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[Special Section: Atka Mackerel]

Longitudinal Growth Differences and the Influence of Diet Quality on Atka Mackerel of the Aleutian Islands, Alaska: Using a Bioenergetics Model to Explore Underlying Mechanisms

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Abstract.—Atka mackerel *Pleurogrammus monopterygius* make up the single largest biomass of groundfish in the Aleutian Islands, Alaska, and are an important component of this marine ecosystem. Atka mackerel show a significant decrease in size from east to west. We compared fish from two study areas reflecting this size cline: Seguam Pass in the eastern Aleutians and Amchitka Island in the western Aleutians. At any given age, the Atka mackerel at the former location are larger than those at the latter (e.g., 5-year-old fish average 732 g and 39 cm fork length at Seguam Pass but only 575 g and 36 cm at Amchitka Island). Our objectives were to determine the mechanisms underlying the observed differences in growth, such as prey availability, prey quality, and thermal experience. We used a bioenergetics model to examine the effects of diet and temperature on growth. The model estimates of consumption fell within the range of those observed for Atka mackerel, suggesting that the model was an appropriate tool for exploring these effects. The results obtained with the model suggest that prey quality is the main factor in the observed size differences. At Seguam Pass Atka mackerel ate a more energetically rich diet consisting of euphausiids and fish, whereas at Amchitka Island copepods dominated the diet and there was little to no fish consumption. The model results also suggest that thermal experience contributed less to the observed differences in growth than did the composition of the diet. Understanding the mechanisms underlying the growth of Atka mackerel will improve predictions of biomass and yield within the framework of a dynamic ecosystem and a changing climate.

Atka mackerel *Pleurogrammus monopterygius* support an important fishery in the Aleutian Islands, Alaska, serving as both predators and prey in this ecosystem (Lowe et al. 2008). In 2009, the biomass of Atka mackerel age 3 and older was estimated at 410,600 tons (Lowe et al. 2008). Although a fair amount is known about the reproduction of Atka mackerel (McDermott and Lowe 1997; McDermott et al. 2007; Lauth et al. 2007; Cooper et al. 2010, this issue), little has been published about their food habits and growth (Yang 1999; Logerwell et al. 2005). Atka mackerel belong to the greenling family and are semidemersal, migrating vertically in the water column during daylight hours with little to no movement off the bottom at night (Nichol and Somerton 2002). Across their geographic range, the population reaches 50% maturity around 3.6 years of age (McDermott and Lowe 1997). Atka mackerel are demersal spawners; females deposit egg masses in rocky habitats, and males guard nests for prolonged periods (several months), providing protection against predators and egg cannibalism (Zolotov 1993; Lauth et al. 2007). Few details are available on Atka mackerel life history before age 3; however, it is thought that the larvae and juveniles are pelagic and reside in the open ocean, transiting via oceanic currents (Gorbunova 1962; Materese et al. 2003; Mel'nikov and Efimkin 2003). Size at age declines along a longitudinal gradient from east to west across the Aleutian chain (Kimura and Ronholt 1988; Lowe et al. 1998). At Seguam Pass in the east, Atka mackerel average up to 5 cm longer and 150 g heavier than those of the same age found near Amchitka Island in the west. These growth differences are primarily manifested in adult fish (age 3 and older) after recruitment to a particular locality has been

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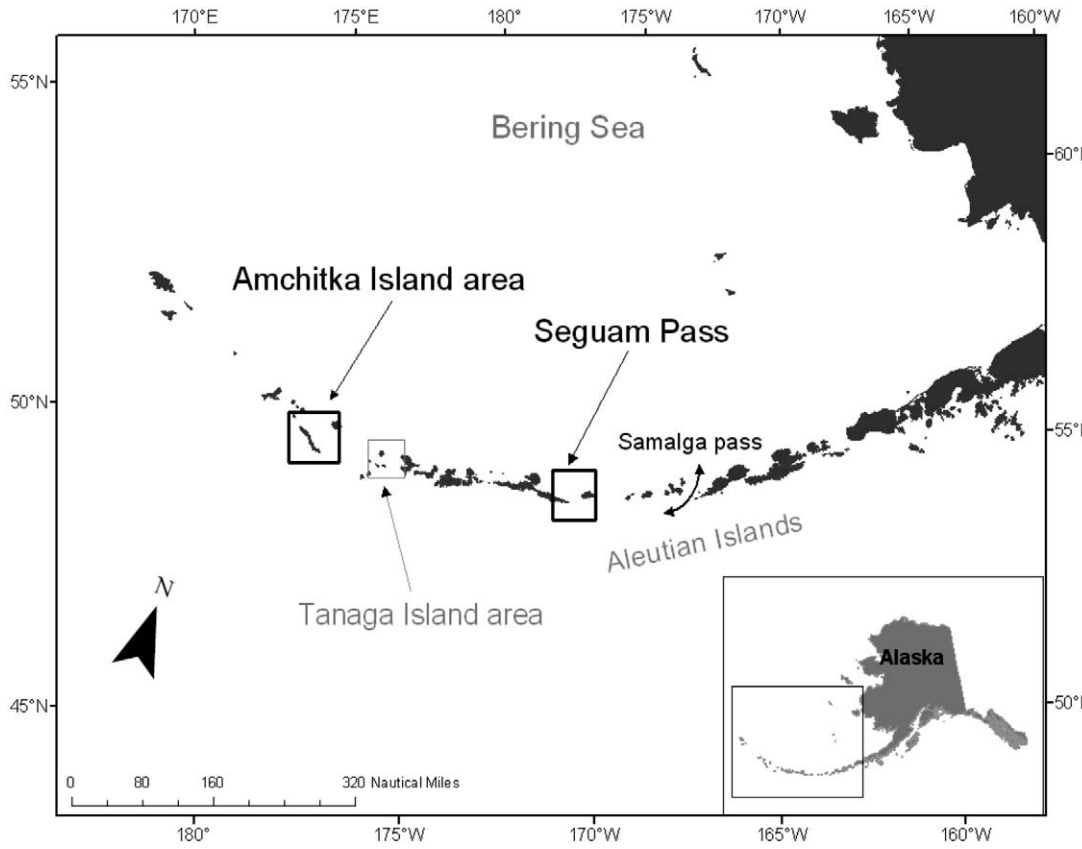


FIGURE 1.—The two study areas (bold boxes) and related areas in the Aleutian Islands. Samalga Pass is an important oceanographic transition zone. The Tanaga Island area contains the Atka mackerel whose energy densities were used as a proxy for those of the Atka mackerel near Amchitka Island.

established (Lowe et al. 2008); therefore, we were interested in determining what factors influenced the observed spatial differences in growth. Although it is often difficult to discern the effects of individual or interacting factors on growth, it is important to identify and understand the mechanisms because body size affects predator–prey relationships, population biomass, and reproductive output.

Fish growth is mediated by prey quality, prey availability (quantity), temperature, body size, and genetic predispositions (Roff 1992). Recent evidence suggests that genetic variation is not responsible for the size differences between Seguam Pass and Amchitka Island (Lowe et al. 1998; Canino et al. 2010, this issue). After eliminating genetic predisposition, we hypothesized that up to three factors contributed to the observed longitudinal growth differences: prey availability (the amount of prey consumed), prey quality (the amount of energy in the prey), and thermal experience. Analyzing how different factors influence the growth of Atka mackerel is the first step toward process-oriented research and ultimately ecosystem modeling.

We used area-specific growth, temperature, and diet data with a bioenergetics model to qualitatively explore the effects of prey availability, prey quality, and thermal experience on the growth of Atka mackerel. The specific objectives of this study were to (1) compare the size at age and growth rates of the Amchitka and Seguam populations using the von Bertalanffy growth equation; (2) compare the underlying diets, thermal experiences, and estimated feeding rates (a surrogate for prey availability) of different age-groups of Atka mackerel at Seguam Pass and Amchitka Island; and (3) explore the area-specific effects of diet and temperature on growth conditions.

Methods

Data Collection

The two study areas were located at Seguam Pass and near Amchitka Island (Figure 1) in the Aleutian

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TABLE 1.—Sample sizes used in the analysis by study area, age, and date. Age-8 fish were only used in model inputs for growth.

	Age					
Date	3	4	5	6	7	8
Amchitka Island						
Jul 2003	1	13	34	44	20	59
Oct 2003	38	130	125	41	23	31
Oct 2004	14	50	67	54	9	2
Seguam Pass						
Jun 2002	27	86	17	20	66	16
Oct 2003	41	212	62	7	2	10
Oct 2004	74	71	98	31	3	6

Island chain. Between 2002 and 2004, the National Marine Fisheries Service chartered commercial fishing vessels for five research cruises primarily to conduct a mark–recapture study during June, July, and October. These cruises served as the platform for all data collection (Table 1). The cruises in June and July were conducted over 12-h daylight periods; the cruises in October were conducted over a 24-h (day and night) periods.

Depth, water column, and bottom temperature data were collected by means of an SBE 39 microbathythermograph (Seabird Electronics) attached to the headrope of the bottom trawl net. Data were logged at 1-s intervals from the time the net was set until the time it was retrieved. When depth data from the SBE 39 were not available for a haul, data were summarized from the ship's sounder via the ECC Globe interface (Electronic Charts Company).

Approximately 10 fish (5 males and 5 females) were randomly sampled from each haul, totaling 1,745 specimens between 2002 and 2004 (Table 1). The data and tissues collected included sex, length (cm), weight (g), stomachs, and age structures (otoliths). Size at age and growth were determined by examination of otoliths (Anderl et al. 1996) at the Alaska Fisheries Science Center. The otoliths from each specimen were sectioned along the dorsal–ventral plane and passed over a flame; the burnt surface was then examined under a microscope.

Stomach samples were fixed in a 10% solution of buffered formalin in the field and neutralized in the laboratory with Neutralex (Tissue-Tek Neutralex). After being neutralized for several hours, the samples were stored in a 70% solution of ethyl alcohol until laboratory analysis. In the laboratory, the stomach contents were excised, excess moisture was blotted, and all nonprey items (e.g., rocks) were removed. If a stomach contained no prey items, it was recorded as empty. The total wet weight of the stomach contents was recorded to the nearest milligram. All of the prey items in each stomach sample were identified to the lowest taxonomic level possible, sorted into prey groups (related taxa), and weighed to the nearest milligram. The major prey species, in terms of contribution to the diet by weight, included Copepoda, Amphipoda, Euphausiidae, arrow worms (Chaetognatha), unidentified fish, lanternfishes (Myctophidae), northern smoothtongue *Leuroglossus schmidti*, unidentified smelts (Osmeridae), Atka mackerel eggs, octopus and squid (Cephalopoda), larvaceans (Larvacea and Copelata) and "other" (e.g., gastropods, polychaetes, and shrimp).

Observed Area-Specific Age and Growth

To verify differences in the size at age of Atka mackerel between the two study areas, the von Bertalanffy growth model was fit to observed length-at-age data for the two areas individually and together, that is,

$$L_t = L_\infty(1 - e^{-k[t-t_0]}), \quad (1)$$

where L_t is fork length at age t, L_∞ is the asymptotic length, k is the Brody growth coefficient, and t_0 is the hypothetical age at which the fish length is zero. The goodness of fit of the model was estimated by nonlinear least-squares regression in S-Plus (S-Plus 1999), as outlined in Hilborn and Walters (1992). The maximum-likelihood ratio test (Kimura 1980) was used to determine whether the parameter estimates for the growth curves best fit each study area separately or the two areas combined.

Bioenergetics Modeling

Bioenergetics models employ an energy balance equation to account for the total energy needs of a consumer, that is, prey consumption (C) equals the sum of growth (G), waste (W), and reproduction and metabolic costs (M) (Winberg 1956; Kitchell et al. 1977). Either growth or consumption can be estimated if the value of the other term is known (Hanson et el. 1997). For this study, we used the Wisconsin Bioenergetics 3.0 model as parameterized for a biologically similar species, walleye pollock *Theragra chalcogramma* (Tables A.1 and A.2 in the appendix; Hanson et al. 1997). The walleye pollock was used as a proxy for Atka mackerel because the two species are semidemersal and overlap considerably in habitat, size range (Barbeaux et al. 2008), and diet composition, euphausiids being the most important prey item by weight for both species (Lang and Livingston 1996; Yang 1999; Adams et al. 2007). The median age at maturity is 3.6 years for Atka mackerel (McDermott et

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TABLE 2.—Percent diet composition of age-3–4 and age-5–7 Atka mackerel by prey energy density at Amchitka Island and Seguam Pass. Observed data were input into the model on days 1, 200, and 300; the final simulation day was day 385.

Prey group	Prey energy density (J/g)	Amchitka 3–4			Amchitka 5–7			Seguam 3–4			Seguam 5–7		
		5.5°C	4.6°C	5.7°C	5.5°C	4.6°C	5.7°C	4.6°C	3.8°C	5.2°C	4.6°C	3.8°C	5.2°C
Copepoda[a]	5,319	0.04	0.60	0.31	0.03	0.43	0.19	0.01	0.46	0.15	0.00	0.08	0.11
Amphipoda[a]	2,787	0.10	0.05	0.01	0.08	0.07	0.01	0.01	0.00	0.00	0.00	0.00	0.00
Euphausiidae[a]	5,949	0.44	0.26	0.39	0.19	0.17	0.38	0.70	0.16	0.78	0.32	0.13	0.68
Chaetognatha[a]	2,062	0.09	0.06	0.11	0.09	0.21	0.06	0.03	0.11	0.02	0.03	0.03	0.01
Osteichthyes[b]	7,500	0.00	0.00	0.00	0.03	0.00	0.02	0.01	0.13	0.00	0.00	0.19	0.01
Myctophidae[c]	7,000	0.00	0.00	0.00	0.00	0.00	0.03	0.01	0.10	0.00	0.02	0.08	0.00
Northern smoothtongue[d]	8,469	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.38	0.00
Osmeridae[e]	4,840	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00
Atka eggs[f]	5,677	0.08	0.00	0.04	0.36	0.00	0.23	0.02	0.00	0.04	0.46	0.00	0.18
Cephalopoda[c]	3,500	0.15	0.00	0.00	0.15	0.02	0.00	0.10	0.00	0.01	0.09	0.03	0.00
Larvacea and Copelata[a]	1,434	0.00	0.00	0.13	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00
Other[c]	3,000	0.09	0.04	0.01	0.08	0.11	0.00	0.10	0.03	0.00	0.07	0.01	0.01

[a] Mazur et al. (2007).
[b] Cauffopé and Heymans (2005).
[c] Hunt et al. (2000).
[d] Davis (2003).
[e] Van Pelt et al. (1997).
[f] Daniel Cooper, Alaska Fisheries Science Center, personal communication.

al. 1997) and between 3 and 4 years for walleye pollock (Wespestad and Terry 1984). In addition, Atka mackerel and walleye pollock often exhibit similar recruitment pulses in stock assessment predictions (Sandra Lowe, Alaska Fisheries Science Center, personal communication).

There were three steps to determining the effects of prey availability, prey quality, and thermal experience on the growth of Atka mackerel in the two study areas. First, we estimated daily and annual consumption rates for two age-groups of Atka mackerel at Amchitka and Seguam by fitting the bioenergetics model to observed growth using area-specific temperatures and area- and age-specific diet composition as inputs; we term these the baseline models. Second, to corroborate the models, we compared the daily consumption estimates generated in step one with independently derived field estimates of daily consumption calculated for June, July, and October. Third, growth responses for a hypothetical 500-g Atka mackerel were simulated for 1 d using different combinations of the diet and thermal regimes observed at Seguam and Amchitka. This allowed us to examine the effects of temperature and diet composition on growth by eliminating those of prey availability and the metabolic costs of spawning over time.

Modeling field consumption.—To construct the baseline models, we used area-specific temperature and diet composition data (Table 2) as inputs in the bioenergetics model to fit consumption to the observed, area-specific annual growth for two age-groups (ages 3–4 and 5–7). Mean bottom temperatures, summarized by area and time period, were used as inputs for thermal experience. Although Atka mackerel undergo diel migrations, the proportion of time that individuals spent in the water column was difficult to discern (Nichol and Somerton 2002), and the temperature differences between the sea floor and the water column depths occupied were small (Dan Nichol, Alaska Fisheries Science Center, personal communication). Therefore, the mean bottom temperature was considered a good representation of the thermal experience at each area.

Diet composition data were available for both Amchitka and Seguam from surveys conducted during the summer and fall in 2002–2004 (Seguam in June 2002, Amchitka in July 2003, and both in October 2003 and 2004). Because the summer diets were for different years, the seasonal diet compositions did not necessarily reflect the actual diet chronology for each area, nor could we account for potential interannual variability in the diets. Therefore, we were forced to assume that any observed differences in summer diet between areas were due to area-specific differences rather than interannual variability. The diet data were the proportions by weight of each prey category in the diet (Table 2). To accurately estimate the diet in each area, the diets of 10 specimens per haul were combined and the proportions from individual hauls in the October 2003 and 2004 collections were weighted by catch per unit effort (CPUE). The latter was estimated as metric tons of Atka mackerel per hour of trawling within the Amchitka and Seguam study areas. The data collected in June and July were not weighted by CPUE because the total weight of the Atka mackerel catch was not recorded.

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TABLE 3.—Input values for all baseline bioenergetics models, from observed Atka mackerel data. See text for additional details.

Model input	Area and age group			
	Amchitka 3–4	Amchitka 5–7	Seguam 3–4	Seguam 5–7
Initial weight (g)	471	591	536	715
Final weight (g)	599	651	655	786
Observed growth (g)	128	60	119	71
Mean prey energy density (J/[g·d])	4,787	4,739	5,464	5,985
Atka mackerel energy density (J/g wet weight)	5,500	5,500	5,500	5,500
% Spawn loss	10.2	16.21	9.16	13.03
Feeding rate	0.15	0.15	0.15	0.15
Biomass (g) of prey eaten during simulation period	1,824	1,781	1,649	1,769

The stomach content data suggested a dietary switch between ages 4 and 5 at both study areas. Therefore, we constructed different diet inputs for four baseline models to account for the differences between the two age-groups; the models were termed Amchitka 3–4, Amchitka 5–7, Seguam 3–4, and Seguam 5–7 (Table 2). Prey energy density values were taken from previous studies in the Bering Sea and Gulf of Alaska (Table 2). Area-specific values for the energy density of prey groups were not available, so the same values were used for both study areas. Although energy density could conceivably vary between areas (which would either dampen or enhance the area-specific differences in growth conditions), we focused on the effects of energetic quality among the different prey taxa.

The growth inputs for the baseline models were calculated as the average observed annual growth increments for age-groups 3–4 and 5–7 at Amchitka and Seguam (Table 3). For example, the growth input for age-group 3–4 was the difference between the weighted-average body mass of age-4 and age-5 fish in October 2004 and that of age-3 and age-4 fish in October 2003. Similarly, the growth input for age-group 5–7 was the difference between the weighted-average body mass of age-6–8 fish in October 2004 and that of age-5–7 fish in October 2003. Data from age-8 fish were only used for growth determinations and were not included in the diet composition analysis (Table 3).

The bioenergetics model allowed a loss in weight due to spawning, and the demands of spawning were used to simulate growth in the baseline models. The total observed energetic loss due to spawning was modeled as the product of the average observed reduction in body mass by sex and age (from June–July to October of the same year) and the energy density of eggs (5,677 J/g wet weight) relative to that of whole fish. Atka mackerel primarily spawn between July and October, and approximately 50% of the population is sexually mature at 3.6 years of age (McDermott and Lowe 1997). For each study area, the average loss in body mass between June–July and October was assumed to be from spawning. It was also assumed that 100% of the fish age 5 and older were sexually mature, along with 80% of the age-4 fish and 20% of the age-3 fish (McDermott and Lowe 1997). The average loss in body mass (as a function of the reduction in body mass and the cost of egg production) for each area and time period was weighted by age-group, sample size, and the percentage of the population that was sexually mature (Table 3).

The energy densities of Atka mackerel differed between the two study areas, that at Seguam being greater (5,892 J/g) than that at Amchitka (4,926 J/g) (Logerwell and Schaufler 2005; Tanaga Pass was used as proxy for Amchitka). To best simulate the effects of temperature and diet on growth, we used the average energy densities from Seguam and Amchitka for all simulations (Table 3).

Age- and area-specific consumption.—To estimate total consumption for approximately 1 year, we used the four baseline models starting on October 1 (simulation day 1) and continuing at daily time steps until October 25 of the following year (simulation day 385). This produced estimates of the biomass of individual prey types and total prey consumed both daily and over the simulation interval using observed data as inputs. It also permitted calculation of the average proportion of maximum consumption (i.e., the feeding rate) required for a consumer to achieve the growth rate observed over the 385-d simulation period. The biomass and corresponding energy of each prey type consumed were summed over the simulation interval to calculate the importance of each type to the annual energy budget of age-3–4 and age-5–7 Atka mackerel at Amchitka and Seguam.

Model corroboration.—To determine whether the bioenergetics model for walleye pollock was a reasonable surrogate for Atka mackerel, we conducted

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a model corroboration by comparing independent estimates of Atka mackerel consumption from the study areas with the estimates generated by the baseline models. The baseline models were initially run with observed area- and age-specific growth, diet, and temperature data (Tables 2, 3) to obtain consumption estimates fitted to the observed annual growth rates. Field-based consumption estimates were then compared with the predicted daily consumption estimates for the same dates to evaluate the accuracy of model simulations.

The field-based consumption estimates were computed from diel stomach fullness and temperature-dependent gut evacuation rates (Ney 1990). Based on the results in Finstad (2005), we concluded that reasonable estimates of daily consumption could be obtained by sampling every 12 h when the temperature was between 5°C and 10°C and once every 24 h when the temperature was less than 5°C. Thus, stomach samples were collected approximately every 4–6 h over 24-h time periods in October and over 12-h periods in June–July. The data were divided into two age-groups, 3–4 and 5–7 years old. Observed consumption (the total weight of prey consumed [g] per day/total fish body weight [g]) was estimated from the daily consumption equation proposed by Bajkov (1935) as modified by Ney (1990) to incorporate a gastric evacuation rate, that is,

$$C = 24RS, \tag{2}$$

where R is the gastric evacuation rate and stomach fullness (S) is calculated as the average amount of prey (in proportion to the consumer's body weight) in the stomach over 24 h, namely,

$$S_i = (A_i/W_i), \tag{3}$$

where A is the weight of the prey (g), W is the weight of the consumer (g), and the subscript i designates the ith consumer. S_i was averaged for each 24-h sampling interval to give

$$S_t = \sum S_i/N, \tag{4}$$

where N is the total number of fish in the sampling interval (~10 fish). S_t was averaged over the number of sampling intervals (T) to derive S, that is,

$$S = \sum S_t/T. \tag{5}$$

The gastric evacuation rate for Atka mackerel, R, was unknown but assumed to be similar to that of walleye pollock based on similarities in the two species' diets and thermal regimes. Gastric evacuation rates for a 50-g walleye pollock were measured at temperatures ranging from 3°C to 9°C and average stomach fullness ranging from 0.5% to 2.5% of body weight (Smith et al. 1989). Values of R were derived from a linear regression model using three gut evacuation rates reported by Smith et al. (1989)—for 3, 6, and 9°C—for a 50-g walleye pollock with a stomach fullness of 1% of body weight, namely,

$$R = 0.003 + 0.010 \cdot \text{Temp},$$

where Temp is the observed average bottom temperature (°C) at each area in which Atka mackerel were assumed to spend the greatest amount of time. The temperature range for Atka mackerel in this study varied from 3.6°C to 6.0°C.

Field-generated daily consumption estimates and 95% confidence intervals were obtained for several days in June 2002, July 2003, and October 2003 and 2004 and compared with the predicted daily consumption from the bioenergetics model simulations (Figure 2). The model predictions fell within the confidence intervals of the majority of the observed consumption estimates for age-3–4 fish at Seguam and age-5–7 fish at both Amchitka and Seguam. The observed consumption estimates for age-3–4 fish at Amchitka were slightly lower than the model predictions near simulation day 10 (Figure 2a); there were too few samples of such fish at Amchitka to estimate observed consumption during the July 2003 sampling period (about simulation day 200).

Simulated growth.—To observe the effects of temperature and diet quality on growth, we simulated growth under three different scenarios. As a starting point, we used the two baseline models for Amchitka (3–4 and 5–7) to simulate the growth of a hypothetical 500-g fish for 1 d and each of the sampling periods (June–July, October 2003, and October 2004). For each scenario, we assumed the same feeding rate (15% of maximum consumption; Table 3). This value was within the range of the estimated feeding rates when growth was fitted in the four baseline models. The results of each simulation scenario were relative to the Amchitka 3–4 and Amchitka 5–7 models. The simulation scenarios were as follows: (1) Seguam Temp, which used the baseline model for Amchitka but switched temperatures between Amchitka and Seguam; (2) Seguam Diet, which used the baseline model for Amchitka but switched diets between Amchitka and Seguam; and (3) Seguam Temp + Diet, which used the baseline model for Amchitka but switched both temperatures and diets between Amchitka and Seguam.

Results

Observed Area-Specific Age and Growth

To demonstrate the observed differences in growth between the study areas, the average weights at age of

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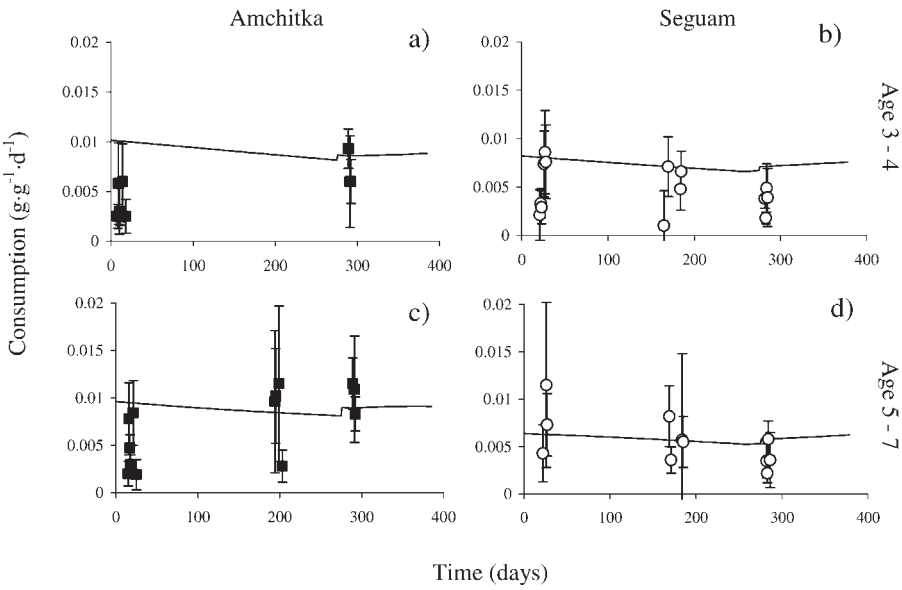


FIGURE 2.—Observed consumption by age-3–4 and age-5–7 Atka mackerel at **(a)** and **(c)** Amchitka Island (squares) and **(b)** and **(d)** Seguam Pass (circles) compared with the estimates derived from the bioenergetics model (horizontal lines). The error bars represent the 95% confidence intervals.

Atka mackerel and 95% confidence intervals are summarized by study area (Figure 3a); there is no overlap between the confidence intervals. The von Bertalanffy growth model was fit to data from Amchitka and Seguam both separately and together (Figure 3b). Based on the maximum-likelihood ratio test, the growth in each area was best described by an area-specific model ($P < 0.01$). Although the growth rates were similar in the two areas, the asymptotic length was greater for Seguam (Table 4); in fact, the estimated ranges for the latter parameter did not overlap (Amchika: 44.0–47.33 cm; Seguam: 48.0–51.18 cm).

Age- and Area-Specific Consumption

The total amount of energy consumed over the simulation period was calculated to illustrate the importance of each prey group to the annual energy budget for age-3–4 and age-5–7 Atka mackerel at Amchitka and Seguam (Figure 4). The biomass of each prey group appeared to be similar to the amount of energy consumed for this prey group and is summarized by the total grams consumed during the simulation period (Table 3). Euphausiids contributed the most energy to the diet of age-3–4 Atka mackerel at both Seguam and Amchitka (Figure 4a). The 3–4-year-old fish at Seguam also consumed fish (which are energetically richer than euphausiids), whereas those at Amchitka consumed very little if any fish (Figure 4a). Similarly, 5–7-year-old Atka mackerel consumed much greater portions of fish at Seguam than at Amchitka (Figure 4b). The 5–7-year-old fish at Seguam consumed more euphausiids than those at Amchitka; however, the 5–7-year-old fish at Amchitka consumed more copepods, which are energetically similar to euphausiids (Figure 4b). Furthermore, the 5–7-year-old Atka mackerel at Seguam consumed northern smoothtongues (included in Osmeridae), an energetically rich species from the deepwater smelt family that was not found in the diet of the 5–7 age-group at Amchitka (Figure 4b).

Simulated Growth

For all three time periods and both age-groups, the growth of a hypothetical 500-g fish was influenced more by diet quality than by temperature (Figure 5). For example, Figure 5a shows that the temperature at Seguam had little effect on the growth of fish in both age-groups (Seguam Temp simulation). However, when the Amchitka diet was replaced by the Seguam diet (Seguam Diet simulation), the 1-d growth increased dramatically for both age-groups from that of the Seguam Temp simulation (Figure 5a). When the diets were switched in the June–July period, the increase in growth was much more pronounced in the age-5–7 group; however, there were increases in both groups (Figure 5b). The results for Seguam Temp + Diet simulation were similar to those for the Seguam

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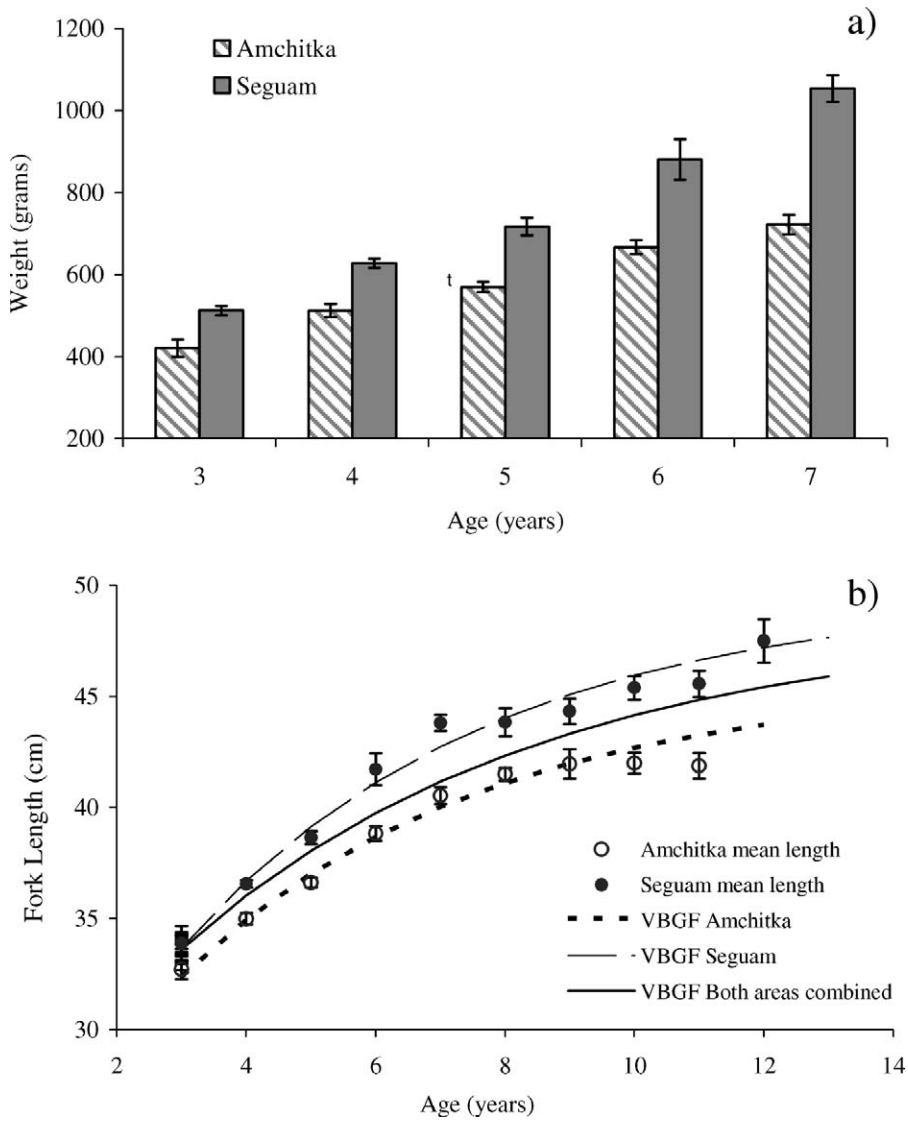


FIGURE 3.—**(a)** Mean weight at age of Atka mackerel at Amchitka Island and Seguam Pass and **(b)** observed mean lengths compared with those derived from von Bertalanffy growth curves (VBGFs). The error bars represent the 95% confidence intervals; data were not available for fish less than 3 years of age.

TABLE 4.—Parameter estimates and mean square errors (MSEs) for the von Bertalanffy growth models for Atka mackerel at Amchitka Island, Sequam Pass, and both sites combined.

Parameter	Amchitka Island	Seguam Pass	Both areas
L_∞ (cm TL)	45.66 (44.0–47.33)	49.59 (48.0–51.18)	48.38 (46.63–50.12)
K	0.21 (0.17–0.26)	0.21 (0.18–0.24)	0.18 (0.15–0.21)
t_0	−2.78 (−3.79 to −1.77))	−2.39 (−2.97 to −1.81))	−3.62 (−4.46 to −2.80))
MSE	3.15	4.14	4.78

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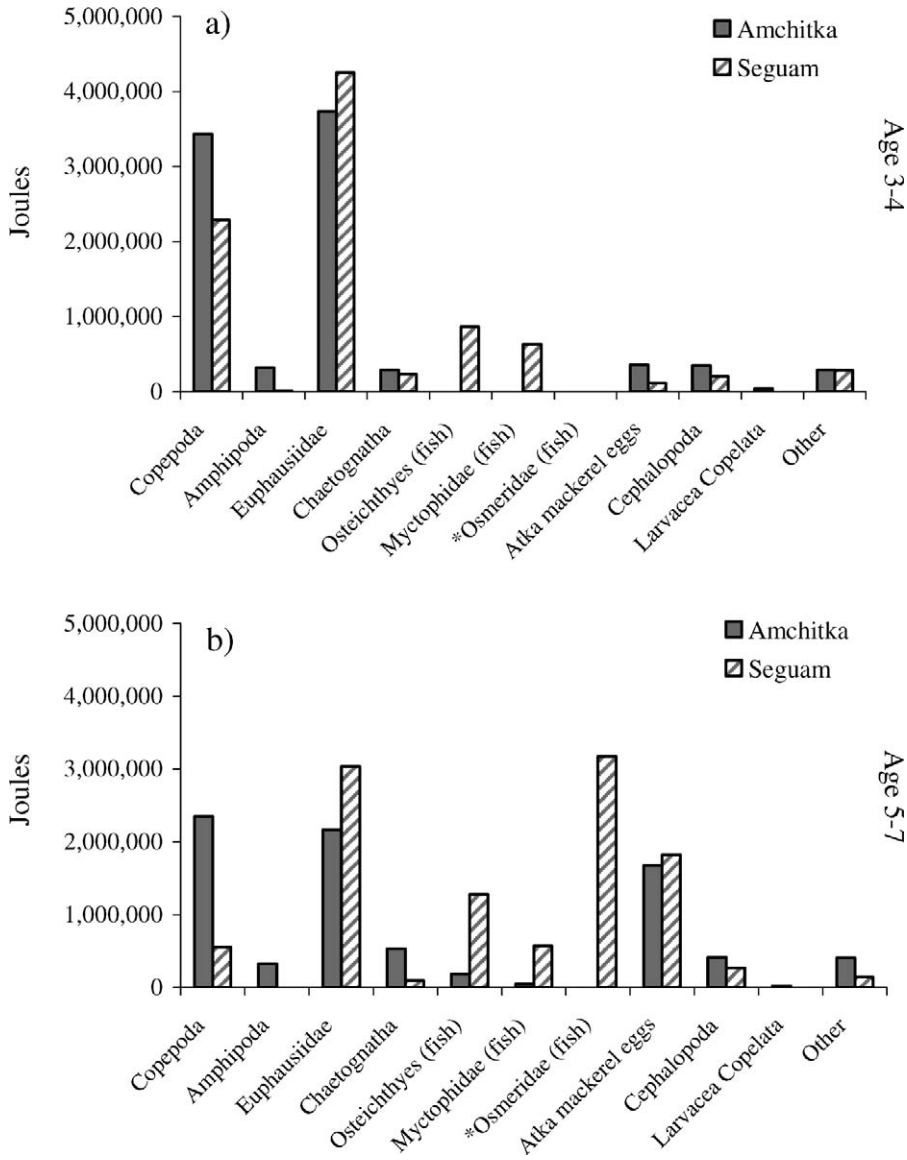


FIGURE 4.—Energy consumed (J) by **(a)** age-3–4 and **(b)** age-5–7 Atka mackerel during a 385-d simulation period based on stomach content analysis and prey energy densities (Table 2). The category Osmeridae includes northern smoothtongues as well as smelt species not further identified.

Diet simulation in that switching temperature did not have a large effect on Atka mackerel growth in these two study areas (Figure 5a–c).

Discussion

In this study, prey quality had a greater effect on predicted Atka mackerel growth than did temperature in all three of the time periods examined. The effects of diet composition on growth were also much higher for 5–7-year-old fish than for 3–4 year olds. This is probably due to the increase in fish consumption in the older age-group during the summertime months. Fish made up a large portion of the summertime diet of 5–7-year-old Atka mackerel at Seguam Pass, but only traces of fish were found in the diets of those near Amchitka Island. On average, the temperature differences between areas were on the order of 1°C. This difference is small, however, as increasing or decreasing the temperature by 1°C and even 2°C produced the same results.

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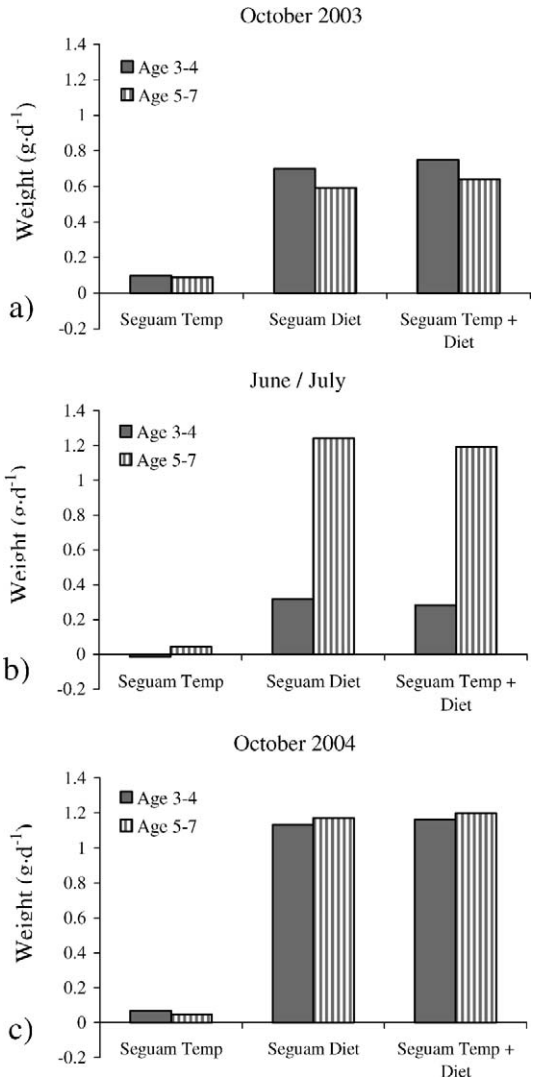


FIGURE 5.—Estimated amount of weight gained by an Atka mackerel in one simulation day in **(a)** October 2003, **(b)** June 2002–July 2003, and **(c)** October 2004. The zero value on the *y*-axis is the baseline growth for a hypothetical Amchitka Island fish initially weighing 500 g. The Seguam Temp simulation involved the substitution of the temperatures at Seguam Pass for those at Amchitka; similarly, the Seguam Diet simulation involved the substitution of the diet at Seguam Pass and the Seguam Temp + Diet simulation the substitution of both the temperatures and diet.

It is difficult to distinguish the effects of prey availability and prey quality on growth in this framework. In our simulations, we assumed that the same amount of prey was consumed in both study areas. Atka mackerel stomach fullness showed little difference between areas, suggesting that the amount of prey consumed (i.e., its availability) in each study area is not a major factor in the observed growth differences.

Few studies have drawn attention to diet composition as the primary driver of growth differences in a marine fish species over its habitat range. Latitudinal growth differences in marine fishes have been well documented (Present and Conover 1992; Yamahira and Conover 2002) and are often due to genetic or temperature clines or shorter growing seasons with increasing latitude (Conover et al. (1997). Longitudinal growth differences are less common, and the mechanisms influencing growth may include other factors (such as diet composition) if the primary habitats have a small temperature ranges and the population shows little if any genetic variation. The results of this analysis convey the importance of diet to fish growth, particularly the total energy content of prey. Similar results were documented by Mazur et al. (2007) in the western Gulf of Alaska, where the effects of prey quality on the growth of juvenile walleye pollock were greater than those of temperature.

Some studies have documented the longitudinal variability in the Aleutian Island ecosystem, including oceanographic conditions between and within Aleutian passes (Ladd et al. 2005; Stabeno et al. 2005), primary production (Mordy et al. 2005), zooplankton production (Coyle 2005), and the distribution of demersal ichthyofauna (Logerwell et al. 2005). A well-documented oceanographic transition takes place at Samalga Pass in the central Aleutian Islands (Figure 1). In the western Aleutians, Amchitka Pass is thought to be another important transition zone, in that oceanographic and biological processes west of the pass differ from those east of it (Logerwell et al. 2005). These transition zones not only differ in oceanographic processes and water transport (coastal or oceanic), they can also differ in the species composition, frequency of occurrence, and abundance of zooplankton (Coyle 2005).

Adapting an adult walleye pollock bioenergetics model to Atka mackerel to gauge the effects of temperature, prey quality, and prey availability on growth was unique. Model corroboration suggested that the walleye pollock bioenergetics model can be a reasonable surrogate. The model was useful in that it simulated seasonal patterns in the absence of observed interannual growth (no observations of growth were available between October 2003 and October 2004) and diet (there were no spring or winter diet data); essentially the model filled in the gaps where there were no field observations. In using the model to estimate the total yearly consumption of Atka mackerel, we were able to synonymously observe the effects that temperature and diet quality had on growth. The model has its limitations, however; it would not be

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appropriate to use it to estimate true Atka mackerel consumption. The thermal experience of Atka mackerel could be improved on by incorporating their diel migration using archival tag data (Nichol and Somerton 2002). To more accurately model Atka mackerel's thermal experience, one should quantify these migrations and incorporate the observed differences between age-groups and sexes (males guard nests in the summer and fall and do not make surface excursions). In addition, obtaining energy content measurements for the prey species found in Atka mackerel diets would greatly improve model estimates.

Understanding the life history and biology of Atka mackerel (such as their feeding, growth, and reproduction) establishes a foundation from which scientists and managers can examine ecosystem dynamics. Growth is especially important because it affects not only reproduction and ultimately spawning biomass but also the predator–prey relationships that are the foundation for ecosystem modeling. For example, the Atka mackerel at Seguam Pass are able to consume fish at an earlier age because of their larger size at age and therefore may impact prey fields differently over their lifespan than those at Amchitka. In addition, the smaller-bodied Atka mackerel at Amchitka may be more susceptible to predators over longer periods.

Relating growth to the environment (temperature) and prey interactions is an important component of ecosystem modeling. Understanding the effects of a dynamic and rapidly changing environment on Atka mackerel growth contributes to our knowledge of life history and essential fish habitat for a species that is integral to an ecosystem as both prey and predator.

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Appendix: Model Specifics

TABLE A.1.—Wisconsin Bioenergetics Model 3.0 used in simulations of Atka mackerel growth (Hanson et al. 1997).

Equation
Consumption
$C = C_{max} \cdot P \cdot f(T)$
$C_{max} = CA \cdot W_t^{CB}$
C = the specific consumption rate ($g \cdot g^{-1} \cdot d^{-1}$)
C_{max} = the maximum specific feeding rate ($g \cdot g^{-1} \cdot d^{-1}$)
P = the proportion of maximum consumption
$f(T)$ = the temperature dependence function (Kitchell et al. 1977; see below)
CA = the intercept of the allometric mass function
CB = the slope of the allometric mass function
$f(T) = V^X \cdot e^{[X \cdot (1-V)]}$
T = water temperature (°C)
$V = (CTM - T)/(CTM - CTO)$
$X = \{Z^2 \cdot [1 + (1 + 40/Y)^{0.5}]^2\}/400$
$Z = \log_e(CQ) \cdot (CTM - CTO)$
$Y = \log_e(CQ) \cdot (CTM - CTO + 2)$
CTM = the maximum water temperature (above which consumption ceases)
CTO = the laboratory temperature preferendum
CQ = the approximate rate at which the function increases at low temperatures
Respiration
$R = RA \cdot W_t^{RB} \cdot f(T) \cdot ACT$
$S = SDA \cdot (C - F)$
R = the specific respiration rate ($g\ O_2 \cdot g^{-1} \cdot d^{-1}$)
RA = the intercept of the allometric mass function
RB = the slope of the allometric mass function
ACT = the activity multiplier
S = the proportion of assimilated energy lost to specific dynamic action
F = the specific egestion rate ($g \cdot g^{-1} \cdot d^{-1}$)
$f(T) = V^X \cdot e^{[X \cdot (1-V)]}$
$V = (RTM - T)/(RTM - RTO)$
$X = \{Z^2\ [1 + (1 + 40/Y)^{0.5}]^2\}/400$
$Z = \log_e(RQ) \cdot (RTM - RTO)$
$Y = \log_e(RQ) \cdot (RTM - RTO + 2)$
RTM = the lethal water temperature
RTO = the temperature at highest respiration
RQ = the approximate rate at which the function increases at low temperatures
Waste
$F = FA \cdot C$
$U = UA(C - F)$
F = fecal waste
FA = intercept of the relationship between the proportion of consumed energy egested as fecal waste and water temperature and ration
U = nitrogenous waste
UA = the proportion of consumed energy egested as nitrogenous waste

TABLE A.2.—Parameter values used in the growth simulations. The derivation of the value for CA is discussed in the footnote; all other values are for walleye pollock and were determined by Mason and coworkers, as cited in Hanson et al. (1997).

Parameter	Value
C	
CA	2.65[a]
CB	−0.5875
CQ	3.5
CTO	8
CTM	15
R	
RA	0.0137
RB	−0.26
RQ	3.3
RTO	15
RTM	18
ACT	1
SDA	0.172
FA	0.2
UA	0.11

[a] The parameter C_{max} is defined as the maximum specific feeding rate ($g \cdot g^{-1} \cdot d^{-1}$) given the body mass and thermal experience of the consumer, that is (Table A.1),

$$C_{max} = CA \cdot W_t^{CB},$$

where CA is a scalar term that controls the relationship between predator mass and the maximum specific feeding rate, W_t is the observed average fish weight, and CB is the slope of the allometric mass function. The model estimates a feeding rate that is proportional to C_{max} based on the input data. Based on the maximum Atka mackerel consumption estimate and a W_t value derived from the observed average weight for Atka mackerel from the Sequam Pass study area, a value of 2.65 was used for CA in all models and simulations.

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