stations included in this study were sampled after dusk. After retrieval of the sampling gear, flexion larvae were preserved in 10% formalin seawater solution for further laboratory analysis.

In the fall of 2008, samples of pelagic juvenile pollock and Pacific cod were provided by the Bering Aleutian Salmon International Survey (BASIS), conducted by the Ted Stephens Marine Research Institute, National Oceanic and Atmospheric Administration (TSMRI, NOAA). Fish were collected with surface (0–20 m) and with midwater rope trawls (targeting acoustic signals; Fig. 1B). Sampling methods are described in more detail by Moss et al. (2009). All BASIS sampling occurred during daylight hours. After retrieval of the gear, fish were identified to species and fixed in 5% buffered formalin-seawater solution. Due to the low available sample size, demersal juvenile Pacific cod were also received from the Fisheries Oceanography Coordinated Investigations (FOCI) at the NOAA AFSC, NMFS (cruise number 3MF08; Fig. 1B); fish were collected with a beam trawl and recovered juveniles were frozen at sea for later processing.

The size range of fish processed for this study was similar across both species in every season with one exception (Table 1). The smallest juvenile Pacific cod (September) were larger than 50 mm TL, while the smallest pollock were just over 36 mm TL. However, only four juvenile pollock were smaller than 50 mm TL.

2.2. Laboratory analyses

All spring and summer fish were measured with calibrated micro-photographic software (Image Pro 3.0) to the nearest 0.1 mm SL, while fall samples were measured with a fish board to the nearest 0.1 mm TL. For each fish, the digestive tract was excised and the stomach was removed. Stomach fullness was visually estimated as: (1) empty, (2) traces, and (3–6) 25%, 50%, 75%, and 100% full (Adams et al., 2007). Stomach contents were gently removed and ingested prey items were examined with a LEICA MZ 16 stereo microscope and a LEICA DM LB2 compound microscope. Prey items were identified to the lowest taxonomic level and developmental stage possible. Total prey wet weight was determined by multiplying a mean prey taxon wet weight, obtained from zooplankton data collected from each respective cruise, by the number of that specific prey taxon in the gut. Spring zooplankton data did not include mean zooplankton wet weight estimates; therefore, volume estimates (%V as a substitute for %W) were calculated using established mensuration formulae (Napp et al., 1999). Published values of mean species and stage specific TL were used to estimate the mean TL of ingested prey.

2.3. Statistical analyses

For each season, cumulative prey curves were used to determine the number of stomachs needed to properly describe the dietary breadth of pollock and Pacific cod (Treloar et al., 2007); all stomachs were randomized 10,000 times to reduce the potential for bias due to sampling order and the mean number of new prey

categories was plotted against the total number of stomachs analyzed. If the curve reached an asymptote, it was assumed that the minimum sample size needed to adequately describe the diet of pollock or Pacific cod had been met. Measures of feeding success for all stomachs were described as numerical feeding intensity (the total number of prey items per stomach), a fullness index (visually assigned values 1–6) (Adams et al., 2007), and feeding incidence (the proportion of fish with at least one ingested item) (Dauvin and Dodson, 1990). Mixed effects models using predator species as a fixed effect and location (station) as a random effect, and their respective null model (dropping the fixed species effect) were compared using a likelihood ratio test to identify significant differences in mean numerical feeding intensity, fullness, and prey size between predator species. Station means were used for all significance testing to avoid the issue of pseudo-replication. Fall numerical feeding intensity and spring and fall prey size data were log transformed to account for strong positive skew, while summer fullness and numerical feeding intensity data were square-root transformed to account for weak positive skew.

Prey composition was expressed as percent number (%N), percent of total prey volume (%V) or percent of total prey weight (%W), and percent frequency of occurrence (%FO) from all non-empty stomachs. Finally, the percentage index of relative importance (%IRI) was calculated from the previous indices (Cortés, 1997). Dietary comparisons were made with PRIMER Version 6 (Clarke and Gorley, 2006). Non-metric multi-dimensional scaling ordination (NMDS) was used to visualize significant dietary differences between species. This approach employed a Bray–Curtis similarity coefficient matrix applied to either square- or fourth-root transformed dietary data, depending on the degree of skewness. Kruskal's stress statistic 1 (Clarke and Gorley, 2006) was used to determine the best spatial representation of the samples. A stress of < 0.2 was considered an acceptable fit (Clarke and Gorley, 2006). Multivariate one-way analysis of similarities (ANOSIM) was performed on the mean dietary composition within species at each station to investigate whether dietary composition differed significantly between species (Clarke and Gorley, 2006). ANOSIM reports a global R statistic that is analogous to an ANOVA F statistic and p-value. Similarity percentages (SIMPER) provides a measure of within species similarity and between species dissimilarity, and was used to isolate dietary categories that were significantly important, or contributed most to observed dissimilarities. The ANOSIM and SIMPER routines were performed on the mean diet of each predator species by station (Picquelle and Mier, 2011). Differences in dispersion, as a measure of diet variability, across groups were tested for significance using a permutation-based procedure (PERMDISP).

3. Results

3.1. Spring

In spring, 54 pollock at 17 stations and 47 Pacific cod at 17 stations were processed for dietary analysis. Cumulative prey curves of pre-flexion pollock and Pacific cod larvae reached an asymptote at approximately 45–50 and 35–40 stomachs, respectively. Twenty three prey types were pooled into 14 categories, 10 of these categories occurred in either pollock or Pacific cod stomachs.

In spite of their spatial and temporal co-occurrence in spring, larval stages of pollock and Pacific cod showed disparate patterns in feeding success and mean prey composition. Pre-flexion pollock larvae had an overall feeding incidence of 67.0%, while pre-flexion Pacific cod larvae reached 71.8%. Pacific cod larvae had a significantly higher mean prey volume of 0.5 ml (SE=0.04) than pollock pre-flexion larvae with a mean prey volume of 0.3 ml (SE=0.01; Table 2). Mean fullness score and numerical feeding intensity were

slightly higher in Pacific cod than in pollock, but not significantly so (Table 2).

The mean dietary composition (Table 3) between pre-flexion pollock and Pacific cod was significantly different (1-way ANOSIM;

Table 2

Feeding intensity of age-0 walleye pollock and Pacific cod expressed as mean prey volume/size, visual fullness index scores, numerical feeding intensity (prey/stomach) and standard errors (SE) for all seasons with corresponding Chi-Square statistics, degrees of freedom (df) and *P*-values (*P*). Bold *P*-values indicate significant differences.

| | Walleye pollock | Pacific cod | Chi-Square | df | <i>p</i> |
|----------------------------|-----------------|-------------|------------|-----|----------------|
| Spring | | | | | |
| Prey volume (ml) | 0.3 (0.01) | 0.5 (0.04) | 8.9 | 3,4 | ≤ 0.01 |
| Fullness (1–6) | 2.7 (0.16) | 3.3 (0.20) | 2.6 | 3,4 | 0.11 |
| Prey stomach ⁻¹ | 1.8 (0.21) | 2.0 (0.12) | 2.7 | 3,4 | 0.10 |
| Summer | | | | | |
| Prey size (mm) | 0.9 (0.02) | 1.7 (0.35) | 24.7 | 3,4 | ≤ 0.001 |
| Fullness (1–6) | 3.4 (0.11) | 4.4 (0.98) | 1.8 | 3,4 | 0.18 |
| Prey stomach ⁻¹ | 6.5 (0.50) | 5.0 (1.83) | 0.02 | 3,4 | 0.87 |
| Fall | | | | | |
| Prey size (mm) | 2.1 (0.04) | 5.3 (0.17) | 290.5 | 3,4 | ≤ 0.001 |
| Fullness (1–6) | 3.9 (0.13) | 4.3 (0.20) | 3.2 | 3,4 | 0.07 |
| Prey stomach ⁻¹ | 74.7 (12.81) | 11.4 (2.61) | 42.5 | 3,4 | ≤ 0.001 |

Table 3

Diet composition of walleye pollock and Pacific cod pre-flexion larvae as percent number (%N), percent volume (%V), percent frequency of occurrence (%FO), and percent index of relative importance (%IRI). “N” represents the sample size of all actively feeding larvae, excluding yolk-sac larvae, empty stomachs, and samples with no identifiable prey. NI–VI: naupliar stages, CI–VI: copepodite stages.

| Prey items | Spring pollock (N=17) | | | | Spring cod (N=17) | | | |
|-----------------------------------|-----------------------|------|------|------|-------------------|------|------|------|
| | %N | %V | %FO | %IRI | %N | %V | %FO | %IRI |
| Copepod eggs | 10.2 | 18.2 | 3.7 | 3.3 | 16.3 | 5.5 | 29.2 | 13.9 |
| <i>Calanus</i> spp. NVI | 0.0 | 0.0 | 0.0 | 0.0 | 2.0 | 1.7 | 4.2 | 0.3 |
| <i>Eucalanus</i> spp. NIII | 4.1 | 5.1 | 7.4 | 2.2 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Metridia pacifica</i> NII–III | 14.3 | 2.2 | 14.8 | 7.8 | 6.1 | 0.2 | 8.3 | 1.2 |
| <i>Metridia pacifica</i> NIV–VI | 20.4 | 36.4 | 18.5 | 33.3 | 28.6 | 9.6 | 45.8 | 38.3 |
| <i>Oithona similis</i> NV–VI | 4.1 | 3.1 | 7.4 | 1.7 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Pseudocalanus</i> spp. NII–III | 22.4 | 2.3 | 29.6 | 23.3 | 8.2 | 0.2 | 16.7 | 3.0 |
| <i>Pseudocalanus</i> spp. NIV–VI | 10.2 | 15.9 | 18.5 | 15.3 | 10.2 | 3.0 | 16.7 | 4.8 |
| <i>Calanus</i> spp. CI–II | 0.0 | 0.0 | 0.0 | 0.0 | 14.3 | 59.6 | 20.8 | 33.7 |
| <i>Metridia pacifica</i> CIII | 0.0 | 0.0 | 0.0 | 0.0 | 2.0 | 16.1 | 4.2 | 1.7 |
| <i>Microcalanus</i> spp. CIV | 2.0 | 2.1 | 3.7 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| Barnacle cyprids | 4.1 | 4.8 | 1.9 | 4.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| Diatoms | 8.2 | 9.9 | 5.6 | 8.5 | 8.2 | 1.7 | 4.2 | 1.7 |
| Euphausiid calyptopis | 0.0 | 0.0 | 0.0 | 0.0 | 4.1 | 2.3 | 8.3 | 1.2 |

Table 4

PRIMER ANOSIM and PERMDISP test results for comparing pollock and cod diets. ANOSIM results are presented as the Global *R* statistic (*R*) across all test groups and the resulting *P* value (*P*). PERMDISP results are presented as the Global *F* statistic (*F*) across all test groups, associated degrees of freedom (df1, 2). Bold values indicate significant differences.

| | ANOSIM | | PERMDISP | | | |
|----------------|----------|----------------|----------|-----|-----|----------------|
| | <i>R</i> | <i>P</i> | <i>F</i> | df1 | df2 | <i>P</i> |
| Spring | | | | | | |
| Pollock vs cod | 0.16 | ≤ 0.05 | 2.07 | 1 | 49 | > 0.05 |
| Summer | | | | | | |
| Pollock vs cod | 0.40 | ≤ 0.01 | 0.63 | 1 | 92 | > 0.05 |
| Fall | | | | | | |
| Pollock vs cod | 0.38 | ≤ 0.001 | 14.34 | 1 | 99 | ≤ 0.001 |

Table 4). SIMPER analysis attributed these differences primarily to a higher consumption of copepod eggs, late stage *M. pacifica* nauplii, and early *Calanus* spp. copepodites by Pacific cod, pollock were consuming higher numbers of smaller and younger naupliar stages, namely *M. pacifica* and *Pseudocalanus* spp. (Fig. 2). Pre-flexion pollock dietary composition had a mean similarity percentage of 18.3%, while the mean dietary composition was 16.4% similar within Pacific cod. While there was a mean dissimilarity of 88.7% between the two species, there was no significant difference in dietary dispersion between pollock and Pacific cod larvae in spring (PERMDISP; Table 4).

3.2. Summer

In summer, 113 flexion pollock larvae at 11 stations were processed for dietary analysis. The low sample size of Pacific cod flexion larvae in summer (5 fish at 4 stations), only allowed for restricted data analysis. Additionally, one Pacific cod larva contained no identifiable prey, effectively restricting the sample size to 4 station means, with each station consisting of only 1 individual. For pollock, the cumulative prey curve reached an asymptote at approximately 50 stomachs, while the cumulative prey curve for Pacific cod failed to reach an asymptote. Thirty five prey types, pooled into 17 categories were identified in the stomachs of flexion pollock and Pacific cod larvae; of these, 13 occurred in the diet of flexion pollock, 8 categories occurred in the diet of flexion Pacific cod larvae.

Despite the low sample size for Pacific cod flexion larvae, comparisons of mean feeding patterns between both species revealed notable differences. Specifically, prey size differed significantly with a mean of 1.7 mm (SE=0.35) for Pacific cod larvae in comparison to 0.9 mm (SE=0.02) for pollock larvae (Table 2). Pollock larvae had an overall feeding incidence of 79.6%, while 100% of Pacific cod were feeding. There were also slight differences in the mean fullness and numerical feeding intensity; however these differences were not statistically different.

The mean dietary composition between flexion pollock and Pacific cod larvae was significantly different (1-way ANOSIM; Table 4), and SIMPER analysis indicated that these differences were primarily due to Pacific cod consuming more early *Calanus* spp. and *Centropages abdominalis* copepodites. In contrast, pollock were consuming higher numbers of late *Acartia longiremis* copepodites, *Oithona similis* copepodites, and mid to adult stages of *Pseudocalanus* spp. (Table 5). Flexion pollock larvae had a mean dietary similarity of 22.3%, while Pacific cod had no within species

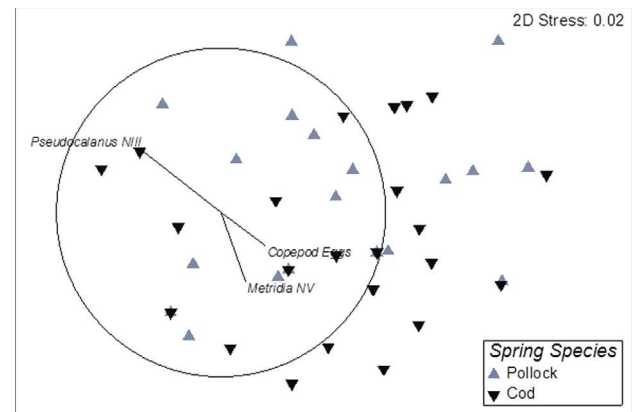


Fig. 2. Non-metric multidimensional scaling (NMDS) ordination of the dietary composition of pre-flexion walleye pollock and Pacific cod larvae collected in spring with Pearson correlation vectors from SIMPER identified prey categories. Two dimensional stress indicates how well the data can be represented in two dimensions (PRIMER: Kruskal stress formula 1).

Table 5

Diet composition of walleye pollock and Pacific cod flexion larvae as percent number (%N), percent volume (%V), percent frequency of occurrence (%FO), and percent index of relative importance (%IRI). "N" represents the sample size of all actively feeding larvae, excluding empty stomachs and samples with no identifiable prey. NII-VI: naupliar stages, CII-VI: copepodite stages.

| Prey items | Summer pollock (N=11) | | | | Summer cod (N=4) | | | |
|------------------------------------|-----------------------|-------|------|-------|------------------|-------|------|------|
| | %N | %W | %FO | %IRI | %N | %W | %FO | %IRI |
| <i>Acartia</i> spp. NIII | 0.2 | < 0.1 | 1.1 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| Calanoid nauplii | 0.5 | < 0.1 | 1.1 | < 0.1 | 5.0 | < 0.1 | 25.0 | 2.2 |
| <i>Pseudocalanus</i> spp. NIV-VI | 23.8 | 1.7 | 32.2 | 15.6 | 5.0 | < 0.1 | 25.0 | 2.2 |
| <i>Acartia longiremis</i> CIV-VI | 18.7 | 12.1 | 37.8 | 22.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Calanus</i> spp. CIII | 1.4 | 7.3 | 2.2 | 0.4 | 20.0 | 3.7 | 25.0 | 10.2 |
| <i>Calanus</i> spp. CIV-VI | 0.5 | 13.2 | 3.3 | 0.9 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Centropages abdominalis</i> CII | 0.0 | 0.0 | 0.0 | 0.0 | 15.0 | 0.8 | 25.0 | 6.8 |
| <i>Centropages abdominalis</i> CV | 0.0 | 0.0 | 0.0 | 0.0 | 15.0 | 1.6 | 25.0 | 7.1 |
| <i>Metridia pacifica</i> CIII-IV | 1.5 | 0.7 | 2.2 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Neocalanus</i> spp. CII-IV | 0.3 | 12.6 | 1.1 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Neocalanus cristatus</i> CV | 0.0 | 0.0 | 0.0 | 0.0 | 5.0 | 74.9 | 25.0 | 34.5 |
| <i>Oithona similis</i> CII-VI | 12.4 | 2.3 | 24.4 | 6.8 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Pseudocalanus</i> spp. CII-III | 16.3 | 5.3 | 28.9 | 11.9 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Pseudocalanus</i> spp. CIV-VI | 22.5 | 38.9 | 35.6 | 41.4 | 30.0 | 1.8 | 50.0 | 27.4 |
| Other copepodites | 1.0 | 5.4 | 4.4 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Themisto pacifica</i> | 0.0 | 0.0 | 0.0 | 0.0 | 5.0 | 17.2 | 25.0 | 9.6 |
| Other | 0.9 | 0.6 | 5.6 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 |

Table 6

Diet composition of walleye pollock and Pacific cod juveniles as percent number (%N), percent volume (%V), percent frequency of occurrence (%FO), and percent index of relative importance (%IRI). "N" represents the sample size of all actively feeding juveniles, excluding empty stomachs and samples with no identifiable prey. CIV-VI: copepodite stages.

| Prey items | Fall pollock (N=13) | | | | Fall cod (N=10) | | | |
|--|---------------------|-------|------|-------|-----------------|-------|------|-------|
| | %N | %W | %FO | %IRI | %N | %W | %FO | %IRI |
| <i>Acartia longiremis</i> CV | 4.2 | 1.7 | 27.1 | 1.7 | 0.2 | < 0.1 | 2.4 | < 0.1 |
| <i>Acartia longiremis</i> CVI | 1.1 | 0.1 | 8.5 | 0.1 | 0.6 | < 0.1 | 2.4 | < 0.1 |
| <i>Calanus</i> spp. CIV-VI | 20.2 | 40.3 | 57.6 | 37.0 | 8.0 | 4.6 | 14.3 | 3.5 |
| <i>Centropages abdominalis</i> CVI | 2.5 | 0.4 | 8.5 | 0.3 | 0.2 | < 0.1 | 2.4 | < 0.1 |
| <i>Epilabidocera amphitrites</i> CV-VI | 1.5 | 1.4 | 13.6 | 0.4 | 1.5 | 0.4 | 7.1 | 0.3 |
| <i>Pseudocalanus</i> spp. CV | 5.8 | 0.4 | 20.3 | 1.3 | 0.4 | < 0.1 | 4.8 | < 0.1 |
| <i>Pseudocalanus</i> spp. CVI | 59.1 | 5.9 | 59.3 | 41.0 | 0.6 | < 0.1 | 7.1 | 0.1 |
| <i>Euphausia pacifica</i> | 0.1 | 0.1 | 1.7 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Thysanoessa</i> spp. | 1.8 | 27.1 | 35.6 | 8.6 | 44.9 | 69.9 | 64.3 | 74.7 |
| <i>Chionoecetes</i> spp. megalopae | 0.0 | 0.0 | 0.0 | 0.0 | 1.3 | 2.9 | 14.3 | 1.1 |
| <i>Themisto pacifica</i> | 0.2 | 1.7 | 11.9 | 0.2 | 3.4 | 7.2 | 16.7 | 3.4 |
| <i>Limacina helicina</i> | 0.1 | < 0.1 | 5.1 | < 0.1 | 32.3 | 0.5 | 14.3 | 9.1 |
| <i>Parasagitta elegans</i> | 2.6 | 20.8 | 37.3 | 9.3 | 6.3 | 14.4 | 19.0 | 7.7 |
| <i>Oikopleura</i> spp. | 0.4 | < 0.1 | 1.7 | < 0.1 | 0.2 | < 0.1 | 2.4 | < 0.1 |
| Other | 0.3 | 0.1 | 8.5 | < 0.1 | 0.2 | < 0.1 | 2.4 | < 0.1 |

similarities. The mean dissimilarity between species was 93.6%. There was no significant difference in dietary dispersion between pollock and Pacific cod larvae (PERMDISP; Table 4), likely due to the low sample size of Pacific cod.

3.3. Fall

In the fall, 62 pollock at 13 stations and 42 Pacific cod at 10 stations were processed for dietary analysis. In the stomachs of juvenile pollock and Pacific cod, 21 prey types pooled into 15 categories were identified; of these, 14 occurred in the diet of either target species. The cumulative prey curves of juvenile pollock and Pacific cod juveniles reached an asymptote at around 20 and 36 stomachs, respectively.

In the fall, dietary patterns were more disparate between juvenile stages of pollock and Pacific cod than earlier in the year. Specifically, mean prey size and mean numerical feeding intensity were both significantly different (Table 2). Pacific cod had a higher mean prey size of 5.3 mm (SE=0.17) and lower mean numerical

feeding intensity of 11.4 (SE=2.61) in comparison to pollock with a mean prey size of 2.1 mm (SE=0.04) and a mean numerical feeding intensity of 74.7 (SE=12.81). Mean fullness index score was slightly higher in Pacific cod than in pollock, but this difference was not significant (Table 2). Juvenile pollock had an overall feeding incidence of 95.2%, while 100% of Pacific cod juveniles were feeding.

Differences in feeding success were also apparent in mean dietary composition (1-way ANOSIM, Table 4), and these differences were primarily due to a higher consumption of late stages of calanoid copepodites by juvenile pollock (Table 6), while Pacific cod juveniles consumed higher numbers of larger crustaceans, such as juvenile stages of the euphausiid *Thysanoessa* spp., the sea snail *Limacina helicina*, and hyperiid amphipods (Fig. 3). The overall mean similarity within juvenile pollock dietary composition was 47.0% and 26.2% for Pacific cod. The mean dissimilarity between species dietary composition was 74.1%. In addition, dietary dispersion was significantly higher in juvenile Pacific cod than in pollock (PERMDISP; Table 4).

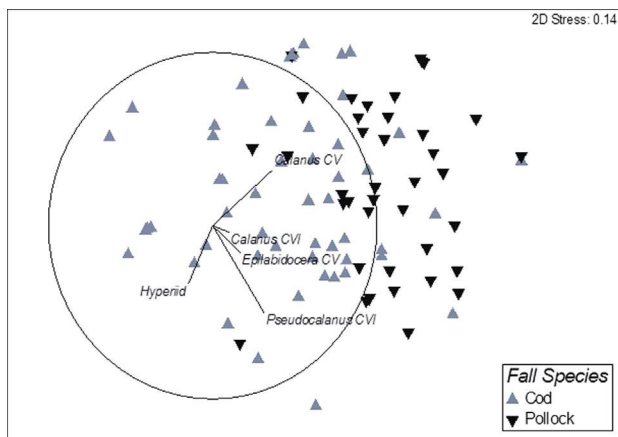


Fig. 3. Non-metric multidimensional scaling (NMDS) ordination depicting the dietary composition of fall-collected walleye pollock and Pacific cod juveniles. Vectors are the same as in Fig. 2.

4. Discussion

Despite sharing ecological preferences, temporal and spatial co-occurrence, and strong correlations in recruitment success (Bacheler et al., 2010; Duffy-Anderson et al., 2006; Hurst et al., 2012; Matarese et al., 2003; Mueter et al., 2011), patterns in feeding success and prey composition differed between all examined early life stages of pollock and Pacific cod during the cold conditions experienced in 2008. However, the number of samples included in this study was limited by availability from other research programs. Increased sampling, particularly from stations where both pollock and Pacific cod co-occurred, would have allowed investigations into sympatric vs. allopatric differences in feeding success and diet composition. Reduced sample sizes were either due to low feeding incidence in the spring, low catches of Pacific cod in the summer, or varying catches of either species in the fall. Further, when they were sampled simultaneously, the number captured or number available of one species was typically smaller than the other. Larger sample sizes with better spatial coverage would have allowed for meaningful two-way comparisons between interspecies size classes, regional domains, and sampling depth intervals; especially in the fall, when juvenile Pacific cod are beginning to settle out to a demersal lifestyle. Investigation into specific spatial domains would likely result in higher within species similarity percentages, and potentially higher between species similarity percentages. Additionally, prey field data were not sufficient to allow selectivity analysis in this study. Microzooplankton data from only two overlapping stations were available from the spring cruise, and the taxonomic resolution did not match this analysis. Summer zooplankton samples were selectively analyzed, and available data only overlapped with this study by approximately half. No zooplankton data were available from fall beam trawl samples or midwater trawl samples.

The diet of pre-flexion Pacific cod larvae in spring in the SEBS differed from that of pollock larvae due to higher consumption of copepod eggs, late calanoid nauplii, and an early inclusion of larger prey items including calanoid copepodites into their diet. A similar pattern was observed in pre-flexion Pacific cod larvae in Mutsu Bay, Japan (Takatsu et al., 2002). The large proportion of copepod eggs consumed by pre-flexion Pacific cod may have artificially inflated measures of fullness and feeding intensity, as pre-flexion pollock in the Gulf of Alaska were reported to display an inability to digest invertebrate eggs (Duffy-Anderson et al., 2002). Similar observations have been made for pre-flexion larval stages of other fish taxa (Conway et al., 1994; Hillgruber and Kloppmann, 2000; Redden and Daborn, 1991), and research has demonstrated that

the ability of eggs to withstand digestion is largely a function of the invertebrate species providing the eggs (Conway et al., 1994; Redden and Daborn, 1991). Whether or not pre-flexion Pacific cod lack the ability to properly digest certain invertebrate eggs is currently not known, but may warrant further research. While no other published data on pre-flexion Pacific cod diet in the SEBS were available, the diet of larval Pacific cod ≤ 5 mm SL in March and April in Mutsu Bay, Japan, was restricted to mainly *Pseudocalanus* spp., *Oithona* spp., and *Metridia* spp. nauplii (Takatsu et al., 1995), larvae of 5–10 mm SL gradually incorporated more copepodite and adult stages of *Pseudocalanus* spp., *A. clausi*, and *Oithona* spp. into their diet.

Differences in dietary patterns between pollock and Pacific cod pelagic flexion larvae continued to be apparent with growth and as the year progressed. While no other studies from the Bering Sea were available for comparison, larval pollock from June of 1987 in the Gulf of Alaska demonstrated a similar dietary composition to their con-specifics in this study. Pollock diet in 1987 had high abundances of *Pseudocalanus* spp. and *Acartia* spp. copepodites and adults (Grover, 1990), though these larvae were larger (10–30 mm SL) than those examined in this study. The similarity in diet composition indicates that feeding patterns described here are typical for pollock flexion larvae at similar latitudes. In contrast, Pacific cod flexion larvae in this study relied most heavily on mid to late calanoid copepodite stages in the SEBS. It is important to remember that the dietary composition for Pacific cod in summer is represented by only 4 fish at 4 stations and a total of 20 identifiable prey items. Thus, results presented here are unlikely to properly describe the overall diet of Pacific cod flexion larvae, and likely overestimates the dietary value of the large copepod *Neocalanus cristatus* (Table 5). The values for %W and %IRI are very likely to be positively biased due to the comparatively large size of this calanoid copepod. However, even with a sample size of 4, Pacific cod were consuming prey items that did not occur in the diet of pollock larvae. Summer Bering Sea Pacific cod diet was similar to that in mid-August in nearshore waters of the Gulf of Alaska (Abookire et al., 2007), which was restricted to unidentified calanoid copepodites, while smaller larvae of 5–10 mm SL still concentrated numerically on copepod nauplii, but were incorporating calanoid copepodite stages as well. The range of ingested prey items in comparison to the range of fish size was similar to this study, thus suggesting a preference of Pacific cod flexion larvae for a larger average prey size than that of similar life stages and size classes of pollock at similar latitudes. Even though the number of Pacific cod larvae collected in the summer was low, the differences in mean dietary composition and mean prey size between the two species were still disparate enough to be statistically significant, suggesting a difference in dietary niche.

Differences in feeding patterns between pollock and Pacific cod were most pronounced in the fall. Pacific cod maintained a slightly higher level of feeding incidence, 100% compared to 95.2% in pollock juveniles. Mean prey size was significantly higher in Pacific cod juveniles, while pollock juveniles were consuming significantly higher numbers of smaller prey items. This is similar to results presented by Lee (1985), in which the length distributions for both predator species overlap with juvenile size ranges in the fall portion of this study. Pacific cod were also reported to have a heavier stomach lining than juvenile pollock of the same size, possibly providing a more robust containment for larger prey (Lee, 1985). Over the collection period from 1981–1983, Pacific cod consistently switched to larger prey items than pollock at around 50 mm TL (Lee, 1985). The smallest juvenile cod in this study were just above 50 mm TL and were already consuming large prey items. Conversely, juvenile pollock dietary composition gradually changed by slowly increasing the maximum prey size, but continuing to consume significant proportions of small calanoid

copepods until well past a total length of 50 mm; both in this study, and in Lee's findings. Additionally, Lee reported that the mean number of prey per stomach decreased with size in Pacific cod, but increased with size in pollock (Lee, 1985), as in our results. Juvenile pollock in Uchiura Bay, Hokkaido, did not switch to a larger prey until approximately 80 mm TL (Kamba, 1977), nearly twice the length at which Pacific cod displayed a similar switch in dietary preference. While the dietary breadth of both species was similar in spring and summer, there was a significant difference in fall, with juvenile Pacific cod utilizing a wider range of prey taxa. This may be a reflection of diverging life history patterns, with Pacific cod moving to a more demersal lifestyle. The mean dietary composition was also different, primarily due to an increased number of large crustacean-type prey items consumed by Pacific cod. This was similar to Pacific cod diet in Mutsu Bay, Japan, where summer juveniles were feeding on comparatively large prey items, such as gammarid amphipods and juvenile pollock (Takatsu et al., 2001). The dietary composition (%W) of juvenile pollock was predominantly large calanoid copepods and euphausiids, similar to results reported for cold conditions in Coyle et al. (2011). The diet of juvenile Pacific cod has similarities to the diet of age-0 Atlantic cod (*Gadus morhua*), both on the eastern coast of the United States, where they were found to be concentrating heavily on mysids, amphipods, and euphausiids at a TL < 100 mm (Link and Garrison, 2002), and in the North Sea where they were also concentrating on crustaceans, such as developmental stages of crab, at concentrations of up to 76% by number (Demain et al., 2011). While juvenile pollock diet focused on small copepods numerically (> 70%), these taxa only accounted for < 9% of the total dietary weight. Conversely, large calanoid copepods only accounted for < 23% of the total number of prey items, but for > 41% of the total dietary weight, with *Calanus* spp. occurring in nearly 60% of all juvenile pollock stomachs. Under warm conditions, with reduced numbers of large prey items, juvenile pollock would likely have to consume higher numbers of small copepods to satisfy their energetic demands.

The prevalent hypothesis predicting variability in pollock recruitment in the SEBS is the Oscillating Control Hypothesis, OCH (Hunt et al., 2002, revised in 2011). The revised OCH postulates bottom-up controls on pollock recruitment during warm periods, resulting in reduced recruitment success. Bottom-up control implies a lack of adequate prey resources, via a late phytoplankton bloom which is propagated throughout the zooplankton community, and positions overlapping populations for potential resource competition. Increased coeval (intra-cohort) cannibalism and overwinter starvation in pollock during warm years is thought to be due to a lack of quality prey items in the previous growing season; namely larger lipid-rich zooplankton taxa such as the copepod *Calanus* spp. and euphausiids (Coyle et al., 2011; Heintz et al., 2013).

Annual differences in feeding performance reported in the literature are likely the result of changes in the prey environment. For example, during the comparatively cold years of 2006–2009, median zooplankton biomass was more than twice that of the previous warm years of 2000–2005 (Stabeno et al., 2012), with an even larger increase in the biomass of large zooplankton species of 5–10 fold in the SEBS, the latter primarily due to an increase in the abundance of *Calanus* spp. (Eisner et al., 2014). Cold conditions have also been beneficial to the recruitment of *Chionoecetes opilio* in the SEBS (Marcello et al., 2012; Parada et al., 2010), a component of the diet of juvenile Pacific cod in this study. Also, there has been a distributional shift to the south of the Arctic hyperiid amphipod *Themisto libellula* since 2006 (Pinchuk et al., 2013). This species, which is primarily restricted to the Middle Domain of the eastern Bering Sea, has a high nutritional value due to its high lipid content (Noyon et al., 2011). Since the onset of the recent cold conditions, *T. libellula* has not only appeared in the eastern Bering

Sea, but also in the diet of age-0 Pacific cod, where it was a substantial component by dietary weight (25–55%) within four years (Pinchuk et al., 2013). The absence of *T. libellula* in juvenile Pacific cod diet in this study may have been due to the low sample size of Pacific cod taken from within the cold pool. *Themisto libellula* is also thought to be a substantial predator on *Calanus* spp. with an estimated average predation impact of 35.8% of the standing stock of *Calanus* spp. per day and a maximum of 225% per day (Pinchuk et al., 2013). Thus, during cold conditions, it appears that not only are the diets of pollock and Pacific cod partitioned by size, but that Pacific cod may, to some extent, alleviate pressure on a preferred and energetically advantageous food source for pollock, while still obtaining energetically advantageous prey themselves.

During warm conditions, the absence of large, high-quality prey items in the Middle Domain results in sub-optimal prey resources for early life stages of Pacific cod and pollock (Coyle et al., 2011). These sub-optimal feeding conditions are reflected in a reduced total energetic content and reduced lipid content for age-0 pollock (Heintz et al., 2013). During warm years, age-0 pollock are displaced from the Outer to the Middle Domain (Smart et al., 2012), placing them in direct proximity to the center of abundance of age-0 Pacific cod (Hurst et al., 2012), thus enhancing the potential for competition due to greater spatial overlap between the two species. Other forage fish species, such as Pacific sand lance (*Ammodytes hexapterus*) and Pacific herring (*Clupea pallasii*), rely heavily on small copepods in the Gulf of Alaska (Purcell and Sturdevant, 2001). The dietary overlap between pollock, herring, and sand lance in that study ranged from 47–84%. Multiple species of gelatinous zooplankton were also relying heavily on small copepods, ranging from 40% numerically in *Pleurobrachia bachei* (Phylum: Ctenophora) to 60% by number in *Aurelia labiata* (Phylum: Cnidaria). Fluctuations in the zooplankton community in response to thermal conditions were most evident in the Middle Domain (Eisner et al., 2014). Thus, in warm years, survival of age-0 pollock may suffer from limited high-quality prey resources and higher rates of predation pressure from conspecifics in the form of cannibalism (Coyle et al., 2011) and from co-occurring age-0 Pacific cod (BASIS, unpublished data).

In the beginning of the production season, pollock exhibit low lipid and total energetic content, probably as a strategy of energy allocation towards somatic growth (Siddon et al., 2013). However, energy allocation patterns in pollock seem to change in late summer (July–September) from favoring somatic growth towards energy storage as a strategy to increase the probability of overwinter survival (Siddon et al., 2013). During warm conditions, total pollock energy densities nearing winter were an average of 35% less than those in cold years, accompanied by a threefold reduction in total lipid content (Heintz et al., 2013). Pacific cod seem to follow a similar pattern (Heintz, pers. comm.). It is likely that these changes in energy content are the result of the differences in the abundance of large and nutritious prey taxa during different thermal conditions (Coyle et al., 2011; Eisner et al., 2014; Heintz et al., 2013; Stabeno et al., 2012).

Trophic interactions between age-0 pollock and Pacific cod in the SEBS appear to be modulated by climate variability, with prey resource partitioning between the two species in cold years, and the potential for competition for sub-optimal prey resources during warm conditions (Coyle et al., 2011; Eisner et al., 2014). The latter may be further complicated by increased pollock mortality due to cannibalism and predation by Pacific cod. Additionally, age-0 pollock experience increased metabolic stress under warm conditions that result in fish that contain only 1/3 the lipid content than their cold condition counterparts (Heintz et al., 2013). These conditions may lead to poor nutritional status of juvenile stages of both species heading into the winter of their first year. Ultimately, these factors are likely to result in poor over-winter survival and subsequent recruitment success (Heintz and Vollenweider, 2010; Kooka and Yamamura, 2012).

Results presented here indicate temporally increasing prey partitioning throughout the first year, suggesting that co-occurring larval and juvenile stages of pollock and Pacific cod avoid competition during cold conditions in the SEBS. While Pacific cod consumed fewer, larger-bodied prey items, especially in the fall, juvenile pollock continued consuming increasing numbers of calanoid copepods, such as *Calanus* spp., *Pseudocalanus* spp., and *A. longiremis*. One potential explanation for the observed differences in prey size may be due to gape size, as morphological differences between Pacific cod and pollock at similar body sizes have been demonstrated (Lee, 1985). A positive relationship for gape size-prey size ratios have been demonstrated for different life stages of a number of marine species, including Atlantic cod (Puvanendran et al., 2004; Scharf et al., 2000). However, the observed partitioning of prey between the two species may be restricted if warmer temperatures lead to a decline in the abundance of large zooplankton species (Coyle et al., 2011; Eisner et al., 2014; Hunt et al., 2011; Stabeno et al., 2012), and consequently the diets of these two gadoid fishes may converge under warm conditions. During warm conditions age-0 Pacific cod may not only potentially compete with pollock, but may also consume pollock directly (Takatsu et al., 2002; BASIS, unpublished data). These scenarios, which could impact recruitment success, warrant further exploration, particularly under the expected warming of the sub-arctic waters of the southeastern Bering Sea (Mueter et al., 2011).

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