Abstract—Juvenile fish in temperate coastal oceans exhibit an annual cycle of feeding, and within this cycle, poor wintertime feeding can reduce body growth, condition, and perhaps survival, especially in food-poor areas. We examined the stomach contents of juvenile walleye pollock (*Theragra chalcogramma*) to explain previously observed seasonal and regional variation in juvenile body condition. Juvenile walleye pollock (1732 fish, 37–250 mm standard length) of the 2000 year class were collected from three regions in the Gulf of Alaska (Kodiak, Semidi, and Shumagin) representing an area of the continental shelf of ca. 100,000 km^2 during four seasons (August 2000 to September 2001). Mean stomach content weight (SCW, 0.72% somatic body weight) decreased with fish body length except from winter to summer 2001. Euphausiids composed 61% of SCW and were the main determinant of seasonal change in the diets of fish in the Kodiak and Semidi regions. Before and during winter, SCW and the euphausiid dietary component were highest in the Kodiak region. Bioenergetics modeling indicated a relatively high growth rate for Kodiak juveniles during winter (0.33 mm standard length/d). After winter, Shumagin juveniles had relatively high SCW and, unlike the Kodiak and Semidi juveniles, exhibited no reduction in the euphausiid dietary component. These patterns explain previous seasonal and regional differences in body condition. We hypothesize that high-quality feeding locations (and perhaps nursery areas) shift seasonally in response to the availability of euphausiids.

Regional variation in the annual feeding cycle of juvenile walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska

Matthew T. Wilson (contact author)[1]
Andre Buchheister[2]
Christina Jump[1]

Email address for contact author: matt.wilson@noaa.gov

[1] Alaska Fisheries Science Center
 National Marine Fisheries Service
 National Oceanic and Atmospheric Administration
 7600 Sand Point Way NE
 Seattle, Washington 98115

[2] Department of Fisheries Science
 Virginia Institute of Marine Science
 College of William & Mary
 Gloucester Point, Virginia 23062

In temperate and subpolar oceans, many coastal fishes exhibit an annual cycle in feeding due to seasonal changes in prey availability and composition (Wootton, 1998). The cyclical low point in feeding conditions often occurs during winter when environmental conditions can adversely affect growth and survival of juveniles and thereby constrain year-class strength (Sogard, 1997; Hurst, 2007). However, juveniles that inhabit prey-rich areas may fare better than those in prey-poor areas because of enhanced accumulations of body reserves before winter, acquisition of energy during winter, or both. Thus, prey-rich areas may support relatively high growth and survival and thereby function as important nurseries for the production of recruits (Dahlgren et al., 2006).

Walleye pollock (*Theragra chalcogramma*) is prominent in many North Pacific ecosystems as a major food web component and fishery resource (Springer, 1992). In the Gulf of Alaska (GOA), juvenile walleye pollock are one of the most abundant neritic forage fishes and are consumed by seabirds, fishes, and marine mammals (Brodeur and Bailey, 1996). Predation-related mortality of juveniles can significantly determine walleye pollock year-class strength in the GOA (Bailey, 2000). Because juveniles require food to grow, and mortality can decrease with body size (Sogard, 1997), description of the annual feeding cycle will provide a trophic context for annual cycles in growth (Brodeur and Wilson, 1996) and mortality (e.g., Hurst, 2007). Furthermore, year after year, specific regions of the GOA support juvenile walleye pollock that are larger (Wilson, 2000; Wilson et al., 2009) and in better body condition (Buchheister et al., 2006) than members of the same year class from other regions, thus raising the possibility that seasonal changes in habitat quality (e.g., food resources) vary geographically.

In the GOA, the principal habitat of juvenile walleye pollock occurs from Kodiak Island to Unimak Pass (Brodeur and Wilson, 1996) (Fig. 1). Young-of-the-year (age-0) juveniles are particularly abundant in the Semidi Bank region because of downstream advection of larvae produced by the large spawning aggregation that forms during early spring in Shelikof Strait (Hinckley et al., 1991). During winter, growth of age-0 juveniles decreases to a negligible rate when epibenthic foraging supplements the acquisition of pelagic prey (Brodeur and Wilson, 1996). In addition,
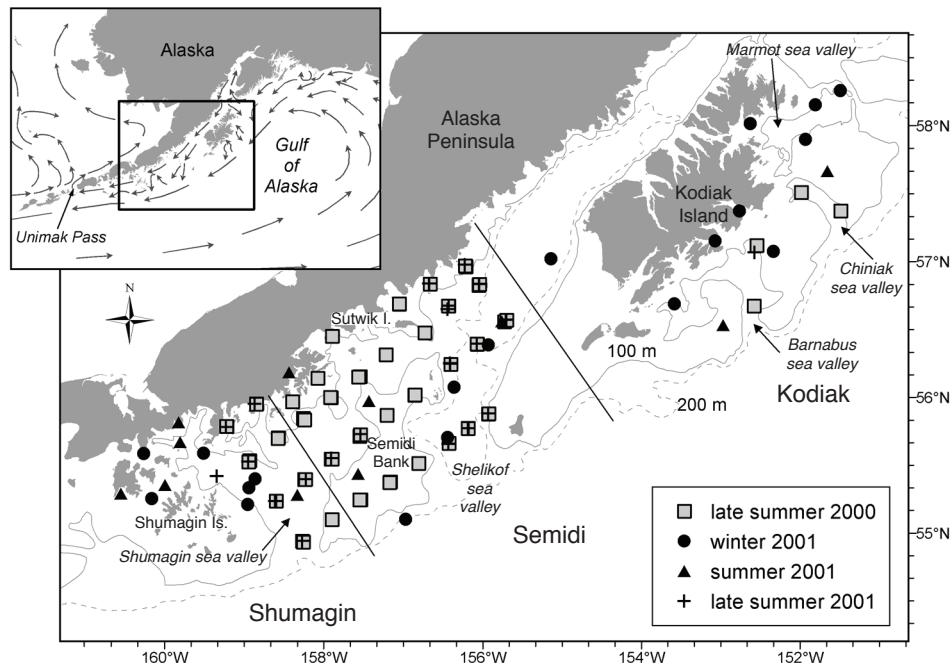
Figure 1

Sites where juvenile walleye pollock (*Theragra chalcogramma*) were collected with trawl nets in the Gulf of Alaska from August 2000 to September 2001. Delineation of season and geographic region follow Buchheister et al. (2006) (see Table 1 for specific sampling dates). Arrows in inset represent the predominant currents in Alaskan waters (Reed and Schumacher, 1986).

a persistent along-shore shift in body length of age-0 juveniles occurs at about Sutwik Island and relatively large juveniles are found northeastward in the Kodiak Island region (Wilson, 2000). In addition to larger body lengths, these juveniles also have greater length-specific weights and are more energy dense than fish from other regions, particularly in late summer and winter (Buchheister et al. 2006). The underlying cause remains unproven but likely involves some aspect of feeding ecology. For example, juveniles collected near Kodiak Island during late summer had a euphausiid-rich diet (Merati and Brodeur, 1996; Wilson et al., 2005; Wilson et al., 2009) and faster growth (Bailey et al., 1996) than individuals collected in the Semidi Bank vicinity. There is currently insufficient evidence in the literature to evaluate the role of food habits in determining regional and cyclical variation in growth, body condition, and perhaps survival of juvenile walleye pollock in the western GOA.

Our objective was to examine the food habits of juvenile walleye pollock for evidence of an annual cycle and to elucidate how these food habits may vary regionally in relation to previously observed geographic variation in juvenile body condition and growth rate. The focus on one year class simply reflects sample availability. Samples of the 2000 year class were available from directed sampling during late summer 2000 (age-0 juveniles) and during late summer 2001 (age-1 juveniles). An additional set of samples was available from oppor-

tunistic sampling. Examining fish from these sample sets enabled us to provide new insight and formulate hypotheses about annual periodicity and regional variation in the food habits of juvenile walleye pollock. Previously, all or a subset of these same samples were used to examine body condition (Buchheister et al., 2006) and growth rates of juvenile walleye pollock (Mazur et al., 2007; Wilson et al., 2011). We conducted a modeling exercise to integrate these previous findings with our observations on food habits and explore the implication of these results on juvenile walleye pollock growth rate.

Materials and methods

Sample collection

Juvenile walleye pollock were collected from 124 trawl catches in the western GOA during August 2000 to September 2001 during nine research cruises conducted by the National Marine Fisheries Service (NMFS). Samples were grouped according to collection location and date according to the method of Buchheister et al. (2006). There were three geographic regions (Kodiak, Semidi, and Shumagin) and four seasons (late summer 2000 [LSum00], winter 2001 [Win01], summer 2001 [Sum01], and late summer 2001 [LSum01]) (Table 1, Fig. 1). The geographic divisions within the experimental study area somewhat arbitrarily distinguished alongshore regions

Table 1

Juvenile walleye pollock (*Theragra chalcogramma*) (1732 fish) were collected in 124 trawl catches (i.e., samples) from three regions of the western Gulf of Alaska during four seasons from August 2000 to September 2001. Fish size is indicated by mean standard length (standard error) and range (minimum–maximum).

Region	Season	Collection date	No. of samples	No. of fish	Standard length (mm)	
					Mean (SE)	Range
Kodiak	Late summer 2000	15–19 Aug 2000	4	63	71 (0.7)	57–88
	Winter 2001	1 Feb–21 Mar 2001	9	78	122 (1.6)	95–158
	Summer 2001	26 Jun–8 Jul 2001	2	20	165 (2.7)	144–182
	Late summer 2001	3 Sep 2001	1	7	200 (2.3)	192–207
Semidi	Late summer 2000	8–19 Sep 2000	45	784	71 (0.4)	37–109
	Winter 2001	2 Feb–23 Mar 2001	4	38	107 (2.1)	83–127
	Summer 2001	9–15 Jun 2001	4	40	118 (1.9)	96–145
	Late summer 2001	8–18 Sep 2001	20	161	198 (2.1)	136–250
Shumagin	Late summer 2000	4–7 Sep 2000	16	374	60 (0.4)	43–86
	Winter 2001	14 Feb–9 Mar 2001	6	58	103 (1.8)	82–153
	Summer 2001	2–7 Jun 2001	5	46	118 (1.7)	95–149
	Late summer 2001	4–7 Sep 2001	8	63	173 (3.3)	127–232

of the shelf according to prominent bathymetric features (Fig. 1) and covered the area alongshore where there is a shift in body length of age-0 walleye pollock (Wilson, 2000). The use of this scheme facilitated integration of our results with those of Buchheister et al. (2006) in our modeling exercise.

Two of the nine cruises were regularly scheduled by NMFS to study juvenile walleye pollock. Samples were collected at predetermined sites between Shelikof Strait and the Shumagin Islands during 3–19 September 2000 and 3–18 September 2001. Samples were collected without regard to time of day with a Stauffer (anchovy) midwater trawl (Wilson et al., 1996). The trawl was equipped with a 3-mm mesh codend liner, and it was fished over double-oblique tows to a depth of 200 m or to 10 m off bottom, whichever was shallowest. These two cruises produced 90 samples. Originally, the data from these samples were obtained for a multiyear study of food habits of walleye pollock (Wilson et al., 2009).

The remaining seven cruises provided all the samples from Win01 and Sum01, and most of the samples from the Kodiak region. Collections of juvenile walleye pollock on these cruises were ancillary to primary cruise objectives (i.e., opportunistic); consequently, we had little control over sampling effort, date, collection site location, and method of sampling (e.g., gear, time of day). On four of these cruises, samples were collected without regard to time of day with midwater and bottom trawls equipped with 32-mm mesh codend liners. On the remaining three cruises, samples were collected during daylight with a poly-nor'eastern bottom trawl equipped with a 32-mm mesh codend liner. These seven cruises produced 34 samples. On all nine cruises, walleye pollock were sorted from the catch and frozen for subsequent examination of their stomach contents in the laboratory.

Stomach content analysis

Fish were selected from thawed samples by standard length (SL) to narrow the focus of our study to members of the 2000 year class. Age-0 individuals were easily identified from historical distinctions in size that separated them from the next older cohort (Brodeur and Wilson, 1996). Age-0 individuals were obtained from samples collected in LSum00 and Win01. Age-1 individuals were obtained from samples collected later in Win01, and in Sum01 and LSum01. The upper SL limit of age-1 fish was estimated from NMFS length-at-age data according to the method of Buchheister et al. (2006).

Fish food habits were characterized by total stomach content weight (SCW) and taxonomic composition (by prey weight and number). Fish were thawed in seawater, measured to the nearest mm SL, blotted dry, and weighed to the nearest 1 mg (as in Wilson et al. [2009]). Stomachs were excised and preserved in 10% formalin. Later, stomachs were dissected and the contents were blotted dry, weighed to the nearest 0.01 mg, and sorted by taxonomic group. Although most copepods were calanoids, some harpacticoids were detected and quantified separately. The calanoids, hereafter referred to as copepods, were further divided by size: 1) small copepods (<2 mm prosomal length [PL]); and 2) large copepods (>2 mm PL). Euphausiids were divided into the following developmental stages: 1) furciliae (≤5 mm length, Siegel [2000]); and 2) juveniles and adults. For each taxonomic group, the total weight and total count of largely intact (ca. <50% digested) individuals were used to estimate mean weight per individual prey item. Items in each group were enumerated and weighed collectively to the nearest 0.01 mg after being blotted dry.

Data analysis

Stomach content data were used to estimate food consumption and diet composition. The amount of food consumed was assessed by using SCW normalized to somatic body weight (whole-body wet weight less stomach content weight) and expressed as percent somatic body weight (%BW). Diet composition was quantified by using prey counts or weights summed across fish and then expressing them as a percentage of total prey count or weight (%No., %W, respectively). We also computed the frequency of occurrence of a particular prey type as the percentage of all stomachs containing that particular prey type (%FO). The cumulative number of prey types detected was examined in relation to the number of fish examined, as in Ferry and Cailliet (1996). We did not incorporate estimates of fish catch in our computations (e.g., cluster sampling estimator [Buckel et al., 1999]) because of uncertainty about how to standardize sampling effort among the different gears, sampling objectives, and methods used during the various cruises.

We conducted a modeling exercise to integrate our observations on feeding with previous findings on body condition (Buchheister et al., 2006) and prey energy density (Mazur et al., 2007) to explore the implications for juvenile walleye pollock growth. The exercise consisted of first estimating daily ration (DR), and then inputting it and other empirical data into a bioenergetics model to output fish growth rate. Daily ration was estimated empirically with a simple evacuation rate model (Elliott and Persson, 1978):

$$C = 24 \cdot E \cdot \bar{S}, \qquad (1)$$

where C = daily food consumption (%BW/d);
24 = the number of hours in a day;
E = the instantaneous rate of evacuation (%BW/h); and
$\bar{S}$ = average SCW over the course of the day.

We used E = 0.28 %BW/h (Merati and Brodeur, 1996). $\bar{S}$ was computed as the average of mean SCW for each 3-h time bin (e.g., 0–3, >3–6, >6–9 h) (Elliott and Persson, 1978). All SCWs were arcsine transformed so that the errors approximated a normal distribution.

Growth rate was estimated with an age-0 walleye pollock bioenergetics model (Ciannelli et al., 1998). Model inputs were fish body weight (g), diet (%W), DR (%BW), predator energy density (J/g, Buchheister et al., 2006), taxon-specific prey energy densities (J/g, Mazur et al., 2007), and water temperature (°C). Fresh fish body weight was estimated from mean whole wet weight of thawed fish by using fresh-frozen weight relationships (Buchheister and Wilson, 2005). Predator energy density was estimated by using fish body weight-energy density relationships (A. Buchheister, unpubl. data, but see Buchheister et al., 2006). Water temperature at a depth of 40 m was measured with a calibrated SBE-19 or SBE-39 temperature profiler (Sea-Bird Electronics, Bellevue, WA), or a microbathy-

thermograph (Richard Brancker Research, Ltd., Ontario, Canada) and averaged across sites where fish were collected. Model output growth rates were based on estimates of excess daily consumption of prey in grams of food per gram of body weight per day (g/g/d) after budgeting for egestion, excretion, respiration, and specific dynamic activity. We used the length-weight relationships from Buchheister et al. (2006) to convert growth rate units to mm SL/d for direct comparison with otolith-based growth rates.

Results

Most of the 1732 juvenile walleye pollock examined were from the Semidi and Shumagin regions during LSum00 (Table 1) when samples were collected with midwater trawl nets. The use of different survey gear (i.e., midwater or bottom trawl nets) among research cruises did not appear to influence fish size or stomach content weight. When compared by season and region, neither mean SL (ANOVA, P = 0.101), nor mean stomach content weight (ANOVA, P = 0.102), differed by survey gear. The bulk of the stomach contents (61%) was composed of juvenile and adult euphausiids, which also did not significantly vary by survey gear (ANOVA, P = 0.426).

Stomach content weight

Overall, SCW averaged 0.72% BW, but season-to-season fluctuations were evident within each region. In all regions, mean SCW decreased from LSum00 to Win01 and then increased into Sum01 before continuing to decline (Fig. 2). The Semidi region was associated with low mean SCW (0.14–0.82% BW) compared to all other regions except Kodiak during LSum01 (0.10% BW), which was represented by only seven fish. The Kodiak region had the highest mean SCW during LSum00 (1.40% BW) and during Win01 (0.56% BW). Later, the Shumagin region had the highest mean SCW during Sum01 (0.76% BW) and LSum01 (0.49% BW), but we acknowledge low confidence in the Shumagin-Kodiak comparison because of the low number of fish available from the Kodiak region. Thus, the region with the highest mean SCW appeared to have shifted from Kodiak to Shumagin after Win01.

Diet

The cumulative number of identifiable prey types encountered in juvenile walleye pollock reached an asymptote at 16 after the contents of about 60 stomachs were examined (Fig. 3). Overall, 19 categories of items were represented in juvenile walleye pollock stomachs, but we did not consider two of these categories to be part of the diet (hard items [e.g., sand] and parasites), and one category consisted of unidentifiable items (Table 2). As the number of stomachs examined decreased below 60, the cumulative number of prey types dropped sharply, causing a negative bias on diet breadth. The smallest sample

sizes were from opportunistic sampling, which occurred during Win01, Sum01, and in the Kodiak region.

Frequently encountered prey types tended to have low individual weights, except for juvenile and adult

Figure 2

Mean stomach content weight (% body weight [BW] ±1 standard error) of juvenile walleye pollock (*Theragra chalcogramma*) collected with trawl nets in three regions (Shumagin, Semidi, and Kodiak) of the western Gulf of Alaska during late summer 2000 (Lsum00), winter 2001 (Win01), summer 2001 (Sum01), and late summer 2001 (Lsum01). The numbers of fish examined are indicated next to each point.

Figure 3

Number of prey types (•) (identified in stomachs of juvenile walleye pollock (*Theragra chalcogramma*) collected in trawl nets in three regions of the western Gulf of Alaska during four seasons (August 2000–September 2001). The *x*-axis is truncated at 100 stomachs.

euphausiids (Table 2). Copepods, larvaceans, and pteropods (Thecosomata) each occurred in >20% of the stomachs and had mean individual prey weights <0.8 mg. Fish (Osteichthyes) were relatively uncommon (4.3% FO) and had the highest mean individual weight (626 mg). In contrast, euphausiid juveniles and adults occurred in half the stomachs and each individual weighed on average 19.9 mg.

The percentage of small-size prey abundance in juvenile walleye pollock diets declined with seasonal progression (Fig. 4A) and with increased predator length (Fig. 4C) and was primarily due to declining percentages of small copepods and larvaceans and increasing percentages of large copepods and euphausiids. For euphausiids, the proportion of furciliae peaked in Sum01, whereas the proportion of juvenile and adult euphausiids peaked later, during LSum01.

Seasonal change in diet composition by weight was most influenced by the proportion of juvenile and adult euphausiids (Fig. 4B), which overall composed 61% of the SCW. In the Shumagin region, the proportional weight of euphausiids increased from 36% in LSum00 to 64% in Sum01; subsequently, in LSum01, 51% of the stomach contents were euphausiid juveniles and adults and 40% were fish. Greater seasonality was observed in the Semidi and Kodiak fish diets. In the Semidi region, euphausiids were more important during late summer (>60%) than during Win01 and Sum01 (<20%) when diets were dominated by large copepods. In the Kodiak region, euphausiids represented >60% of the diet in all seasons except during Sum01 when most (84%) of the diet bulk was fish and other epibenthos (mostly cumaceans). The low number of Kodiak fish examined during Sum01 (20 fish) and LSum01 (7 fish) reduced confidence in the respective diet compositions. Thus, seasonality in diet composition was mostly attributable to euphausiids and was less evident in the Shumagin region than in the Semidi and perhaps Kodiak regions.

Growth rate

Growth rate estimates ranged from −0.38 mm SL/d during Win01 to 0.56 mm SL/d during LSum01, but were not estimated for all season-region combinations (Table 3). For six season-region combinations, coverage of diel periodicity in feeding (e.g., Merati and Brodeur, 1996) was deemed inadequate because <5 of the eight 3-h time bins that compose the diel feeding cycle were represented. Consequently, growth rates were
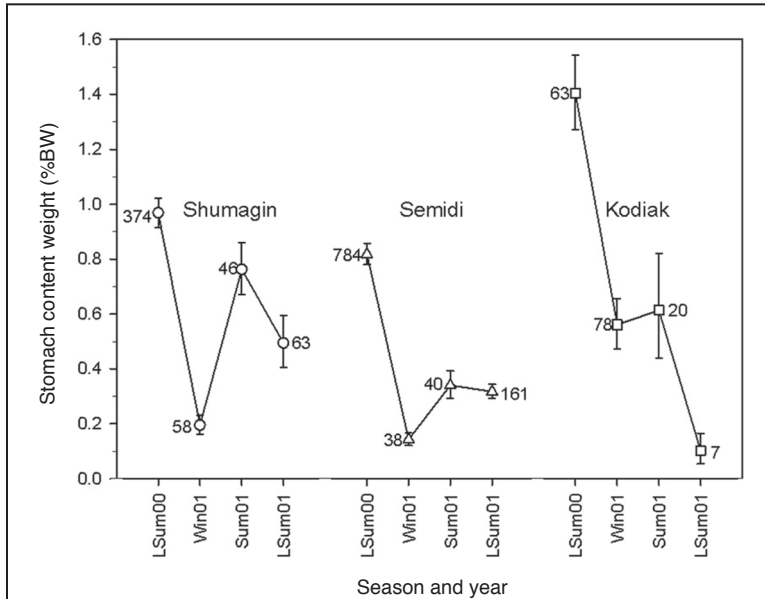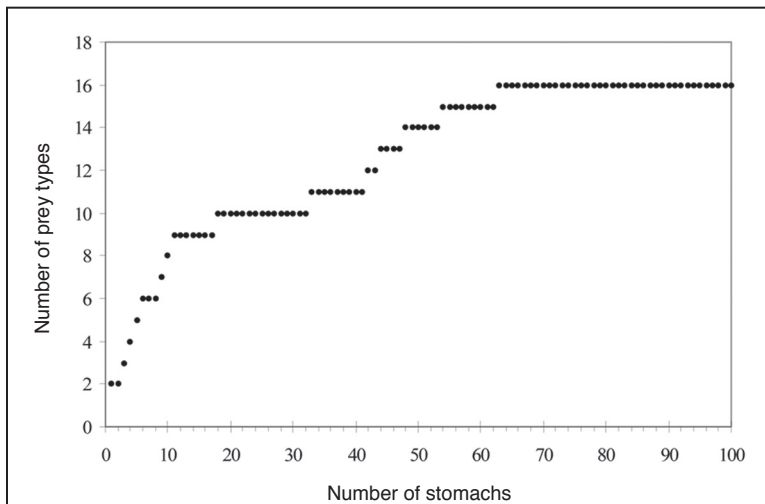
Table 2

Prey groups recovered from the stomach contents of juvenile walleye pollock (*Theragra chalcogramma*) collected during August 2000 to September 2001 by trawling in the western Gulf of Alaska. Diet composition is characterized by percent frequency of occurrence (%FO), percent of total prey count (%No), and percent of total prey weight (%W). Weight (mg) per individual prey item (W per item) indicates relative prey size.

Prey group	%FO	%No	%W	W per item[1]
Amphipoda, epibenthic	6.7	0.47	0.86	4.57
Amphipoda, pelagic	8.8	0.43	0.42	2.37
Cirripedia larvae	5.7	1.72	0.07	0.08
Copepoda, <2 mm PL	56.4	44.59	2.30	0.11
Copepoda, >2 mm PL	42.4	14.04	5.84	0.76
Chaetognatha	12.5	0.55	1.93	9.54
Euphausiacea furciliae	10.0	1.85	0.58	0.25
Euphausiacea juveniles and adults	49.6	7.53	61.32	19.91
Larvacea	32.7	17.24	0.96	0.12
Mysidacea	0.9	0.03	0.24	14.52
Natantia	2.1	0.06	1.13	65.09
Osteichthyes	4.3	0.10	14.35	626.48
Reptantia	20.4	1.04	2.24	5.77
Thecosomata	21.3	6.94	0.85	0.16
miscellaneous prey (e.g., Ostracoda)	3.7	0.31	0.05	0.12
hard items (e.g., sand)	0.9	0.00	0.18	2.70
other epibenthic prey (e.g., Cumacea, harpacticoids)	5.1	2.06	3.35	1.92
parasites (e.g., Nematoda)	10.4	0.33	0.68	3.62
unidentified prey	45.4	0.71	2.65	0.15
Groups combined	100	100	100	2.72

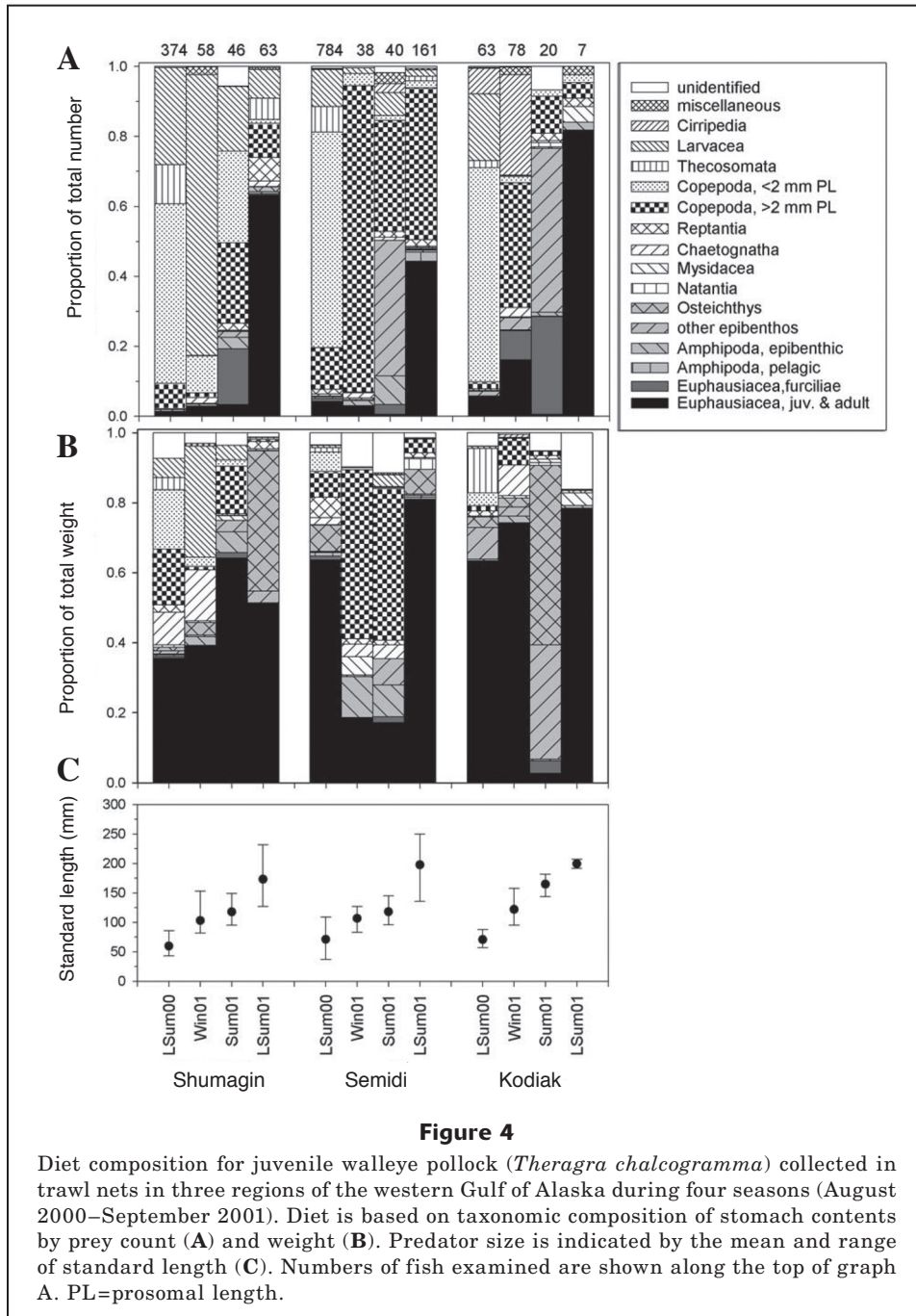[1] Per item weight (W/No.) was computed with only items that were <50% digested

estimated for only the six remaining season-region combinations.

Absolute growth rate (mm SL/d) generally increased with seasonal progression, except during Win01 when growth in the Shumagin region was negative. Compared to the growth of Kodiak fish, the negative growth of Shumagin fish was associated with relatively small-fish body weight, low daily ration, and an energy-poor diet. In terms of specific growth rate, the negative wintertime growth equates to a daily loss of 1% BW for Shumagin juveniles; in contrast, the positive wintertime growth of the Kodiak juveniles equates to a daily gain of 1% BW. It therefore appears that the higher daily ration and energy-rich diet observed among juveniles in the Kodiak region during Win01 resulted in a relatively high season-specific growth rate.

Discussion

Our results show that members of the largest population of juvenile walleye pollock in the GOA exhibit seasonal fluctuations in stomach content weight similar to those of other cold-water fishes (Wootton, 1998). Because these were growing juveniles, the feeding cycle was superimposed on marked increases in fish body size. Body size is an important consideration because increases in body size generally correspond with decreases in the specific weight of stomach contents (Wootton, 1998). Thus, the late summer-to-winter and the summer-to-late summer declines in %BW can be at least partly explained by increasing fish length. However, a length effect does not explain the winter-to-summer rebound in stomach content weight, which might alternatively be explained by a postwinter rebound from relatively poor wintertime feeding conditions. We acknowledge that the Kodiak region in particular was represented by few fish, which increases uncertainty in our observations, but the seasonal pattern was similar among regions and was consistent with a postwinter recovery in body condition (Buchheister et al., 2006) and acceleration in growth rate (Wilson et al., in press). The increase in water temperature from winter to summer may have stimulated feeding by increasing gastric evacuation and systemic demand (Wootton, 1998). Another contributing factor might have been prey availability. Zooplankton population density in the GOA increases during spring owing to an early summer peak in copepod abundance before declining from summer to winter (Coyle and Pinchuk, 2003). Prey availability was thought to influence positively stomach content weights of walleye pollock in the Bering Sea (Dwyer et al., 1987).

Figure 4

Diet composition for juvenile walleye pollock (*Theragra chalcogramma*) collected in trawl nets in three regions of the western Gulf of Alaska during four seasons (August 2000–September 2001). Diet is based on taxonomic composition of stomach contents by prey count (**A**) and weight (**B**). Predator size is indicated by the mean and range of standard length (**C**). Numbers of fish examined are shown along the top of graph A. PL=prosomal length.

Stomach content weight and diet were not strictly independent because euphausiids were a principal dietary component. A similar association was inferred off Japan when a postwinter rebound in juvenile walleye pollock stomach fullness was thought to reflect seasonal increase of euphausiid abundance (Yamamura et al., 2002). Euphausiids are a preferred prey item (Wilson et al., 2006) and the large ones especially are a beneficial dietary addition because their caloric density is higher than that of most other prey (Mazur et al., 2007). However, the consumption of large euphausiids

may be constrained by fish mouth gape width (Brodeur, 1998). The constraint relates to body size (Wilson et al., 2009). Given the negligible overwinter growth, from age-0 to age-1 (Brodeur and Wilson, 1996), we hypothesize that poor wintertime food habits resulted at least partly from juvenile walleye pollock being too small to consume all sizes of euphausiids.

The annual cycle of euphausiids in juvenile walleye pollock diet likely reflects the predator-prey size relationship superimposed on annual cycles of fish growth and euphausiid production. In the GOA, euphausiids

are spawned during spring (Pinchuk et al., 2008) and then develop and grow during the subsequent summer (Pinchuk and Hopcroft, 2007). This can explain why the peak proportion of furciliae in fish stomachs preceded that of juvenile and adult euphausiids. Euphausiid population density appears to peak during autumn (Coyle and Pinchuk, 2005) or winter (Cooney, 1986) owing perhaps to prespawning aggregation behavior and sampling bias (e.g., Siegel, 2000). We contend that some fraction of these euphausiids were too big to be available as prey of late age-0 and early age-1 walleye pollock. Any starvation-related shrinkage in euphausiid body size (Pinchuk and Hopcroft, 2007) might therefore benefit juvenile walleye pollock. Sometime between the period when walleye pollock growth resumes in early spring (Wilson et al., in press) and the period when they consume large euphausiids in late summer (Wilson et al., 2009), yearling walleye pollock gain the ability to consume all sizes of the euphausiids within their foraging ambit. Because juvenile walleye pollock and euphausiid size compositions vary geographically (e.g., Wilson et al., 2009), we predict that regional variation occurs in the timing when juveniles gain full access to all sizes of euphausiids, which are a principal determinant of food-related habitat quality.

Superior feeding conditions before and during winter in the Kodiak region can explain why resident juveniles were bigger and in better body condition than other juveniles (Buchheister et al., 2006). Superior feeding conditions were indicated by a euphausiid-rich diet and fuller stomachs. Euphausiid-rich diets may simply reflect the advantage of a body size that enabled the consumption of large euphausiids. However, recent research during late summer indicates that euphausiid populations in the Kodiak region can be substantially denser than in the Shumagin and Semidi regions (senior author, unpubl. data) and perhaps reflect different oceanographic characteristics. The Kodiak region is characterized by onshore flow into sea valleys, which were associated with euphausiid concentrations (Logerwell et al., 2010). In contrast, much of the shelf area in the Shumagin and Semidi regions is occupied by Semidi Bank, which causes offshore flow (Schumacher and Reed, 1986). Few euphausiids occur inshore of and over Semidi Bank, although concentrations are found over the adjacent continental slope and sea valleys (Wilson, 2009). Euphausiids may also experience less grazing pressure in the Kodiak region than in the Shumagin and Semidi regions where juvenile walleye pollock can be more abundant (senior author, unpubl. data).

During summer 2001, the best food-related habitat quality for juvenile walleye pollock appeared to have shifted to the Shumagin region. The Shumagin juveniles experienced the strongest postwinter rebound in stomach fullness and no decline in the dietary proportion of euphausiids. This shift in habitat may reflect the relatively high abundance of small-size euphausiids observed later in the region (Wilson et al., 2009). In contrast, Semidi and Kodiak juveniles exhibited a relatively weak postwinter rebound in stomach fullness

and relatively low euphausiid dietary proportions. The high proportion of epibenthic animals (e.g., cumaceans) among Kodiak fish during summer 2001 may be indicative of supplemental feeding during times of pelagic prey scarcity (Brodeur and Wilson, 1996). The better habitat quality in the Shumagin region may have been transitory as the diets of juveniles in the Semidi and Kodiak areas again became relatively euphausiid rich during late summer 2001, although the Shumagin mean SCW stayed relatively high. We acknowledge that our interpretation of apparent differences between Shumagin and Kodiak is tenuous given the paucity of Kodiak fish examined—a paucity that can bias dietary breadth (Ferry and Cailliet, 1996) and reduce estimate precision, but our interpretation is consistent with season and region differences in body condition.

Additional support of a postwinter shift in the region of most-favorable feeding habitat is provided by regional differences in whole-body energy density. In concert with their relatively strong postwinter rebound in stomach content weight, Shumagin fish exhibited a stronger rebound in whole-body energy density than Semidi and Kodiak juveniles, and the Shumagin juveniles had high energy densities during summer 2001 (Buchheister et al., 2006). We therefore hypothesize that the area most favorable for juvenile walleye pollock feeding is determined by euphausiid availability and shifts from the Kodiak region during winter to the Shumagin region during summer. Whether this change extends to seasonal shifts in walleye pollock nursery location, as distinguished from less productive juvenile habitat (Dahlgren et al., 2006), depends on the impact that the variation in food habits has on growth and survival.

In the field context of the present study, juvenile walleye pollock food habits and associated body condition have direct implications for growth rate. The relevance of food to growth was underscored by the similarity of our growth estimates from food-based modeling with those from independent otolith-based studies. Otolith growth of age-0 walleye pollock 5 days before capture in late summer 2000 indicated body growth rates of 0.03 to 0.19 g/d (Mazur et al., 2007), which encompass our estimates of 0.03 and 0.04 g/d (see Table 3, multiply the specific growth rate by body weight). During 2001, the peak growth rate of yearling walleye pollock estimated from growth increments in otoliths was 0.59 mm SL/d (Wilson et al., in press), which was slightly above our late summer 2001 estimates of 0.39 and 0.56 mm SL/d. We found no estimates of growth rate during winter, but the average of our two new wintertime estimates (–0.03 mm SL/d) is consistent with the negligible change in body length of juveniles throughout the western GOA (Brodeur and Wilson, 1996). The difference between our winter estimates reflects the difference in dietary proportion of euphausiids associated with differences in stomach content weight and diet energy density. We speculate that similar region-specific dietary differences explain the previously observed faster growth (Bailey et al., 1996) and larger body length

Table 3

Growth rate for juvenile walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska by season and region (see Fig. 1, Table 1) was estimated with a bioenergetics model. Model inputs included mean water temperature at 40-m depth, predator body weight, predator energy density, and daily food ration. Daily ration (%BW/d) was estimated with a simple evacuation model (see text). Diet energy density and specific growth rate (grams of growth per gram of body weight per day, [g/g/d]) are included. LSum00=late summer 2000, Win01=winter 2001, and LSum01=late summer 2001.

				Energy density (J/g)			Growth rate	
Season	Region	Temp (°C)	Body wt (g)	Predator	Diet	Daily ration	mm SL/d	g/g/d
LSum00	Semidi	9.0	3.6	3999	5094	4.99	0.26	0.011
LSum00	Shumagin	8.3	2.0	3441	4070	6.62	0.27	0.013
Win01	Kodiak	5.0	15.2	4284	5261	3.46	0.33	0.008
Win01	Shumagin	4.5	9.3	4187	3530	1.30	−0.38	−0.011
LSum01	Semidi	9.8	81.4	4782	5578	2.43	0.39	0.006
LSum01	Shumagin	9.3	55.0	4576	4725	3.45	0.56	0.010

(Wilson, 2000) of age-0 juveniles in the Kodiak region during late summer. Fish body size and water temperature are other relevant factors because they affect respiration, which in the bioenergetics model was the largest use of input energy. Respiration decreases with fish size, but increases with water temperature. Thus, the wintertime size-related reduction in respiration of Kodiak fish allowed more energy for growth than that for Shumagin fish although water in the Shumagin region was 0.5° C cooler. In addition to physiological conditions, body size directly affects the acquisition of large euphausiids (Wilson et al., 2009) and consequent energy input (Mazur et al., 2007). For summer 2001 and late summer 2001, too few samples were available to estimate the growth rates of Kodiak yearlings for comparison with the Shumagin region and therefore we were unable to explore seasonal shifts in the region of most-favorable growth. Nevertheless, the direct implication of seasonal and regional variation in food habits on growth rate leads us to speculate that the region most favoring rapid growth of juvenile walleye pollock varies with year in response to ecological determinants of euphausiid availability and oceanographic effects on local euphausiid abundance.

Opportunistic sampling enabled us to obtain the sample set necessary to formulate hypotheses, but rigorous control over sampling effort and site location was lacking. This was least a concern during winter when sampling effort was relatively high and most sites were located in close proximity to sea valleys where yearlings likely concentrate (e.g., Hollowed et al., 2007; Wilson, 2009). However, the number of stomachs available during winter from the Semidi region was <60; therefore the apparent number of prey types consumed (i.e., dietary breadth) was probably biased low (Ferry and Cailliet, 1996). Similarly insufficient stomach numbers were available in each region sampled during summer 2001, but the negative bias was probably most extreme for Kodiak during summer and late summer 2001 when only 20 and 7 fish were examined, respectively. It was

encouraging, however, that the late summer 2001 resurgence in the dietary proportion of euphausiids among Kodiak fish was mirrored in the diet of Semidi fish, which was represented by ample stomachs. Site location in the Kodiak region during summer and late summer (2000 and 2001) was generally farther offshore than in winter. Therefore, the available samples did not represent the nearshore where juvenile walleye pollock population density can be high (Wilson et al., 2005). Previously, at least for age-0 juveniles, no significant difference was found between nearshore and shelf sites regarding stomach content weight, and dietary differences were attributed to nearshore prey (e.g., crab larvae) rather than euphausiids (Wilson et al., 2005), which in the present study were primarily responsible for diet variation. Another problem with using opportunistic sampling was the variety of cruise objectives and collection methods (e.g., gear), which created uncertainty about how to quantify the population fraction represented by each sample. Clearly, there are many drawbacks to using opportunistically collected samples; however, those samples provided the empirical information necessary to formulate our hypotheses.

Conclusions

In summary, an annual cycle in juvenile walleye pollock food habits was primarily evident as a postwinter rebound in stomach content weight that was not explained by a body-size effect. We hypothesize that seasonal changes in stomach content weight were driven by the combined effects of juvenile growth, predator-prey size constraints, and the cycle of euphausiid abundance and growth. Further, we hypothesize that the most-favorable feeding area cycles annually from the Kodiak region during winter to the Shumagin region during summer in response to euphausiid availability. The similarity in growth rate between food-based model output and independent otolith-based estimates imply that the

observed seasonal and regional variation in food habits and body condition directly affect juvenile walleye pollock growth rates. Given that food habits, body condition, and growth rate are relevant to the survival of juveniles, the location of walleye pollock nurseries, as opposed to less productive juvenile habitat (Dahlgren et al., 2006), may vary with annual periodicity.

Acknowledgments

Literature cited

Bailey, K. M.
  2000.   Shifting control of recruitment of walleye pollock *Theragra chalcogramma* after a major climatic and ecosystem change.   Mar. Ecol. Prog. Ser. 198:215–224.
Bailey, K. M., A. L. Brown, M. M. Yoklavich, and K. L. Mier.
  1996.   Interannual variability in growth of larval and juvenile walleye pollock *Theragra chalcogramma* in the western Gulf of Alaska, 1983–91.   Fish. Oceanogr. 5(suppl. 1):137–147.
Brodeur, R. D.
  1998.   Prey selection by age-0 walleye pollock, *Theragra chalcogramma*, in nearshore waters of the Gulf of Alaska.   Environ. Biol. Fishes 51:175–186.
Brodeur, R. D., and K. M. Bailey.
  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 (Y. Watanabe, Y. Yamashita, and Y. Oozeki, eds.), p. 245–259.   A.A. Balkema, Rotterdam, Netherlands.
Brodeur, R. D., and M. T. Wilson.
  1996.   A review of the distribution, ecology and population dynamics of age-0 walleye pollock in the Gulf of Alaska.   Fish. Oceanogr. 5 (suppl. 1):148–166.
Buchheister, A., and M. T. Wilson.
  2005.   Shrinkage correction and length conversion equations for *Theragra chalcogramma, Mallotus villosus* and *Thaleichthys pacificus*.   J. Fish. Biol. 67:541–548.

Buchheister, A., M. T. Wilson, R. J. Foy, and D. A. Beauchamp.
  2006.   Seasonal and geographic variation in condition of juvenile walleye pollock in the western Gulf of Alaska.   Trans. Am. Fish. Soc. 135:897–907.
Buckel, J. A., D. O. Conover, N. D. Steinberg, and K. A. McKown.
  1999.   Impact of age-0 bluefish (*Pomatomus saltatrix*) predation on age-0 fishes in the Hudson River estuary: evidence for density-depended loss of juvenile striped bass (*Morone saxatilis*).   Can. J. Fish. Aquat. Sci. 56:275–287.
Ciannelli, L., R. D. Brodeur, and T. W. Buckley.
  1998.   Development and application of a bioenergetics model for juvenile walleye pollock.   J. Fish Biol. 52:879–898.
Cooney, R. T.
  1986.   Zooplankton.   *In* The Gulf of Alaska physical environment and biological resources (D. W. Hood and S. T. Zimmerman, eds.), p. 285–303.   OCS Study MMS86-0095.   Minerals Management Service, Springfield, VA.
Coyle, K. O., and A. I. Pinchuk.
  2003.   Annual cycle of zooplankton abundance, biomass and production on the northern Gulf of Alaska shelf, October 1997 through October 2000.   Fish. Oceanogr. 12:327–338.
  2005.   Seasonal cross-shelf distribution of major zooplankton taxa on the northern Gulf of Alaska shelf relative to water mass properties, species depth preferences and vertical migration behavior.   Deep-Sea Res., pt. II, Top. Stud. Oceanogr. 52:217–245.
Dahlgren, C. P., G. T. Kellison, A. J. Adams, B. M. Gillanders, M. S. Kendall, C. A. Layman, J. A. Ley, I. Nagelkerken, and J. E. Serafy.
  2006.   Marine nurseries and effective juvenile habitats: concepts and applications.   Mar. Ecol. Prog. Ser. 312:291–295.
Dwyer, D. A., K. M. Bailey, and P. A. Livingston.
  1987.   Feeding habits and daily ration of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea, with special reference to cannibalism.   Can. J. Fish. Aquat. Sci. 44:1972–1984.
Elliott, J. M., and L. Persson.
  1978.   The estimation of daily rates of food consumption for fish.   J. Anim. Ecol. 47:977–991.
Ferry, L. A., and G. M. Cailliet.
  1996.   Sample size and data analysis: Are we characterizing and comparing diet properly?   *In* Feeding ecology and nutrition in fish: proceedings of the symposium on the feeding ecology and nutrition in fish; international congress on the biology of gishes, July 14–18, 1996 (D. MacKinlay and K. Shearer, eds.), p. 71–80.   Am. Fish. Soc., San Francisco, CA.
Hinckley, S., K. M. Bailey, S. J. Picquelle, J. D. Schumacher, and P. J. Stabeno.
  1991.   Transport, distribution, and abundance of larval and juvenile walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska.   Can. J. Fish. Aquat. Sci. 48:91–98.
Hollowed, A. B., C. D. Wilson, P. J. Stabeno, and S. A. Salo.
  2007.   Effect of ocean conditions on the cross-shelf distribution of walleye pollock (*Theragra chalcogramma*) and capelin (*Mallotus villosus*).   Fish. Oceanogr. 16:142–154.
Hurst, T.
  2007.   Causes and consequences of winter mortality in fishes.   J. Fish Biol. 71:315–345.
Logerwell, E. A., J. Duffy-Anderson, M. Wilson, and D. McKelvey.
  2010.   The influence of pelagic habitat selection and inter-

specific competition on productivity of juvenile walleye pollock (*Theragra chalcogramma*) and capelin (*Mallotus villosus*) in the Gulf of Alaska. Fish. Oceanogr. 19:262–278.

Mazur, M. M., M. T. Wilson, A. B. Dougherty, A. Buchheister, and D. A. Beauchamp.
    2007. Temperature and prey quality effects on growth of juvenile walleye pollock *Theragra chalcogramma* (Pallas): a spatially explicit bioenergetics approach. J. Fish Biol. 70:816–836.

Merati, N., and R. D. Brodeur.
    1996. Feeding habits and daily ration of juvenile walleye pollock in the western Gulf of Alaska. *In* Ecology of juvenile walleye pollock (R. D. Brodeur, P. A. Livingston, T. R. Loughlin, and A. B. Hollowed, eds.), p. 65–79. NOAA Tech. Rep. NMFS-126.

Pinchuk, A. I., K. O. Coyle, and R. R. Hopcroft.
    2008. Climate-related variability in abundance and reproduction of euphausiids in the northern Gulf of Alaska in 1998–2003. Prog. Oceanogr. 77:203–216.

Pinchuk, A. I., and R. R. Hopcroft.
    2007. Seasonal variations in the growth rates of euphausiids (*Thysanoessa inermis, T. spinifera,* and *Euphausia pacifica*) from the northern Gulf of Alaska. Mar. Biol. 151:257–269.

Reed, R. K., and J. D. Schumacher.
    1986. Physical oceanography. *In* The Gulf of Alaska physical environment and biological resources (D. W. Hood and S. T. Zimmerman, eds.), p. 57–75. OCS Study MMS86-0095. Minerals Management Service, Springfield, VA.

Schumacher, J. D., and R. K. Reed.
    1986. On the Alaska Coastal Current in the western Gulf of Alaska. J. Geophys. Res. 91(C8):9655–9661.

Siegel, V.
    2000. Krill (Euphausiacea) life history and aspects of population dynamics. Can. J. Fish. Aquat. Sci. 57(suppl. 3):130–150.

Sogard S.
    1997. Size-selective mortality in the juvenile stage of teleost fishes: A review. Bull. Mar. Sci. 60:1129–1157.

Springer, A. M.
    1992. A review: Walleye pollock in the North Pacific—how much difference do they really make? Fish. Oceanogr. 1:80–96.

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. Fish. Bull. 98:823–834.

Wilson, M. T.
    2009. Ecology of small neritic fishes in the western Gulf of Alaska. I. Geographic distribution in relation to prey density and the physical environment. Mar. Ecol. Prog. Ser. 392:223–237.

Wilson, M. T., R. D. Brodeur, and S. Hinckley.
    1996. Distribution of age-0 walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. *In* Ecology of juvenile walleye pollock (R. D. Brodeur, P. A. Livingston, T. R. Loughlin, and A. B. Hollowed, eds.), p. 11–24. NOAA Tech. Rep. NMFS-126.

Wilson, M.T., A. L. Brown, and K. L. Mier.
    2005. Geographic variation among age-0 walleye pollock (*Theragra chalcogramma*): evidence of meso-scale variation in nursery quality? Fish. Bull. 103:207–218.

Wilson, M. T., C. M. Jump, and A. Buchheister.
    2009. Ecology of small neritic fishes in the western Gulf of Alaska. II. Consumption of krill in relation to krill standing stock and the physical environment. Mar. Ecol. Prog. Ser. 392:239–251.

Wilson, M. T., C. M. Jump, and J. T. Duffy-Anderson.
    2006. Comparative analysis of the feeding ecology of two pelagic forage fishes: capelin *Mallotus villosus* and walleye pollock *Theragra chalcogramma*. Mar. Ecol. Prog. Ser. 317:245–258.

Wilson, M. T., K. Mier, and A. Dougherty.
    2011. The first annulus of otoliths: a tool for studying intra-annual growth of walleye pollock (*Theragra chalcogramma*). Environ. Biol. Fishes. doi:org/10.1007/s/0641-011-9815-1.

Wootton, R. J.
    1998. Ecology of teleost fishes, 2nd edn. Fish and fisheries series, vol. 24, 386 p. Kluwer Academic Publs., Dordrecht, The Netherlands.

Yamamura, O., S. Honda, O. Shida, and T. Hamatsu.
    2002. Diets of walleye pollock *Theragra chalcogramma* in the Doto area, northern Japan: ontogenetic and seasonal variations. Mar. Ecol. Prog. Ser. 238:187–198.