



Effect of region on the food-related benefits to age-0 walleye pollock (*Theragra chalcogramma*) in association with midwater habitat characteristics in the Gulf of Alaska

Matthew T. Wilson*, Kathryn L. Mier, and Christina M. Jump

Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7600 Sand Point Way NE, Seattle, WA 98115, USA

*Corresponding author: tel: +1 206 526 6522; fax: +1 206 526 6723; e-mail: matt.wilson@noaa.gov.

Wilson, M. T., Mier, K. L., and Jump, C. M. 2013. Effect of region on the food-related benefits to age-0 walleye pollock (*Theragra chalcogramma*) in association with midwater habitat characteristics in the Gulf of Alaska – ICES Journal of Marine Science, 70: 1396–1407.

Received 19 March 2013; accepted 18 July 2013; advance access publication 16 August 2013.

In the western Gulf of Alaska (GOA), we compared age-0 juvenile walleye pollock body weight, food habits, and expected growth rates between two regions during 3 years. The benefit to rearing off Kodiak Island vs. in the Semidi Islands vicinity increased among years with body length because larger fish consumed more euphausiids, and euphausiids were apparently more available in the Kodiak region. This explains previously observed regional variation in body size, condition, and growth rates within the GOA population and points to potential importance of the Kodiak region as a walleye pollock nursery. During September 2005, 2007, and 2009, Kodiak midwater was cooler and saltier than Semidi midwater, presumably due to a relatively narrow continental shelf and greater oceanic influence. Zooplankton composition differed between regions with the greater euphausiid population density off Kodiak being most relevant to walleye pollock food habits. As found historically, age-0 walleye pollock abundance was lower in the Kodiak region than in the Semidi region. However, the Kodiak fish were larger in both length and length-specific weight, and had fuller stomachs than Semidi fish, although differences were not significant in all years. Regional differences were most pronounced during the relatively warm year 2005 when fish were particularly large. Fish dietary mass was dominated by euphausiids, especially for Kodiak fish ≥ 55 mm standard length. Bioenergetics model output suggests that the greater euphausiid dietary proportion translates into faster growth of the Kodiak fish. The midwater habitat off Kodiak Island might therefore support above-average production of recruits to the GOA adult population due to better condition and likely survival of walleye pollock juveniles, especially when fish are large and thus able to more fully exploit euphausiids, but confirmation of above-average production of recruits depends on our ability to determine spatial structure in juvenile-adult population connectivity.

Keywords: abundance, bioenergetics, body size, diet, fish, food habits, growth, marine, nursery.

Introduction

Fish nurseries have long been recognized as critical for production of juveniles that recruit to adult populations. Nurseries have been defined as habitats where production of recruits (Dahlgren *et al.*, 2006) or recruits per unit area (Beck *et al.*, 2001) is above average. For many species, the habitats frequented by juveniles are known, but determining habitat- or area-specific productivity is complicated by the difficulty of following specific groups to recruitment (Gillanders *et al.*, 2003); consequently, the specific location of many nurseries remains elusive. Despite this difficulty, it is worthwhile to try to identify high-production areas (i.e. nurseries) because success will enable subsequent biological and ecological research to focus on geographic

areas where most recruits are produced (Sheaves *et al.*, 2006). One approach is to compare juveniles among geographic regions, assuming no migration, for evidence of regional differences in biology and ecology that are relevant to growth and survival; for example, food quantity and quality. An underlying assumption is that fuller stomachs and a calorie-rich diet contribute to faster growth and greater accumulation of energy reserves, which can reduce vulnerability to predation and improve survival during adverse environmental conditions (e.g. lipid accumulation before overwinter prey scarcity). We used this approach to compare the food-related benefits that juvenile walleye pollock (*Theragra chalcogramma*) accrue from residing in each of two coastal regions in the Gulf of Alaska (GOA).

Walleye pollock, a semi-demersal gadid, is an economically and ecologically prominent fish in coastal North Pacific ecosystems. As adults, walleye pollock support large commercial fisheries, and are a major trophic component in many areas due to their high abundance and their consumption of zooplankton and small fish (Springer, 1992). As juveniles, walleye pollock are a major dietary component of many fish, marine mammals, and seabirds (Brodeur and Bailey, 1996).

In the GOA, the results of extensive research show that juvenile walleye pollock are abundant over the western shelf with considerable geographic variation in their biology and ecology (Brodeur and Wilson, 1996; Wilson, 2009). Few individuals are found beyond the shelf break because, presumably, they avoid the colder, more saline Alaskan Stream, a fast-flowing boundary current that could quickly transport individuals to the southwest (Stabeno *et al.*, 2004; Wilson, 2009). During September, many young-of-the-year (age-0) juveniles occur in the Semidi Islands vicinity southwest of Shelikof Strait (Brodeur and Wilson, 1996) (Figure 1). This reflects downstream

transport of larvae in the Alaska Coastal Current from Shelikof Strait where the largest spawning aggregation of walleye pollock in the GOA forms each spring (Bacheler *et al.*, 2009). Some age-0 juveniles also occur along the Gulf-side of Kodiak Island (Wilson *et al.*, 2005), which is not downstream from Shelikof Strait, perhaps reflecting production from other spawning aggregations. Late-summer population densities have historically been lower off Kodiak than in the Semidi region, but the Kodiak population includes age-0 juveniles that are larger than Semidi fish, and recruitment is better predicted by population density in the Kodiak region than in the Semidi region (Wilson, 2000). The number of recruits produced from the Kodiak region is unknown, but it could be substantial if juvenile survival is highly relative to elsewhere in the GOA; furthermore, production from it and other less-populated areas might contribute to spawning stock diversity (Olsen *et al.*, 2002).

Age-0 walleye pollock are predominantly zooplanktivorous and preliminary evidence indicates that late-summer juveniles in the

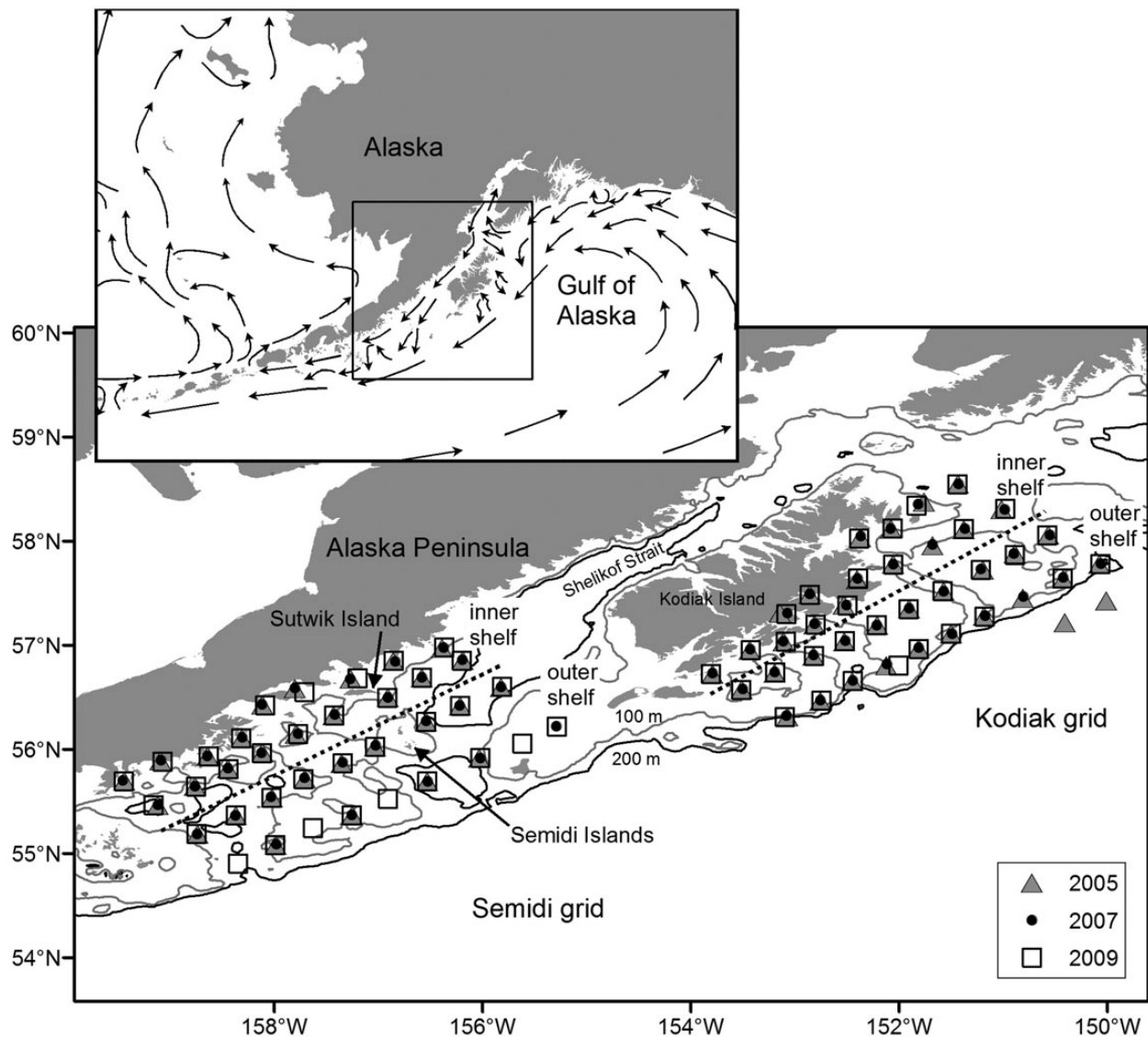


Figure 1. Map of ocean currents (top, from Reed and Schumacher, 1986) and sites in the GOA (bottom) where sampling was conducted during September 2005, 2007, and 2009 to measure water temperature and salinity, and to collect zooplankton and age-0 walleye pollock. Each grid is divided (dotted line) into inner-shelf and outer-shelf area.

Kodiak region consume more euphausiids than those in the Semidi region (Merati and Brodeur, 1996; Wilson *et al.*, 2011). Because euphausiids are energy-rich relative to most other prey (Mazur *et al.*, 2007), consuming large portions of them could explain the better body condition (Buchheister *et al.*, 2006) and larger size (Wilson, 2000) of the Kodiak juveniles. Although the larger body size of the Kodiak juveniles could reflect spawn timing rather than a region-specific, food-related effect, available evidence indicates that Kodiak (Wilson *et al.*, 2005) and Semidi (Dougherty *et al.*, 2012) juveniles have similar hatch dates and that the Kodiak fish can grow faster (Brown and Bailey, 1992; Bailey *et al.*, 1996). Faster growth reduces the length of time fish are vulnerable to size-selective predation (Sogard, 1997), and predation on juveniles is thought to be a major factor controlling walleye pollock recruitment dynamics (Bailey, 2000). A euphausiid-rich diet might also promote overwinter survival by allowing age-0 juveniles to accumulate storage reserves before winter when prey densities are low (Heintz *et al.*, 2013). We therefore wanted to examine whether age-0 walleye pollock benefit more from residing off Kodiak Island when compared with in the Semidi region, which has historically had higher age-0 walleye pollock abundance. If so, more research is warranted to determine whether the Kodiak region qualifies as a walleye pollock nursery, and what the actual contribution of each nursery is to the adult population. Thus, our objective was to compare the food habits and body size of age-0 walleye pollock between regions in association with region-specific midwater physical and prey-field characteristics.

Methods

Study area

The study area consisted of two grids of predetermined collection sites situated in regions of known age-0 walleye pollock habitat (Figure 1). The Kodiak grid was situated off the Gulf side of Kodiak Island and the Semidi grid encompassed Semidi Bank; each grid represents $\sim 30\,000\text{ km}^2$. Sites were occupied by sampling along inshore–offshore lines of stations beginning at the northernmost site in the Kodiak region and ending at the southwesternmost line of the Semidi grid. At each site, we first characterized the local habitat in terms of water temperature, salinity, and zooplankton composition, then sampled the local age-0 walleye pollock population to determine local abundance, size composition, and to collect fish for subsequent laboratory determination of body weight, stomach weight, and diet. Sampling occurred 24 h d^{-1} during September 2005, 2007, and 2009 aboard the NOAA ship *Miller Freeman*.

Water temperature and salinity

Water temperature and salinity measurements were taken using a calibrated Sea-Bird Electronics (SBE) 19 plus SeaCat profiler, which was deployed on the tow wire immediately above the zooplankton sampling array. The profiler was used to monitor real-time depth of the array and to measure water temperature ($^{\circ}\text{C}$) and salinity (practical salinity units, psu) during the up-cast portion of each tow. The accuracy of the profiler was verified by comparison to data collected with a Sea-Bird 911+ CTD during several casts made at the start, middle, and end of each cruise.

The measurements taken at 40-m water depth were used to characterize the temperature and salinity of the midwater habitat. Based on these measurements, we divided each of our sampling grids (Kodiak, Semidi) into a warm inner-shelf area and a relatively

cold, saltier outer-shelf area (Figure 1). This delineation was incorporated as a cross-shelf effect in statistical tests of regional differences in zooplankton community composition and age-0 walleye pollock abundance, size, and food habits.

Zooplankton

Zooplankton was collected with a ringnet (25.4 cm diameter mouth opening, $153\text{-}\mu\text{m}$ mesh net) and a 1-m^2 Tucker trawl ($333\text{-}\mu\text{m}$ mesh). The ringnet was mounted in the drogue net of the Tucker trawl and fished on the descent to collect small zooplankton. The drogue net was closed at depth (200 or 5 m off bottom, whichever was shallowest). Larger zooplankton were collected in the Tucker trawl during the ascent. All nets were equipped with calibrated flowmeters. Each zooplankton sample was sorted and enumerated at the Polish Plankton Sorting and Identification Center (Szczecin, Poland) using protocol established by the Alaska Fisheries Science Center (Siefert and Incze, 1991). Taxa were grouped following previous age-0 walleye pollock prey field studies (Wilson, 2009). Catches were standardized to volume filtered (no m^{-3}). Standardized catches were fourth-root transformed to normalize the error structure; we report back-transformed means.

Multivariate analyses were used to determine the statistical significance of Kodiak–Semidi differences in zooplankton community composition. Within each year, the regional difference was tested for statistical significance using an analysis of similarity (ANOSIM) implemented in PRIMER v6 software (Clarke and Gorley, 2006). ANOSIM is a non-parametric, multivariate analysis analogous to a univariate analysis of variance (ANOVA) (Clarke and Warwick, 2001). Bray–Curtis similarities were computed from population densities after fourth-root transformation, which was applied to give less weight to very abundant species and more weight to the mid-range species so that the computed Bray–Curtis similarities/dissimilarities were more meaningful (Clarke and Green, 1988). The ANOSIM was followed by a SIMPER (Similarity Percentages) analysis to determine group-specific contributions to regional differences in the prey field (Clarke and Warwick, 2001). A two-dimensional nonmetric multidimensional scaling (NMDS) ordination plot was used to graphically show the differences in community composition between Kodiak and Semidi. NMDS is an iterative ordination method that projects multivariate data onto two dimensions preserving, as much as possible, the rank order of the dissimilarity measure.

Walleye pollock

Fish were collected with a small-mesh midwater trawl from the upper 200 m or where shallower from the sea surface to 5 m off bottom (Wilson, 2009). Walleye pollock were sorted by body length into two age groups. Age-0 ($\leq 140\text{ mm}$ standard length, SL) individuals were distinctly smaller than older age-1+ ($\geq 140\text{ mm}$, SL) fish. Age-0 walleye pollock were enumerated and SL measured. Large catches (>100 individuals) were randomly subsampled to obtain ~ 100 individuals, which were measured at sea to the nearest millimetre SL. A random sample of individuals was frozen at -80°C and stored at -20°C for later examination in the laboratory.

In the laboratory, body weight and food habits of age-0 walleye pollock were determined using fish frozen at sea. Samples collected during 2007 and 2009 were thawed and processed within 3 months of collection. For 2005, however, some samples were processed within 3 months of collection, but most (34 of 40) samples were thawed and processed 10 months after collection; this delay was incorporated in statistical analyses by including a process-month effect as detailed later. For small samples (≤ 20 fish), all individuals

were examined; otherwise, 20 individuals were selected for determination of body weight. Each of the 1349 selected fish was measured to the nearest millimetre SL, blotted dry, and weighed to the nearest milligramme. For determination of food habits, stomachs were excised between the oesophagus and pylorus and stored individually in a sodium borate-buffered 10% formalin solution. All stomachs up to a maximum of 20 per sample were used to determine food habits during 2005; the maximum was reduced to 10 fish per sample for 2007 and 2009 due to laboratory resource constraints. The total number of stomachs examined was 1135. For each stomach, content weight (SCW) was measured to the nearest 0.01 mg. The contents were then sorted into prey groups based on taxonomy, size, and digestion following Wilson *et al.* (2009). For each prey group, all individuals were counted, blotted dry, and collectively weighed to the nearest 0.01 mg. Weights and counts of groups consisting of largely intact prey were used to indicate prey size, which was computed as group weight divided by prey count (i.e. mean individual weight). Thus, fish abundance and size composition were determined at sea, and fish body weight, SCW, and diet were determined from samples examined in the laboratory.

Statistical tests were used to detect regional differences in the univariate (abundance, body length and weight, and SCW) and multivariate (diet) data. Regional variation in abundance (no m^{-2}) was tested using a simple ANOVA; a fourth-root transformation was applied to normalize the error structure, but we report back-transformed means. Abundance was computed following Wilson (2009).

Regional variation in body length, length-specific body weight, and SCW was tested using a mixed model analysis with haul (nested within region and cross-shelf area) as a random factor, and year and cross-shelf as fixed effects. For the body weight and SCW analyses, length was included as a covariate. The body weight analysis was based on log-transformed data to linearize the model. SCW was expressed as proportion of somatic weight ($\text{SCW}/[\text{body weight} - \text{SCW}]$) and arcsine-transformed to normalize the error structure. For 2005, when 34 of the 40 samples were processed 10 months after collection, process month was incorporated into the body weight and SCW models as a fixed factor. Each variable (body length, body weight, and SCW) was weighted by abundance. The abundance weight was computed as age-0 walleye pollock abundance at a site, within year, divided by the number of observations from the sample collected at that site.

Regional variation in age-0 walleye pollock diets was analysed using Bray–Curtis similarities between samples in the PERMANOVA (permutational MANOVA) procedure in PRIMER 6 (Clarke and Gorley, 2006) with PERMANOVA+ software (Anderson *et al.*, 2008). The procedure was used to examine prey count and prey weight, which for each of the 1035 fish were expressed as per cent of total prey; 100 fish were excluded from the diet analysis because each contained only unidentified prey or miscellaneous items (e.g. fish scale). A fourth-root transformation was applied to reduce the influence of highly abundant species relative to less-abundant species on the computed Bray–Curtis similarities/dissimilarities (Clarke and Green, 1988). PERMANOVA is a highly flexible and robust procedure that accounted for the nested structure of the sampling design where fish were nested within hauls, and hauls were nested within region and cross-shelf area. This procedure also allowed inclusion of the covariate, SL, which can affect diet (Wilson *et al.*, 2009). A SIMPER (similarity percentages) procedure (Clarke and Warwick, 2001) in PRIMER was used to determine prey group contributions to dissimilarity between regions.

We used a bioenergetics model to estimate daily growth rate from observed year- and region-specific water temperature and diet, and to identify the diet component (prey group) most responsible for regional differences in the expected growth rate. In the model, which was parameterized for juvenile walleye pollock (Ciannelli *et al.*, 1998), the energy available for growth equals the total energy consumed minus the energy lost to waste, activity, and respiration; maximum consumption and metabolism scaled allometrically to body mass and water temperature. Inputs were fish body weight (g), diet (%W), daily ration (%BW, Wilson *et al.*, 2011), predator energy density (J g^{-1} , Buchheister *et al.*, 2006), taxon-specific prey energy densities (J g^{-1} , Mazur *et al.*, 2007), and water temperature ($^{\circ}\text{C}$). To control for fish length, we input the body weight of a 70-mm SL fish, a body length common to all regions and years, estimated using region-specific length–weight relationships (Buchheister *et al.*, 2006). The output was daily growth rate. To determine each prey group's effect on region-specific growth rate each year, we reran the model multiple times and each time equated the proportions of one prey group between regions. For example, for 2005, the effect of euphausiids on the expected growth rates of Kodiak fish and Semidi fish was determined by inputting fish diet as observed for each region except that euphausiid weight was equated (averaged) between regions before computing prey-group proportions. We similarly examined the effect of water temperature on the difference in growth rate.

Results

Water temperature and salinity

The coastal ocean at 40-m depth was consistently colder and slightly more saline in the Kodiak region than in the Semidi region (Figure 2). Off Kodiak, the water averaged 8.4°C and 32.1 psu when compared with 9.2°C and 31.7 psu in the Semidi region. Water temperature was warmest during 2005, and cross-shelf gradients were evident in both regions. Thus, while cross-shelf gradients were prominent in both regions, the midwater habitat in the Kodiak region was generally colder and more saline reflecting greater oceanic influence than in the Semidi region.

Zooplankton

The zooplankton collection consisted of 207 samples collected over all stations and years. A total of 18 groups was represented in the collection. Four groups of gelatinous zooplankton were omitted from subsequent analysis because they were not found in the stomach contents of age-0 walleye pollock; so, we did not consider them part of the prey field of age-0 walleye pollock.

Each year, numerical composition of the zooplankton samples differed between regions. Initial ANOSIM test results were complicated by significant differences in composition across the shelf ($p < 0.05$); therefore, subsequent between-region tests were conducted within each year and cross-shelf area. Composition of the zooplankton community differed significantly between Kodiak and Semidi regions ($p < 0.05$), except for 2007 outer shelf, which was marginally not significant ($p = 0.06$, Table 1). However, R -values were small (< 0.2) for all tests except 2005 inner shelf indicating weak separation. Yearly NMDS plots further illustrate the strength of these differences (Figure 3). Five groups accounted for $> 70\%$ of the total dissimilarity: barnacle larvae, larvaceans, thecosomate pteropods (Thecosomata), pre-juvenile euphausiids, and small copepods (Table 2). The mean densities of thecosomate pteropods, small copepods, and crab larvae (Reptantia) were highest in the Semidi region, whereas the cooler, more-saline Kodiak habitat

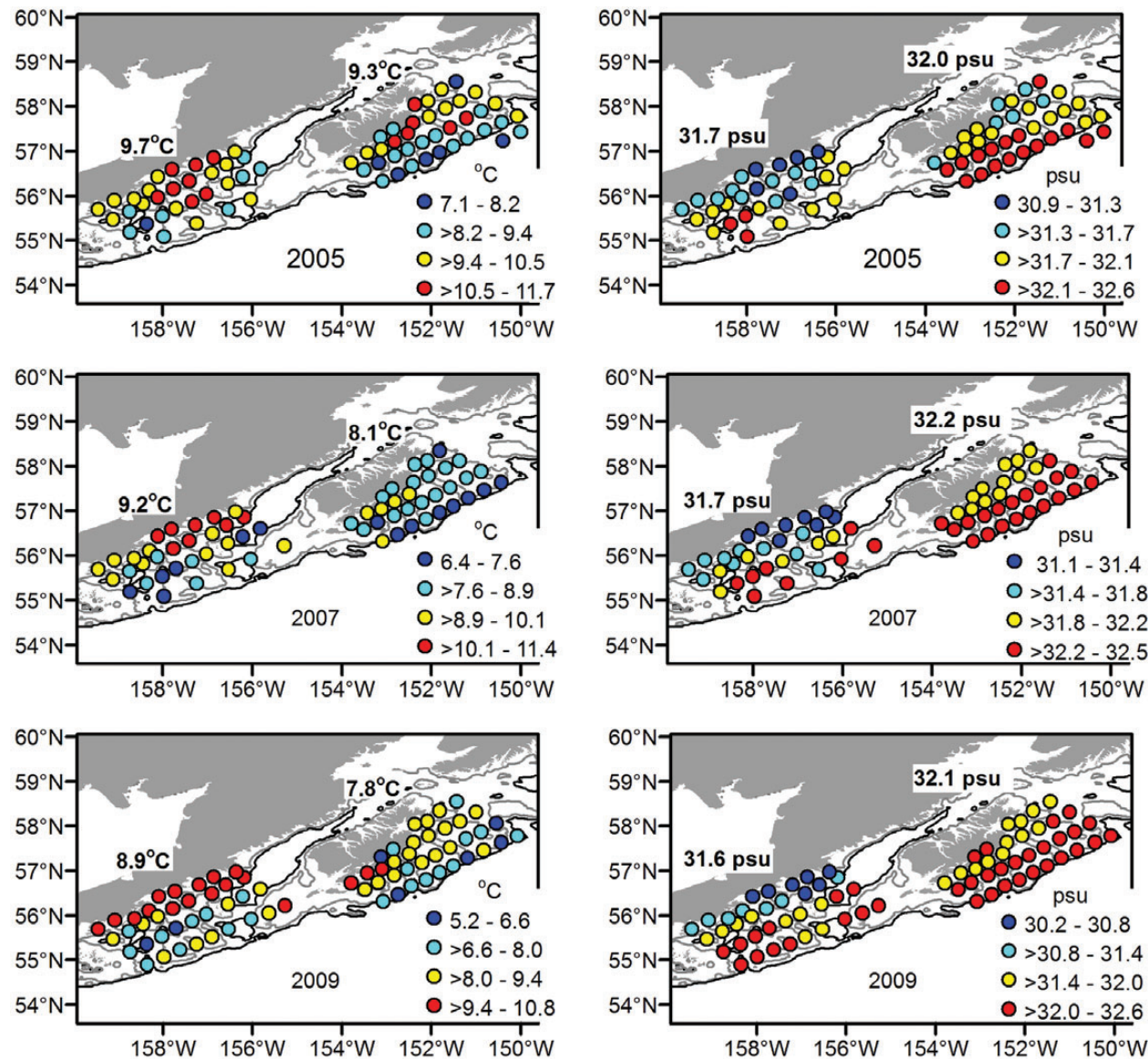


Figure 2. Water temperature (°C) and salinity (psu) were measured at 40-m water depth where sampling occurred in the western GOA during September 2005, 2007, and 2009 (means are indicated by year and region). A colour version of this figure can be accessed online.

Table 1. ANOSIM test results of the difference between the Kodiak and Semidi regions in composition of *n* zooplankton samples collected in Tucker trawls during September 2005, 2007, and 2009 in the western GOA.

Year	<i>n</i>	Inner shelf		Outer shelf	
		<i>p</i> -value	<i>R</i>	<i>p</i> -value	<i>R</i>
6–18 September 2005	69	0.001	0.599	0.011	0.195
5–15 September 2007	66	0.040	0.101	0.060	0.082
6–19 September 2009	72	0.006	0.143	0.027	0.066

Tests were conducted within collection year and cross-shelf area (inner shelf, outer shelf). *R* is a measure of separation between regional groups of samples (separation increases as *R* approaches 1).

had higher mean densities of pre-juvenile euphausiids and barnacle larvae (Table 3). Regional differences in population density of larva-ceans were not consistent among years. Interestingly, the mean

density of pre-juvenile euphausiids decreased from 2005 to 2009 during the study; similarly, larger euphausiids (juvenile and adult) decreased from 2005 to 2009 and although this latter group contributed less to total dissimilarity based on numerical abundance, they also tended to be densest off Kodiak, which was relevant to age-0 walleye pollock food habits.

Walleye pollock

Consistent with historical observations, data from 207 trawl hauls indicated that there were fewer age-0 walleye pollock in the Kodiak region than around the Semidi Islands and average body length of the Kodiak individuals was larger. The regional effect on abundance was significant regardless of year, but the larger mean length of the Kodiak fish was significant only during 2005 and 2009 (Table 4). Across the shelf, large fish seemed to concentrate more over the inner shelf in the Kodiak region than in the Semidi

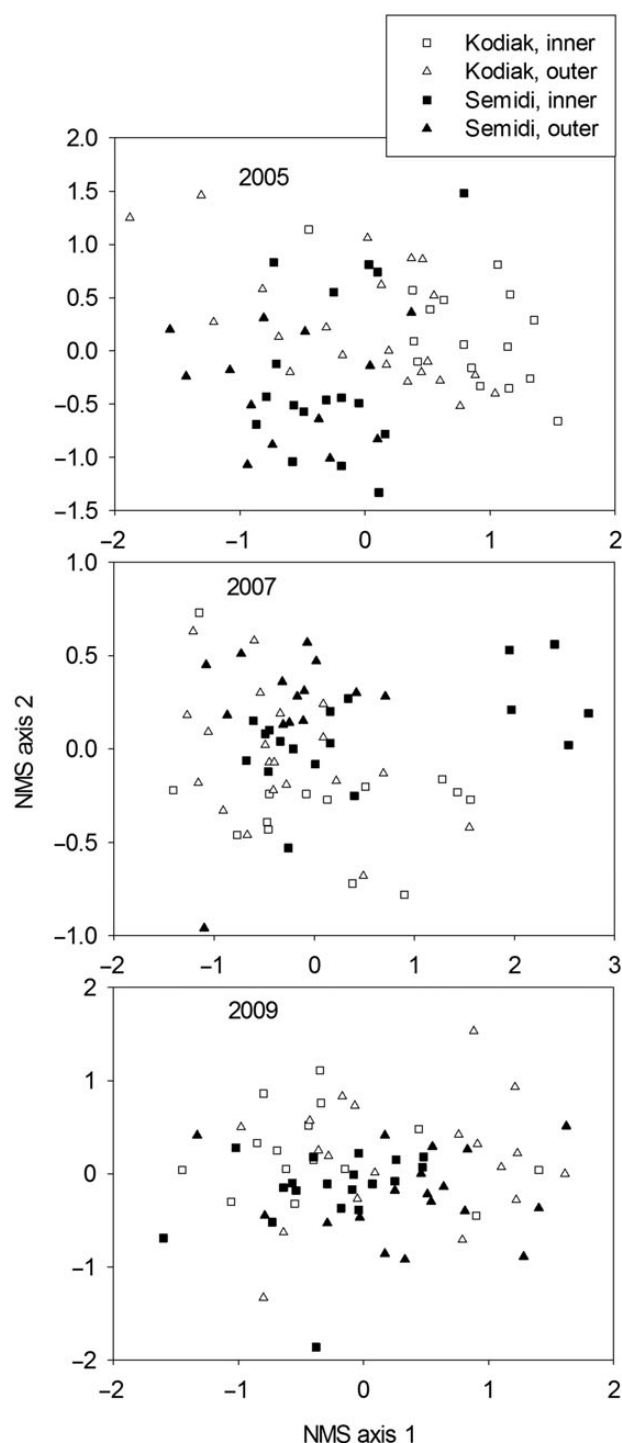


Figure 3. For each year, NMDS (non-metric multidimensional scaling) ordination of zooplankton samples by taxonomic composition. Samples were collected in the Kodiak and Semidi regions of the western GOA during September 2005, 2007, and 2009. Within each year and region, symbols distinguish samples collected over the inner shelf from those collected over the outer shelf.

region; however, no cross-shelf differences in abundance or length were statistically significant ($p > 0.05$) in either region.

Length-specific body weight differed between Kodiak and Semidi fish during 2005 ($p = 0.003$) and 2009 ($p = 0.013$), but

not during 2007 ($p = 0.502$). The Kodiak fish were heavier than Semidi fish by 8% in 2005 and by 4% in 2009 (Table 5). The difference found for 2005 was limited to samples processed in July, when samples from both regions were processed, due to a significant process-date effect ($p = 0.010$). The cross-shelf effect was marginally not significant during 2007 ($p = 0.089$) and not significant in 2005 or 2009. Interestingly, the regional difference in body weight increased among years with body length (Table 4), suggesting that in 2007, fish were too small to exploit any regional difference in food resource.

Age-0 walleye pollock SCW differed between regions during 2005 ($p = 0.006$). The process-date effect ($p = 0.735$) and cross-shelf effect ($p = 0.340$) were not significant and therefore dropped from the model. Stomach content weight of the Kodiak fish in 2005 was 1.7% of somatic body weight (back-transformed, abundance-weighted mean) when compared with 0.8% for the Semidi fish. No difference in SCW was detected between Kodiak and Semidi regions during 2007 ($p = 0.786$, overall mean = 0.6%) or 2009 ($p = 0.208$, overall mean = 1.1%). Thus, the greatest difference in SCW between regions occurred during 2005 when fish were larger and the density of euphausiids in the zooplankton was higher than in 2007 and 2009.

The overall diet of age-0 walleye pollock consisted of 17 prey groups (Table 6), including miscellaneous and unidentified prey, but prey composition changed with fish length and between regions. Diet transitioned with increasing predator length to include larger prey, such as juvenile and adult euphausiids (Figure 4). We therefore compared diet between regions within 10-mm fish length bins. Clearly, a region effect was superimposed on the length-related transition due most noticeably to greater proportions of juvenile and adult euphausiids in the Kodiak region for fish ≥ 55 mm SL (Figure 4). Statistically, PERMANOVA test results indicated that the length and region effects were significant during 2005 (Table 7) and 2009 (length effect, $p = 0.001$; region effect, $p < 0.024$), but not 2007 (length effect, $p > 0.20$; region effect, $p > 0.18$). We only tabulated the PERMANOVA results of the 2005 prey-count data analysis because other significant test results were similar. For 2007, the absence of large fish (> 84 mm SL) (Figure 4) could have contributed to the non-significance of the length effect. SIMPER results indicated that juvenile and adult euphausiids contributed most (30%) to the dissimilarity in diet between the Kodiak and Semidi regions during 2005 (Table 8) and 2009. Thus, age-0 walleye pollock underwent a size-related dietary transition, but fish in the Kodiak region consumed proportionally more juvenile and adult euphausiids than did Semidi fish.

In addition to a relatively euphausiid-rich diet, the Kodiak fish consumed juvenile and adult euphausiids that were larger than those consumed by Semidi fish. The mean individual weight of juvenile and adult euphausiids, which were recovered intact from fish representing 52 samples, significantly differed between Kodiak and Semidi regions ($p < 0.006$). The region-year interaction was not significant ($p = 0.653$), indicating that the Kodiak fish consistently consumed larger euphausiids (Figure 5). Interestingly, the year effect was significant ($p < 0.001$) due to the mean euphausiid weight being about twice as heavy during 2005 than during 2007 and 2009, which were not different ($p = 0.585$). This regional and interannual variation was not likely due to differences in digestion or fish size because we considered only prey that were recovered intact from stomachs of fish 65–84 mm SL, a size range that was fully represented in each year. Thus, the euphausiids recovered from fish stomachs were on average larger and contributed more

Table 2. For each year and cross-shelf area (inner, outer), SIMPER (Similarity Percentages) per cent contribution by each zooplankton group to the Bray–Curtis dissimilarity in zooplankton composition between Kodiak and Semidi regions.

Group	2005		2007		2009	
	Inner	Outer	Inner	Outer	Inner	Outer
Amphipoda	3.45	3.70	1.72	3.33	6.08	4.87
Chaetognatha	3.17	2.41	1.98	2.85	6.88	4.56
Cirripedia	19.18	12.40	11.76	11.26	12.51	9.49
Copepoda, lg	5.19	6.27	3.31	6.10	4.79	7.48
Copepoda, sml	10.47	13.64	30.37	22.80	19.49	21.14
Euphausiacea, juv. + adult	5.94	4.07	2.59	3.50	3.58	4.96
Euphausiacea, pre-juv.	11.25	15.53	7.25	8.04	2.14	0.97
Larvacea	16.52	17.72	17.66	15.35	17.30	18.12
Mysidacea	1.61	0.71	0.94	0.65	2.26	0.81
Natantia	4.42	4.37	No data ^a	No data ^a	4.83	2.74
Osteichthyes larvae	0.32	0.22	1.44	1.19	0	0
Ostracoda	0	1.30	0.43	4.34	0	2.71
Reptantia	5.55	3.29	1.44	3.24	4.34	3.28
Thecosomata	12.93	14.39	19.09	17.34	15.80	18.88

^aNatantia were erroneously not sorted from the catch in 2007.

Table 3. Back-transformed mean density (no·m⁻³) of zooplankton groups by year and region (Kodiak, Semidi) as estimated from Tucker trawl samples collected in the western GOA during September 2005, 2007, and 2009.

	2005		2007		2009	
	Kodiak	Semidi	Kodiak	Semidi	Kodiak	Semidi
Amphipoda	0.05	0.02	0.03	0.10	0.05	0.08
Chaetognatha	1.95	2.44	2.31	2.13	0.14	1.17
Cirripedia	17.35	0.32	54.51	3.01	1.51	0.30
Copepoda, lg	24.00	42.30	35.58	34.00	23.52	28.44
Copepoda, sml	1884.27	2625.07	13 176.95	28 087.22	5518.33	7958.26
Euphausiacea, juv. + adult	6.77	2.30	2.70	0.95	0.82	0.98
Euphausiacea, pre-juv.	31.90	2.65	7.69	0.33	<0.01	<0.01
Larvacea	186.52	48.09	516.35	2079.78	122.75	104.02
Mysidacea	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Natantia	0.74	0.26	No data ^a	No data ^a	0.21	0.14
Osteichthys larvae	<0.01	0	0.09	0.02	0	0
Ostracoda	<0.01	0	<0.01	<0.01	<0.01	<0.01
Reptantia	0.44	0.65	0.59	1.90	1.46	2.17
Thecosomata	4.02	17.08	69.41	1822.27	43.14	267.86

^aNatantia were erroneously not sorted from the catch in 2007.

Table 4. Back-transformed mean abundance and abundance-weighted mean standard length of age-0 walleye pollock collected in *n* samples from the GOA during September 2005, 2007, and 2009.

Year	<i>n</i>	Abundance (no.100 m ⁻²)			Length (mm SL)		
		Kodiak	Semidi	<i>p</i> -value	Kodiak	Semidi	<i>p</i> -value
6–18 September 2005	69	0.157	8.503	0.003	84.8	76.9	0.001
5–15 September 2007	68	0.001	2.459	<0.001	68.1	63.1	0.264
6–19 September 2009	70	0.026	1.172	0.001	77.5	68.7	<0.001

p < 0.05 indicates significant difference between Kodiak and Semidi regions.

to the diet of age-0 walleye pollock in the Kodiak region than in the Semidi region.

Bioenergetics model output indicated that our observed regional differences in diet translated into growth rates that were faster for the Kodiak fish than for the Semidi fish, and that this was primarily due to the greater proportion euphausiids in the diet of Kodiak fish. Our region-specific estimates of growth rate ranged from 0.12 mm d⁻¹ (0.016 g d⁻¹) to 0.50 mm d⁻¹ (0.071 g d⁻¹) (Figure 6).

Depending on year, the Kodiak fish were predicted to grow faster than Semidi fish by 0.02–0.37 mm d⁻¹. Equating the euphausiid proportions had a much greater effect on reducing or reversing the between-region difference in growth rate than any other dietary component or water temperature (Figure 6). The euphausiid effect on growth rate estimates was also evident from the comparatively low growth rates estimated for the Semidi region during 2007, when the dietary proportion of euphausiids for 70-mm fish was

Table 5. Mixed-model test results by year of region (Kodiak, Semidi) and cross-shelf (inner, outer shelf) effects on the body weight [Ln(Wt)] of 1349 age-0 walleye pollock collected during September 2005, 2007, and 2009 by trawling in the western GOA.

Year	Fixed effect	p-value	Equation
2005	Ln(SL)	<0.001	Kodiak: $\text{Ln(Wt)} = -12.133 + 3.119 \times \text{Ln(SL)} + \text{RHE}$
	Region	0.003	Semidi: $\text{Ln(Wt)} = -12.213 + 3.119 \times \text{Ln(SL)} + \text{RHE}$
2007	Ln(SL)	<0.001	Regions combined $\text{Ln(Wt)} = -12.448 + 3.194 \times \text{Ln(SL)} + \text{RHE}$
2009	Ln(SL)	<0.001	Kodiak: $\text{Ln(Wt)} = -12.197 + 3.140 \times \text{Ln(SL)} + \text{RHE}$
	Region	0.013	Semidi: $\text{Ln(Wt)} = -12.235 + 3.140 \times \text{Ln(SL)} + \text{RHE}$

Highly non-significant terms were eliminated; equations include the covariate, ln-transformed standard length [Ln(SL)], and the random haul effect (RHE).

Table 6. Prey groups recovered from the stomachs of 1135 age-0 walleye pollock collected during September 2005, 2007, and 2009 by trawling in the western GOA.

Prey group	%FO	%No	%W	Wt per item ^a
Amphipoda	19.82	1.42	1.52	2.66
Chaetognatha	11.37	0.70	1.24	5.16
Cirripedeae	3.61	0.73	0.02	0.05
Cladocera	0.70	0.04	<0.01	–
Copepoda, < 2 mm pro.	27.93	26.39	1.43	0.11
Copepoda, > 2 mm pro.	43.70	22.02	8.36	0.67
Euphausiacea, juv. + adult	58.85	9.62	76.96	21.96
Euphausiacea, pre-juvenile	6.17	1.17	0.50	1.11
Larvacea	18.77	30.60	1.56	0.07
Mysidacea	1.41	0.13	0.51	7.70
Natantia	1.15	0.05	0.80	35.47
Osteichthyes	0.97	0.04	1.15	162.35
Ostracoda	0.35	0.01	0.01	0.80
Reptantia	11.28	1.10	1.65	3.37
Thecosomata	16.30	4.35	1.75	0.96
Miscellaneous	4.32	0.20	0.18	1.73
Unidentified	21.32	1.43	2.37	–
Total prey No and W per fish	–	23.78	0.039	–

Diet composition is characterized by per cent frequency of occurrence (%FO), per cent of total prey count (%No), and per cent of total prey weight (%W). Groups are ordered by weight (mg) per individual prey item (W per item).

^aPer item weight (W/No.) only includes items that were <50% digested.

the lowest of all region-year combinations (24% vs. ≥65%, Figure 4). While we did not explicitly incorporate the fish size-related dietary transition, similar outcomes were obtained using the diet of 60 or 80 mm SL fish. Thus, for age-0 walleye pollock ≥55 mm SL, it appears that the euphausiid dietary proportion was mostly responsible for the faster growth of the Kodiak fish.

Discussion

Our results indicate that during years when age-0 walleye pollock were relatively large, they realized more food-related benefit from residing in the Kodiak region than in the Semidi region. Regional differences in fish length-specific body weight, SCW, and diet were significant during 2005 when the mean fish length was large as opposed to 2007 when the mean fish length was small. During 2009, the mean fish length was intermediate and the corresponding food-related responses were intermediate. Fish length also affects diet. We suggest that age-0 walleye pollock must undergo their size-related dietary transition before they are able to exploit juvenile and adult euphausiids and consequently benefit more from residing in the Kodiak region than in the Semidi region. Effects on interannual variation in fish size are therefore likely to affect how much age-0 walleye pollock benefit from inhabiting the Kodiak region.

Consider, for example, water temperature, which relates positively to fish length (Wilson, 2000; Dougherty *et al.*, 2007). During 2005, water temperature was warm and probably contributed to fish lengths being on average larger than in 2007 and 2009, both relatively cold years. The larger size in 2005 probably facilitated an earlier dietary transition onto a euphausiid-based diet with greater consequent region-specific effects on body weight and SCW relative to fish collected during 2007 and 2009. Admittedly, the disparity in the mean fish length between 2007 and 2009 is not explained by water temperature because the warmer year (2007) had the smaller mean length, but other possible effects on fish length include spawn and hatch timing, prey availability, and size-selective losses.

The Kodiak fish responded to the euphausiid-rich habitat by increasing their dietary proportion of euphausiids. This size-related dietary transition is attributed at least partly to predator mouth gape constraints on prey size selection (Brodeur, 1998). Compared with other prey, euphausiids are preferred by age-0 walleye pollock (Wilson *et al.*, 2006) perhaps due to their high caloric density (Mazur *et al.*, 2007) and more suitable sizes (Brodeur, 1998; Wilson *et al.*, 2009). The benefit was especially pronounced during 2005 when there were about 7 euphausiids m^{-3} in the Kodiak midwater as opposed to ~2 euphausiids m^{-3} in other years; furthermore, the euphausiids that were ingested during 2005 were on average larger than those ingested in other years. Consuming large euphausiids is energetically beneficial because the caloric density of euphausiids increases with body size (Mazur *et al.*, 2007). If the late-summer availability of euphausiid biomass significantly affects the growth and survival of age-0 walleye pollock, then the Kodiak region may contribute above-average production of recruits.

The bioenergetic model output growth rate estimates were reasonable compared with previous empirical estimates, which bolstered our confidence that the observed regional difference in diet translated into regional differences in growth rate. Our region-specific estimates (0.016–0.071 g d^{-1}) were similar to the growth rates estimated from recent otolith growth by Mazur *et al.* (2007) (0.026–0.190 g d^{-1}). Historically, otolith-based estimates of growth rate indicate that, on average, Kodiak age-0 walleye pollock grow 0.16 mm d^{-1} faster than their Semidi counterparts (Bailey *et al.*, 1996), which is within our range of estimates (0.02–0.37 mm d^{-1}). We acknowledge that cryptic or easily digested prey such as larvaceans might have been underrepresented in our observations relative to more prominent prey such as large euphausiids. Nevertheless, we are confident that the euphausiid-rich diet best explains the previously observed faster growth of age-0 walleye pollock in the Kodiak region relative to their counterparts in the Semidi region. It is more difficult to explain regional differences in body length, which integrate the effects of growth rate, hatch date, and size-selective loss.

Faster growth is generally thought to benefit juvenile fish by decreasing mortality (Sogard, 1997). This has particular relevance to GOA walleye pollock because recruitment is currently thought to

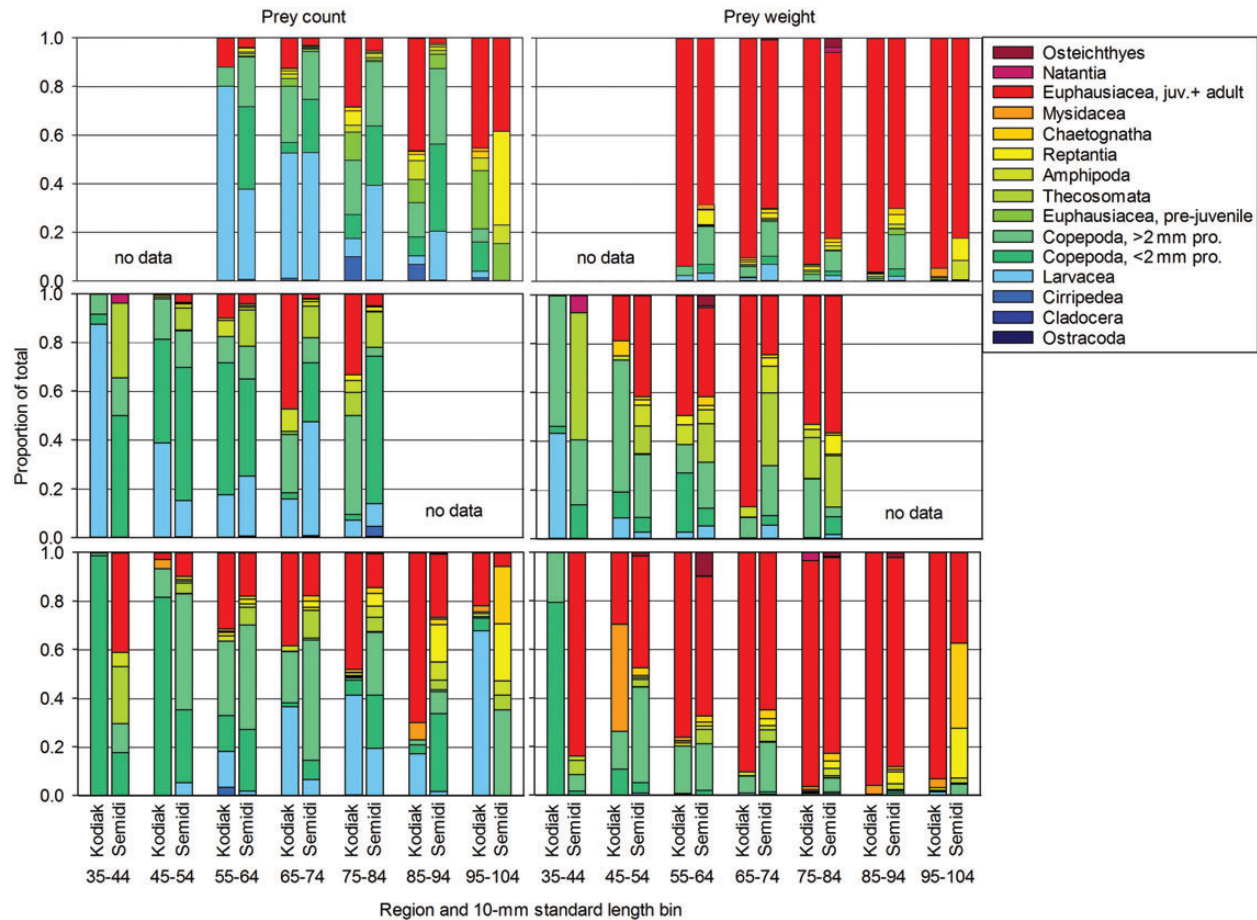


Figure 4. Age-0 walleye pollock diet in terms of prey count (left panels) and prey weight (right panels) is compared between regions (Kodiak vs. Semidi) within 10-mm SL bins (e.g. 35 – 44, 45 – 54 mm, etc) of fish collected in the western GOA during September 2005 (top panels), 2007 (middle panels), and 2009 (bottom panels). Miscellaneous and unidentified prey, are omitted.

Table 7. Permutational MANOVA results of the difference in age-0 walleye pollock diets (by per cent number, %No) between the Kodiak and Semidi regions during September 2005.

Source	d.f.	SS	MS	pseudo-F	p (perm)	Unique perms
Fish length	1	70 072	70 072	8.7363	0.001	996
Region	1	51 119	51 119	3.2275	0.024	998
Station (region)	35	4.85E5	13 870	6.9959	0.001	997
Residual	477	9.46E5	19 82.5	–	–	–
Total	514	1.55E6	–	–	–	–

be regulated by predation on juveniles (Bailey, 2000). We therefore suggest that for growth of age-0 walleye pollock ≥ 55 mm SL, the midwater habitat off Kodiak Island supports faster growth than the Semidi Islands vicinity due to higher euphausiid availability. It remains to be seen whether the food-related growth benefit is offset, in terms of recruit production, by lesser abundance, higher predation, or both.

Although difficult to explain conclusively, the sometimes greater abundance of euphausiids off Kodiak Island relative to the Semidi region might reflect accumulations stemming from favourable oceanographic processes, reduced grazing pressure, or both. The cooler, saltier water off Kodiak suggests a stronger oceanic influence, facilitated perhaps by a relatively narrow continental shelf and

Table 8. Per cent contribution of each prey group to dissimilarity in age-0 walleye pollock diets (by per cent number, %No) between the Kodiak and Semidi regions during September 2005.

Group	Avg. %No		% contribution to dissimilarity
	Kodiak	Semidi	
Euphausiacea, juv. + adults	0.52	0.28	30.18
Copepoda, large	0.15	0.26	18.65
Larvacea	0.04	0.19	16.58
Copepoda, small	0.06	0.14	11.97
Reptantia	0.08	0.03	7.78
Amphipoda	0.05	0.05	5.31

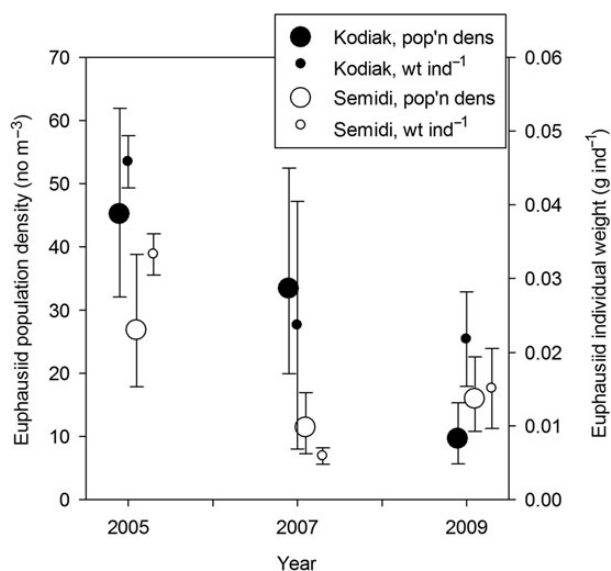


Figure 5. Mean (± 1 standard error) population density and individual weight of juvenile and adult euphausiids recovered mostly intact from the stomachs of age-0 walleye pollock (65–84 mm SL) collected during September 2005, 2007, and 2009. Symbol position along the x-axis is offset for clarity.

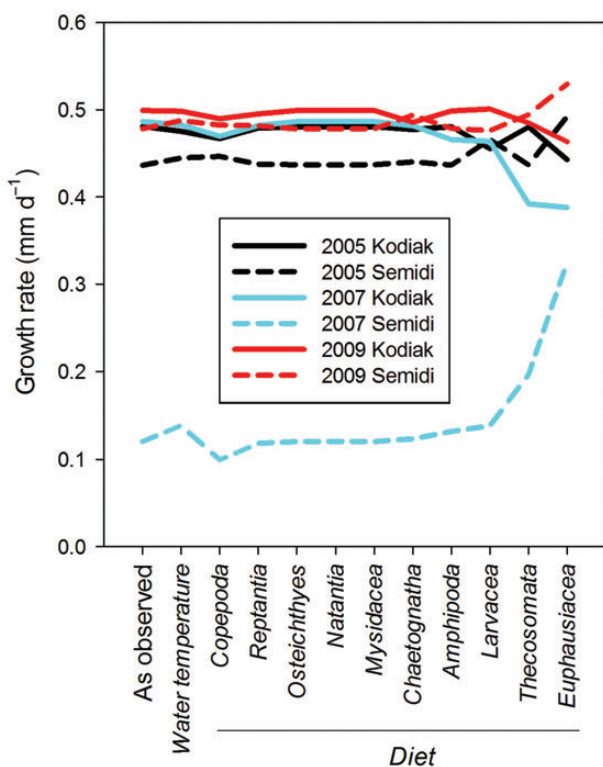


Figure 6. Bioenergetics model-based estimate of growth rate of a 70-mm SL age-0 walleye pollock with the observed weight-based diet (Figure 4) at observed water temperatures (as observed). Lines show how growth rate estimates were affected when water temperature or the proportion of each dietary component was, in turn, equated between regions (Kodiak, Semidi). A colour version of this figure can be accessed online.

at-depth shoreward flow in sea valleys (Stabeno *et al.*, 2004). Euphausiids are often abundant along the shelf break (Simard and Mackas, 1989; Mackas and Coyle, 2005) and shoreward transport can explain euphausiid concentrations that have been observed in sea valleys over the Kodiak shelf (Logerwell *et al.*, 2010). In the northern GOA, the euphausiid *Euphausia pacifica* can be transported by shoreward flow onto the shelf (Pinchuk *et al.*, 2008). The euphausiids that we could identify belonged to the genus *Thysannoessa*, although many others were too digested and could not be identified with certainty. Perhaps a reduction in shoreward transport occurred during 2009, despite being a relatively cold year, such that the Kodiak region was not enriched by oceanic influxes of euphausiids. Grazing pressure is another determinant of euphausiid abundance (Dalpadado and Skjoldal, 1996; Yamamura, 2004). Lower grazing pressure off Kodiak Island could be attributed to lower age-0 walleye pollock abundance, but we did not census other euphausiid predators. Euphausiids might also grow faster in the Kodiak region due to high sea-surface chlorophyll throughout summer (Stabeno *et al.*, 2004; Pinchuk and Hopcroft, 2007) perhaps explaining why the euphausiids consumed by Kodiak fish were heavier than those consumed by similar-size Semidi fish. Thus, interannual variation in favourable oceanographic conditions, and perhaps lower grazing pressure, might explain why euphausiids were sometimes more abundant and apparently larger off Kodiak Island than in the Semidi region.

The apparent dependence of habitat quality on euphausiid availability is a common feature of many coastal ecosystems. Euphausiids are a common dietary staple of many neritic fish in the Barents Sea (Dalpadado and Skjoldal, 1996), southeast Atlantic (Pillar *et al.*, 1992), and North Pacific (Robinson, 2000; Yamamura, 2004). In the Bering Sea, food-related body condition of age-0 walleye pollock before winter seems to relate directly to subsequent survival (Heintz *et al.*, 2013) in the absence of supplemental winter feeding (Kooka *et al.*, 2009). However, the effect of regional variation in feeding conditions on survival is difficult to ascertain because there is currently no way to track walleye pollock through the recruitment process, determine where recruits were as juveniles, or identify what they had eaten as age-0 juveniles.

Given that food-related benefits accrue to age-0 walleye pollock in the Kodiak region, why is the Kodiak population not larger than the population in the Semidi region, which is similar in area (ca. 30 000 km²)? This can be largely explained by the fact that the Kodiak region is not directly downstream of the large spawning aggregation of walleye pollock in Shelikof Strait; consequently, it does not receive similarly large influxes of larvae each spring. Origin of the Kodiak fish is uncertain, but probably includes local spawning and inputs from upstream spawning locations such as Prince William Sound (Wilson, 2000). Conceivably, the Kodiak region might also be populated by Semidi fish moving upstream in search of prey. Such north-eastward movement could be facilitated by current reversals and areas of low velocity, such as over the middle and outer shelf (Stabeno *et al.*, 2004) where net current velocities are less than the 1–2 body length s⁻¹ cruising speed of age-0 walleye pollock (Ryer *et al.*, 2002). The smaller Kodiak population might also reflect relatively heavy predation, but regional variation in predation pressure has not been studied.

In summary, greater apparent oceanic influence off Kodiak Island was associated with a sometimes higher population density of euphausiids when compared with farther downstream in the Semidi Islands vicinity. Age-0 juvenile walleye pollock in the Kodiak region consumed proportionally more euphausiids and

depending on year were heavier and had fuller stomachs than their similar-size Semidi counterparts. Bioenergetic modelling highlighted the singular importance of euphausiids as the driver of faster growth of the Kodiak fish relative to Semidi fish. Larger fish generally consumed greater proportions of euphausiids; consequently, the region effect was most pronounced among fish >55 mm SL. During 2005, relatively warm water was associated with large fish lengths and pronounced regional differences in length-specific weight, SCW, and diet underscoring the potential for interannual variation in fish length to cause regional differences in food-related benefits and perhaps survival. For the Kodiak region to be considered a nursery, production of recruits (Dahlgren *et al.*, 2006) or recruits per unit area (Beck *et al.*, 2001) would need to exceed the mean production of all habitats utilized by juvenile walleye pollock in the GOA. While it is not yet possible to quantify region-specific production throughout the GOA, our results point out that age-0 walleye pollock accrue food-related benefits from inhabiting the Kodiak shelf and thus have the potential to contribute above-average numbers of recruits to the adult population.

Acknowledgements

We thank all cruise personnel from the NOAA ship *Miller Freeman* involved in the collection of samples and data, the Research Fishing Gear and MACE programmes at the AFSC for gear and logistic support, and C. Harpold for help accessing zooplankton data. Comments from D. Cooper, J. Duffy-Anderson, G. Lang, J. Napp, the AFSC Publications Unit, and three anonymous reviewers improved the manuscript. This research is contribution EcoFOCI-0799 to NOAA's Ecosystems and Fisheries-Oceanography Coordinated Investigations. It was supported by NOAA's North Pacific Climate Regimes and Ecosystem Productivity Programme.

References

- Anderson, M. J., Gorley, R. N., and Clarke, K. R. 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth, UK.
- Bacheler, N. M., Bailey, K. M., Ciannelli, L., Bartolino, V., and Chan, K-S. 2009. Density-dependent, landscape, and climate effects on spawning distribution of walleye pollock *Theragra chalcogramma*. *Marine Ecology Progress Series*, 391: 1–12.
- Bailey, K. M. 2000. Shifting control of recruitment of walleye pollock *Theragra chalcogramma* after a major climatic and ecosystem change. *Marine Ecology Progress Series*, 198: 215–224.
- Bailey, K. M., Brown, A. L., Yoklavich, M. M., and Mier, K. L. 1996. Interannual variability in growth of larval and juvenile walleye pollock *Theragra chalcogramma* in the western Gulf of Alaska, 1983–91. *Fisheries Oceanography*, 5(Suppl. 1): 137–147.
- Beck, M. W., Heck, K. L., Jr, Able, K. W., Childers, D. L., Eggleston, D. B., Gillanders, B. M., Halpern, B., *et al.* 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience*, 51: 633–641.
- Brodeur, R. D. 1998. Prey selection by age-0 walleye pollock, *Theragra chalcogramma*, in nearshore waters of the Gulf of Alaska. *Environmental Biology of Fishes*, 51: 175–186.
- Brodeur, R. D., and Bailey, K. M. 1996. Predation on the early life stages of marine fish: a case study on walleye pollock in the Gulf of Alaska. In *Survival Strategies in Early Life Stages of Marine Resources: Proceedings of an International Workshop*, Yokohama, Japan, 11–14 October 1994, pp. 245–259. Ed. by Y. Watanabe, Y. Yamashita, and Y. Oozeki. A. A. Balkema, Rotterdam, The Netherlands. 367 pp.
- Brodeur, R. D., and Wilson, M. T. 1996. A review of the distribution, ecology and population dynamics of age-0 walleye pollock in the Gulf of Alaska. *Fisheries Oceanography*, 5(Suppl. 1): 148–166.
- Brown, A. L., and Bailey, K. M. 1992. Otolith analysis of juvenile walleye pollock *Theragra chalcogramma* from the western Gulf of Alaska. *Marine Biology*, 112: 23–30.
- Buchheister, A., Wilson, M. T., Foy, R. J., and Beauchamp, D. A. 2006. Seasonal and geographic variation in condition of juvenile walleye pollock in the western Gulf of Alaska. *Transactions of the American Fisheries Society*, 135: 897–907.
- Ciannelli, L., Brodeur, R. D., and Buckley, T. W. 1998. Development and application of a bioenergetics model for juvenile walleye pollock. *Journal of Fish Biology*, 52: 879–898.
- Clarke, K. R., and Gorley, R. N. 2006. PRIMER Version 6: User Manual/tutorial. PRIMER-E, Plymouth.
- Clarke, K. R., and Green, R. H. 1988. Statistical design and analysis for a “biological effects” study. *Marine Ecology Progress Series*, 46: 213–226.
- Clarke, K. R., and Warwick, R. M. 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, 2nd edn. PRIMER-E, Plymouth.
- Dahlgren, C. P., Kellison, G. T., Adams, A. J., Gillanders, B. M., Kendall, M. S., Layman, C. A., Ley, J. A., *et al.* 2006. Marine nurseries and effective juvenile habitats: concepts and applications. *Marine Ecology Progress Series*, 312: 291–295.
- Dalpadado, P., and Skjoldal, J. R. 1996. Abundance, maturity and growth of the krill species *Thysanoessa inermis* and *T. longicaudata* in the Barents Sea. *Marine Ecology Progress Series*, 144: 175–183.
- Dougherty, A., Bailey, K. M., and Mier, K. L. 2007. Interannual differences in growth and hatch date distributions of age-0 year walleye pollock *Theragra chalcogramma* (Pallas) sampled from the Shumagin Islands region of the Gulf of Alaska, 1985–2001. *Journal of Fish Biology*, 71: 763–780.
- Dougherty, A., Bailey, K., Vance, T., and Cheng, W. 2012. Underlying causes of habitat-associated differences in size of age-0 walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska. *Marine Biology*, 159: 1733–1744.
- Gillanders, B. M., Able, K. W., Brown, J. A., Eggleston, D. B., and Sheridan, P. F. 2003. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. *Marine Ecology Progress Series*, 247: 281–295.
- Heintz, R. A., Siddon, E. C., Farley, E. V., Jr, and Napp, J. M. 2013. Correlation between recruitment and fall condition of age-0 pollock (*Theragra chalcogramma*) from the eastern Bering Sea under varying climate conditions. *Deep Sea Research II*. <http://dx.doi.org/10.1016/j.dsr2.2013.04.006>.
- Kooka, K., Yamamura, O., Ohkubo, N., and Honda, S. 2009. Winter lipid depletion of juvenile walleye pollock *Theragra chalcogramma* in the Doto area, northern Japan. *Journal of Fish Biology*, 75: 186–202.
- Logerwell, E. A., Duffy-Anderson, J., Wilson, M., and McKelvey, D. 2010. The influence of pelagic habitat selection and interspecific competition on productivity of juvenile walleye pollock (*Theragra chalcogramma*) and capelin (*Mallotus villosus*) in the Gulf of Alaska. *Fisheries Oceanography*, 19: 262–278.
- Mackas, D. L., and Coyle, K. O. 2005. Shelf-offshore exchange processes, and their effects on mesozooplankton biomass and community composition patterns in the northeast Pacific. *Deep-Sea Research II*, 52: 707–725.
- Mazur, M. M., Wilson, M. T., Dougherty, A. B., Buchheister, A., and Beauchamp, D. A. 2007. Temperature and prey quality effects on growth of juvenile walleye pollock *Theragra chalcogramma* (Pallas): a spatially explicit bioenergetics approach. *Journal of Fish Biology*, 70: 816–836.
- Merati, N., and Brodeur, R. D. 1996. Feeding habits and daily ration of juvenile walleye pollock in the western Gulf of Alaska. In *Ecology of Juvenile Walleye Pollock*, pp. 65–79. Ed. by R. D. Brodeur, P. A. Livingston, T. R. Loughlin, and A. B. Hollowed. US Department of Commerce, NOAA Technical Report NMFS-126. 227 pp.
- Olsen, J. B., Merkouris, S. E., and Seeb, J. E. 2002. An examination of spatial and temporal genetic variation in walleye pollock (*Theragra*

- chalcogramma*) using allozyme, mitochondrial DNA, and microsatellite data. Fishery Bulletin US, 100: 752–764.
- Pillar, S. C., Stuart, V., Barange, M., and Gibbons, M. J. 1992. Community structure and trophic ecology of euphausiids in the Benguela ecosystem. South African Journal of Marine Science, 12: 393–409.
- Pinchuk, A. I., Coyle, K. O., and Hopcroft, R. R. 2008. Climate-related variability in abundance and reproduction of euphausiids in the northern Gulf of Alaska in 1998–2003. Progress in Oceanography, 77: 203–216.
- Pinchuk, A. I., and Hopcroft, R. R. 2007. Seasonal variations in the growth rates of euphausiids (*Thysanoessa inermis*, *T. spinifera*, and *Euphausia pacifica*) from the northern Gulf of Alaska. Marine Biology, 151: 257–269.
- Reed, R. K., and Schumacher, J. D. 1986. Physical Oceanography. In The Gulf of Alaska: Physical Environment and Biological Resources, pp. 57–75. Ed. by D. W. Hood, and S. T. Zimmerman. Ocean Assessment Division, National Oceanic and Atmospheric Administration, Seattle. 655 pp.
- Robinson, C. L. K. 2000. The consumption of euphausiids by the pelagic fish community off southwestern Vancouver Island, British Columbia. Journal of Plankton Research, 22: 1649–1662.
- Ryer, C. H., Lawton, A., Lopez, R. J., and Olla, B. L. 2002. A comparison of the functional ecology of visual vs. nonvisual foraging in two planktivorous marine fishes. Canadian Journal of Fisheries and Aquatic Sciences, 59: 1305–1314.
- Sheaves, M., Baker, R., and Johnston, R. 2006. Marine nurseries and effective juvenile habitats: an alternative view. Marine Ecology Progress Series, 318: 303–306.
- Siefert, D. W., and Incze, L. S. 1991. Zooplankton of Shelikof Strait, Alaska, April and May 1989: data from Fisheries Oceanography Coordinated Investigations (FOCI) cruises. NOAA AFSC Proc. Rep. 91–16, US Dept. of Commerce, Alaska Fisheries Science Center, National Marine Fisheries Service, Seattle, WA.
- Simard, Y., and Mackas, D. L. 1989. Mesoscale aggregations of euphausiids sound scattering layers on the continental shelf of Vancouver Island. Canadian Journal of Fisheries and Aquatic Sciences, 46: 1238–1249.
- Sogard, S. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science, 60: 1129–1157.
- Springer, A. M. 1992. A review: walleye pollock in the North Pacific—how much difference do they really make? Fisheries Oceanography, 1: 80–96.
- Stabeno, P. J., Bond, N. A., Hermann, A. J., Kachel, N. B., Mordy, C. W., and Overland, J. E. 2004. Meteorology and oceanography of the northern Gulf of Alaska. Continental Shelf Research, 24: 859–897.
- Wilson, M. T. 2000. Effects of year and region on the abundance and size of age-0 walleye pollock, *Theragra chalcogramma*, in the western Gulf of Alaska, 1985–1988. Fishery Bulletin US, 98: 823–834.
- Wilson, M. T. 2009. Ecology of small midwater fishes in the western Gulf of Alaska. I. Geographic distribution in relation to prey density and hydrography. Marine Ecology Progress Series, 392: 223–237.
- Wilson, M. T., Brown, A. L., and Mier, K. L. 2005. Geographic variation among age-0 walleye pollock (*Theragra chalcogramma*): evidence of mesoscale variation in nursery quality? Fishery Bulletin US, 103: 207–218.
- Wilson, M. T., Buchheister, A., and Jump, C. 2011. Regional variation in the annual feeding cycle of juvenile walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. Fishery Bulletin US, 109: 316–326.
- Wilson, M. T., Jump, C. M., and Buchheister, A. 2009. Ecology of small neritic fishes in the western Gulf of Alaska. II. Consumption of krill in relation to standing stock and the physical environment. Marine Ecology Progress Series, 392: 239–251.
- Wilson, M. T., Jump, C. M., and Duffy-Anderson, J. T. 2006. Comparative analysis of the feeding ecology of two pelagic forage fishes: capelin *Mallotus villosus* and walleye pollock *Theragra chalcogramma*. Marine Ecology Progress Series, 317: 245–258.
- Yamamura, O. 2004. Trophodynamic modeling of walleye pollock (*Theragra chalcogramma*) in the Doto area, northern Japan: model description and baseline simulations. Fisheries Oceanography, 13(Suppl. 1): 138–154.

Handling editor: Manuel Hidalgo