

Caloric Value of High-Seas Salmon Prey Organisms and Simulated Salmon Ocean Growth and Prey Consumption

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To investigate the relationship between salmon prey consumption and growth, this study used recent field data on salmon food habits and growth, experimental caloric determinations of salmon and salmon prey organisms, and a published bioenergetics model. Salmon and their prey were collected at sea, and caloric density determined by bomb calorimetry. Calorimetry results indicated that small medusae had low caloric density. Copepods, euphausiids, hyperiid amphipods, pteropods, and appendicularians had values in the middle range for caloric density, and squid and fish were calorically dense. Whole-body caloric values of high-seas caught immature sockeye salmon and maturing pink and coho salmon were higher than for immature chum salmon.

Bioenergetic models were used to estimate growth and daily ration for common age and maturity groups of sockeye, chum, pink, and coho salmon caught in the central North Pacific Ocean and Bering Sea in summer. Assuming a constant daily ration for 60 days in June and July and a temperature of 5-9°C, an immature ocean age .1 sockeye salmon (361-568 g) required a daily ration of 3.6-4.1% wet body weight (bw)/day, an immature ocean age .2 chum salmon (1042-1547 g) required 3.3-3.9% bw/day, and a maturing ocean age .1 pink salmon (912-1313 g) required 2.7-3.1% bw/day. A maturing ocean age .1 coho salmon (1909-2975 g) required 2.6-2.9% bw/day at 9-11°C. Model simulations indicate that salmon are feeding at a rate close to their physiological maximum. Therefore, any decrease in daily ration could cause significant decreases in growth over a time period as short as two months. We suggest that when prey is abundant, conditions favorable to salmon growth may be bounded at high temperatures by metabolic rates and at low temperatures by consumption rates.



INTRODUCTION

A climatic regime shift that occurred in 1976-77 may have led to favorable environmental conditions for northern salmon stocks and an increase in the abundance of sockeye (*Oncorhynchus nerka*), pink (*O. gorbuscha*), and chum (*O. keta*) salmon (Trenberth 1990; Beamish and Bouillon 1993; Miller et al. 1994; Hare and Francis 1995). In the last decade, researchers have documented a gradual decrease in size of Asian and North American stocks of chum and pink salmon (Kaeriyama 1989; Kaeriyama and Urawa 1992; Ishida et al. 1993; Helle and Hoffman 1995; Bigler et al. 1996).

Investigations of the relationship between the increase in salmon abundance and the decrease in body size throughout the North Pacific have led scientists to hypothesize that salmon may be showing evidence of density-dependent growth. The feeding efficiency of salmon in the ocean has a major effect on salmon production. For example, the biomass of returning sockeye salmon adults can be almost 25 times greater than the biomass of out-migrating smolts (Brett 1986).

Food habits of immature and maturing salmon in offshore waters have been investigated in the Gulf of Alaska (LeBrasseur 1966; Manzer 1968; Pearcy et al. 1988; Walker 1993; Myers et al. 1996), the

Bering Sea (Nishiyama 1970, 1977; Kanno and Hamai 1972; Davis et al. 1996), the North Pacific Ocean (Allen and Aron 1958; Andrievskaya 1957, 1966; Ito 1964; Takeuchi 1972; Sobolevskii and Senchenko 1996; Tadokoro et al. 1996), and the Okhotsk Sea (Gorbatenko and Chuchukalo 1989). Brodeur (1990) summarized marine food habits and feeding ecology of salmon by species and life-history type, and concluded that, despite differences in prey organisms, salmon may be non-selective feeders within a preferred prey size range. Studies have indicated that the prey composition of chum salmon can change in response to the abundance of pink salmon (Andrievskaya 1966, 1970; Shuntov et al. 1993; Tadokoro et al. 1996). Tadokoro et al. (1996) observed that when pink salmon abundance was low, chum salmon fed on a diet similar to the prey ingested by sockeye and pink salmon, but when pink salmon abundance was high, chum salmon increased the proportion of gelatinous zooplankton and reduced the proportion of crustacean prey in their diet.

Bioenergetic models are useful tools for extrapolating from stomach contents data to estimate prey consumption through time. Two researchers used bioenergetics to investigate the prey rations of adult salmon in offshore waters. Nishiyama (1970, 1977) examined the bioenergetics of maturing sockeye salmon in the Bering Sea as they migrate into Bristol Bay on their spawning run, and estimated that the daily ration required for a 2211-g female was 39 kcal/kg/day and for a 2546-g male was 54 kcal/kg/day. Brett (1983, 1986) developed a bioenergetics model of the life history of Babine Lake sockeye salmon, and estimated the average daily ration for maturing fish was 41.4 kcal/kg/day. He suggested the ocean growth of salmon was maximal and could exceed those observed under laboratory conditions (Brett 1983).

In this study, we use field observations on sea surface temperatures and salmon food habits in summer in the central North Pacific Ocean and Bering Sea, data on caloric density of salmon and salmon prey determined from bomb calorimetry, and a published fish bioenergetics model to simulate salmon growth and estimate prey consumption over a 60-day period. Growth estimates from the model were compared with summer monthly mean weights of high-seas caught salmon to evaluate daily ration. Gross conversion efficiency (growth/consumption), mean consumption rate (g prey/day), total consumption by prey category (g), and total energy consumed (kcal) were estimated at the end of the 60-day simulated period.

MATERIALS AND METHODS

Bomb Calorimetry

Common salmon prey, including medusae, copepods, hyperiid amphipods, euphausiids, pteropods, cephalopods, urochordates, and fish were collected from net tows and salmon stomachs during high-seas salmon research cruises in the central North Pacific Ocean, Bering Sea, and Gulf of Alaska in 1992-1995. Immature sockeye and chum, and immature and maturing pink and coho salmon were collected in the North Pacific and Gulf of Alaska. These samples were frozen at sea (approximately -20°C), then thawed and blotted to determine wet weights in the laboratory. When body size was small, i.e., amphipods, copepods, and euphausiids, prey organisms were whole-body samples of numerous individuals. When body size was large, i.e., squid and fish, prey were whole-body samples of single individuals. Wet weight sample sizes ranged from approximately 5 to 150 g. Salmon were ground and homogenized whole, from which subsamples of approximately 50 to 80 g wet weight were collected. Samples were freeze-dried in a Virtis freeze drier (Freeze Mobile 6, Gardiner, NY) for three to four days. The dried samples were ground to a powder. Approximately 1 g of powder was pressed into pellets (to increase the likelihood of complete burning of the sample) and used to determine the gross energy content. One sample per organism was burned at 30 atm of oxygen in a Parr oxygen bomb calorimeter (Model 1341, Moline, IL). Formation of acids following combustion under pressure in the calorimeter produces heat, but acid correction of the bomb washings was not included because of the small degree of error expected for marine animal species (<2%; Paine 1964, 1971).

The proportion of prey energy content that was indigestible by salmon was calculated based on proximate and moisture content from other studies of the same or closely related prey species. The gross energy content and the digestible energy content of each prey species were calculated. The gross energy values for protein (5640 cal/g on a dry weight basis[dwb]), lipid (8700 cal/g dwb), and carbohydrates (4111 cal/g dwb; Higgs et al. 1995) was multiplied by the proximate composition determined by other authors (McBride et al. 1959; Ikeda 1972; Nishiyama 1977; Higgs et al. 1995). To determine the digestible energy content, the energy digestible by salmon of protein (5091 cal/g dwb), lipid (8508 cal/g dwb) and carbohydrate (3800 cal/g dwb; Higgs et al. 1995) was multiplied by the proximate composition particular to each prey species. Dividing the digestible energy content by

the gross energy content gave the proportion of digestible energy available in each prey organism. The proportion of indigestible energy was calculated by subtracting the proportion of digestible energy from one.

Bioenergetics Modeling

Growth and prey consumption were calculated using the fish bioenergetics Model 2 (Hewett and Johnson 1992). Model 2 uses a balanced energy equation where energy consumed in the diet equals energy expended for metabolism, waste elimination, and fish growth. Factors that affect the energy budget are water temperature, fish size, predator and prey energy density, and prey availability. Model 2 input and output values are on a wet weight basis (wwb), computations are specific rates (per unit body weight), and fish weight and consumption are computed on a daily basis in the simulation. Consumption is estimated from an allometric weight function giving the maximum specific consumption rate, modified by a proportionality constant representing prey availability and a temperature function (Appendix 1). The temperature algorithm is the product of two curves: the first curve is the relationship whereby consumption increases with increasing temperature up to a cut-off temperature, and the second is the relationship whereby consumption decreases above the cut-off temperature. This consumption algorithm simulates cold-water fish at low temperatures (Thornton and Lessem 1978). Respiration is determined by calculating the standard (resting) metabolism from an allometric weight function and modifying it for the effect of temperature, an activity factor, and specific dynamic action (metabolic heat loss from digestion of food; Appendix 1). Egestion is a function of temperature and ration and includes a correction factor for the indigestible portion of each prey category. Excretion is a function of temperature, ration, and a proportion of consumption minus egestion (Appendix 1).

The physiological parameter values provided with Model 2 software included values for pink and sockeye salmon (identical values), and coho salmon (Appendix Table 1). Because there were no parameter values given for chum salmon, we used the same parameter values given for pink and sockeye salmon and made a modification to the CA parameter (intercept for weight dependence of maximum consumption). The CA parameter was increased from 0.303 to 0.394 (30%) because preliminary simulations indicated the consumption estimates were too low for chum salmon. This modification of the CA parameter was justified because the specific size of chum stomachs is larger

than other salmon, enabling them to have a higher consumption rate (Azuma 1995; Welch 1997).

Pacific salmon are not equally abundant in all areas of the Subarctic North Pacific Ocean (Pearcy 1992). Summertime gillnet and longline salmon catches in the central Bering Sea are dominated by sockeye, chum, and, in odd-years, pink salmon (Davis et al. 1996). We attempted to model growth and consumption for sockeye, chum, and pink salmon in conditions that closely resemble the central Bering Sea (52°-58°N, 180° and 177°E to 177°W) in summertime. Seawater temperatures frequently encountered in surface waters (0 to 30 m) in the Bering Sea range from 5° to 9°C. For coho salmon, we modeled summertime conditions in the central North Pacific Ocean (44°-47°N, 180°) because coho salmon are abundant in catches in this area (Davis et al. 1996). Seawater temperatures in the surface waters (0 to 40 m) of the central North Pacific frequently range from 7° to 11°C. Details of how salmon move within these regions and change their thermal habitat on a monthly basis have not yet been determined. Therefore, temperature was held constant for each 60-day simulation and separate simulations were run for each 1°C interval across the range of temperatures (Table 1).

To determine the salmon prey composition for use in the bioenergetics model, salmon stomach contents from salmon caught in the central North Pacific Ocean and Bering Sea were used (Davis et al. 1996). Sockeye and pink salmon in the central Bering Sea have similar prey organisms found in their stomach contents including euphausiids, copepods, amphipods, squid, pteropods, and fish. The difference between sockeye and pink salmon stomach contents is that sockeye salmon contain more copepods and hyperiid amphipods while pink salmon contain more squid and fish (Davis et al. 1996). Chum salmon caught in the Bering Sea commonly feed on many of the same prey as sockeye and pink salmon, including euphausiids, amphipods, pteropods, and fish, but chum salmon have a broader assortment of prey organisms found in their stomachs because they also feed on medusae and appendicularians (Davis et al. 1996; Tadokoro et al. 1996). Coho salmon in the central North Pacific Ocean feed primarily on squid and secondarily on hyperiid amphipods (Davis et al. 1996). The prey composition used for the bioenergetics model was the mean percent composition of the common prey categories observed from 1991 to 1996 for sockeye, chum, and pink salmon caught in the Bering Sea, and coho salmon caught in the central North Pacific Ocean normalized to equal 100% (Table 1; Davis et al. 1996).

The caloric value for medusae used in the

Table 1. Environmental temperatures, salmon, and prey characteristics used as input values to simulate conditions in the central North Pacific Ocean and the Bering Sea. Grams are expressed on a wet weight basis. Prey caloric density is the gross energy content, and the mean prey caloric density is weighted by the prey composition.

Salmon Predator	Predator Caloric Density (cal/g)	Region	Temperature Range (°C)	Prey Category	Prey Composition	Prey Caloric Density (cal/g)	Proportion Indigestible
Sockeye	1633-1665*	Bering Sea	5° to 9°	Euphausiids	0.14	743	0.1035
				Copepods	0.13	627	0.0904
				Amphipods	0.24	589	0.1299
				Squid	0.25	732	0.0891
				Pteropods	0.08	624	0.0907
				Fish	0.16	1185	0.0898
				mean		749	
Chum	1376	Bering Sea	5° to 9°	Euphausiids	0.26	743	0.1035
				Amphipods	0.12	589	0.1299
				Pteropods	0.11	624	0.0907
				Fish	0.12	1185	0.0898
				Medusae	0.27	169	0.1125
				Appendicularians	0.12	759	0.0926
mean		611					
Pink	1702-1752*	Bering Sea	5° to 9°	Euphausiids	0.15	743	0.1035
				Copepods	0.08	627	0.0904
				Amphipods	0.09	589	0.1299
				Squid	0.30	732	0.0891
				Pteropods	0.04	624	0.0907
				Fish	0.34	1185	0.0898
				mean		862	
Coho	2083	Central North Pacific	7° to 11°	Squid	0.83	1550	0.0775
				Amphipods	0.17	589	0.1299
				mean		1387	

* predator energy density is a linear function of body weight.

bioenergetics model was the average of the values determined in our study and the caloric value for *Aglantha digitale* collected in the Bering Sea by Ikeda (1972; Table 2). The squid (unidentified spp.) eaten by pink and sockeye salmon in the Bering Sea were not well represented by the squid collected in our study of caloric value, because our squid samples were collected from stomachs of coho salmon caught south of the Aleutian Islands. Therefore, we used the published caloric value for squid eaten by sockeye salmon caught in Bristol Bay (Table 2; Nishiyama 1977). The caloric value used for the squid prey category of coho salmon was based on that of *Berryteuthis* spp. determined by calorimetry in this study. The caloric values for copepods, euphausiids, hyperiid amphipods, pteropods, and appendicularians used in the model were determined in our study (Table 1). The fish prey category used for simulations of the sockeye, chum, and pink salmon was the mean value for juvenile *Hemilepidotus* spp. and Atka mackerel (*Pleurogrammus monopterygius*), both commonly

found in salmon stomachs in the Bering Sea. The predator energy density for pink and sockeye salmon was defined to be a function of weight (following Hewitt and Johnson 1992), and values of 1375 cal/g ww and 2083 cal/g ww were used for chum and coho salmon (Table 1).

The life history stages we selected for the simulations represent common ages and maturity stages of salmon caught in the Bering Sea and central North Pacific Ocean during recent summertime cruises of the *Wakatake maru* (Davis et al. 1996). Bering Sea salmon catches were primarily composed of sockeye, chum, and pink salmon, and immature ocean age .1 sockeye and ocean age .2 chum salmon were selected because these life history groups were common. All pink and coho salmon caught by the *Wakatake maru* are maturing ocean age .1s, the life-history stage for our simulations. Individual salmon weights used in the simulations were the mean weights for June through July (60 days) for immature ocean age .1 sockeye (growing from 361 to 568 g), immature

Table 2. Gross caloric density (cal/g wet weight) for high-seas salmon prey organisms, and the estimated proportion of prey that is indigestible for salmon.

Organism or Group	cal/g Wet Weight	Proportion Indigestible	Reference
Cnidaria			
<i>Aglantha digitale</i>	202	0.1125	Ikeda 1972
Copepoda			
<i>Neocalanus cristatus</i>	717	0.0886	Nishiyama 1977
<i>N. cristatus</i>	910	0.1094	Ikeda 1972
Copepods	1104	0.0731	Higgs et al. 1995
Euphausiacea			
<i>Thysanoessa raschii</i>	928	0.1103	Ikeda 1972
<i>Thysanoessa</i> spp.	1117	0.0966	Nishiyama 1977
<i>Euphausia pacifica</i>	1107	0.1018	Nishiyama 1977
Euphausiacea	1130	0.1053	Higgs et al. 1995
Amphipoda			
<i>Parathemisto pacifica</i>	665	0.1151	Nishiyama 1977
<i>P. libellula</i>	716	0.1204	Nishiyama 1977
<i>P. libellula</i>	975	0.1541	Ikeda 1972
Gastropoda			
<i>Limacina helicina</i>	636	0.0850	Nishiyama 1977
<i>Clione limacina</i>	563	0.0744	Nishiyama 1977
<i>C. limacina</i>	520	0.1127	Ikeda 1972
Cephalopoda			
Squid	732	0.0891	Nishiyama 1977
Squid	1134	0.0659	Higgs et al. 1995
Teleostei			
<i>Clupea harengus pallasi</i>	2341	0.0774	McBride et al. 1959
<i>Mallotus villosus</i>	1179	0.0945	Higgs et al. 1995
<i>Tarletonbeania</i>	1060	0.1029	Nishiyama 1977
<i>crenularis</i>	1633	0.0844	Higgs et al. 1995
Unidentified Fish			

ocean age .2 chum (growing from 1042 to 1547 g), and maturing pink (growing from 912 to 1313 g) and coho salmon (growing from 1909 to 2975 g) calculated from data collected aboard Japanese research vessels operating in the North Pacific and Bering Sea (1972-1995). These weights are an approximation of what the specific age and maturity groups might gain over the summer. The true initial weight and growth of an individual salmon from the Bering Sea and central North Pacific Ocean might be different from these values because the mean values are pooled over a large geographical area and from different salmon stocks. It is possible that an individual salmon feeding and residing in different oceanographic habitats would have significantly different growth rates than the

average values used in these simulations.

Daily ration levels used in the simulations included daily maintenance (daily ration resulting in zero growth), daily percent of body weight (1%, 2%, 3%, 4% of wet body weight [bw]), and the physiological maximum ration. The physiological maximum is calculated daily and is expressed as a percentage of body weight, decreasing as the fish grows. Over the 60-day period, net production (g), gross conversion efficiency (%; cumulative growth [g]/cumulative consumption [g]), and average consumption rate (total prey consumed g/60 days) were calculated. Prey consumption was summarized by total weight (g) of each prey category consumed and the total energy consumed (kcal) over the 60-day period.

RESULTS

Caloric Determinations

Calorimetric determinations of salmon prey organisms indicated that small medusae had a low energy content and a high water content (136 cal/g ww; 94% water; Table 3). Copepods (627 cal/g ww), euphausiids (743 cal/g ww), hyperiid amphipods (589 cal/g ww), pteropods (624 cal/g ww), and appendicularians (759 cal/g ww) had

values in the middle range for caloric density (Table 3). Squid and fish were calorically dense prey groups, in the range of 896-2041 cal/g ww (Table 3). The caloric value of *Beryteuthis* spp. squid increased with size from 978 (28 to 38 mm mantle length) to 1550 cal/g ww (66-100 mm mantle length; Table 3). Small threespine sticklebacks (*Gasterosteus aculeatus*, <45 mm standard length [sl]), capelin (*Mallotus villosus*), Atka mackerel, blue lanternfish (*Tarletonbeania crenularis*, 65-75 mm sl), and walleye pollock (*Theragra chalcogramma*)

Table 3. Gross energy values of salmon and common prey organisms determined by bomb calorimetry. Caloric values for each prey category are determined from a single 1-g sample combustion. Size (mm): mxl=maximum length, shl=shell length, ml=mantle length, sl=standard length, fl=fork length, bw=body weight (g). Sex: F=female, M=male, imm=immature, mat=mature, gw=gonad weight. Sample area: GOA=Gulf of Alaska, NPO=North Pacific Ocean, BS=Bering Sea, Aleut=Aleutian Islands.

Organism or Group	cal/g Wet Weight	cal/g Dry Weight	% Water	Size, Sex, or Maturity	Month	Sample Area
Cnidaria small medusae	136	2231	93.9	whole; mxl=10-13	June-July	NPO and BS
Copepoda <i>Neocalanus cristatus</i>	627	5504	88.6	whole; mxl=7-8	June-July	NPO and BS
Euphausiacea <i>Thysanoessa</i> spp.	743	4675	84.1	whole; mxl=11-26	June-July	NPO and BS
Amphipoda Hyperiid amphipods	589	3952	85.1	whole; mxl=3-6	July	BS
Gastropoda <i>Limacina</i> spp.	624	3547	82.4	whole; shl=3	June-July	NPO, BS, GOA
Cephalopoda <i>Beryteuthis</i> spp.	978	5147	81.0	whole; ml=28-38	June-July	NPO and BS
<i>Beryteuthis</i> spp.	1550	5983	74.1	whole; ml=66-100	June-July	NPO and GOA
<i>Gonatopsis borealis</i>	1125	5259	78.6	whole; ml=42-59	June-July	NPO and BS
<i>G. borealis</i>	1155	5224	77.9	whole; ml=62	Nov-Dec	NPO
<i>Gonatus</i> spp.	1877	6680	71.9	whole; ml=57-71	June-July	BS
<i>Onychoteuthis borealijaponica</i>	1201	5046	76.2	whole; ml=45-61	June, Nov, Dec	NPO
Urochordata Appendicularians	759	4414	82.8	whole	June	NPO
Teleostei (non-salmonids) Bathymasteridae <i>Clupea harengus pallasii</i>	1153	4487	74.3	whole; sl=42-48	July	BS
<i>Cololabis saira</i>	1914	5907	67.6	whole; sl=97-104	October	GOA
<i>Gasterosteus aculeatus</i>	1536	5224	70.6	whole; sl=177	October	GOA
<i>G. aculeatus</i>	1166	4049	71.2	whole; sl=32-44	October	GOA
<i>Hemilepidotus</i> sp.	1533	4367	64.9	whole; sl=56-62	October	GOA
<i>Mallotus villosus</i>	1184	4520	73.8	whole; sl=18-31	July	Aleut Is and BS
<i>Pleurogrammus monopterygius</i>	1277	5277	75.8	whole; sl=63-71	October	GOA
<i>Stenobrachius leucopsarus</i>	1186	4841	75.5	whole; sl=42-70	June-July	NPO, BS, GOA
<i>Tarletonbeania crenularis</i>	2041	6398	68.1	whole; sl=32-90	June-July	NPO and BS
<i>T. crenularis</i>	896	4435	79.8	whole; sl=24-50	June	NPO
<i>Theragra chalcogramma</i>	1283	4771	73.1	whole; sl=65-75	June	NPO
	1101	4554	77.8	whole; sl=75-95	October	GOA
Teleostei (salmonids) <i>Oncorhynchus nerka</i>	1342	5326	74.8	fl=413; bw=693; F; imm; gw=5	Nov-Dec	NPO
<i>O. nerka</i>	1920	5926	67.6	fl=426; bw=854; M; imm; gw=1	Nov-Dec	NPO
<i>O. nerka</i>	2331	6420	63.7	fl=500; bw=1366; F; imm; gw=6	Nov-Dec	NPO
<i>O. keta</i>	1212	5203	76.7	fl=217; bw=112; F; imm; gw=1	January	NPO
<i>O. keta</i>	1188	5186	77.1	fl=355; bw=362; F; imm; gw=2	Nov-Dec	NPO
<i>O. keta</i>	1854	6100	69.6	fl=420; bw=701; F; imm; gw=3	Nov-Dec	NPO
<i>O. keta</i>	1249	5205	76.0	fl=513; bw=1215; M; imm; gw=1	Nov-Dec	NPO
<i>O. gorbuscha</i>	1300	5307	75.5	fl=242; bw=137; F; imm; gw=2	January	NPO
<i>O. gorbuscha</i>	1796	5986	70.0	fl=473; bw=1122; M; mat; gw=4	July	GOA
<i>O. gorbuscha</i>	1785	5833	69.4	fl=532; bw=1838; F; mat; gw=144	July	GOA
<i>O. kisutch</i>	2083	5917	64.8	fl=548; bw=2656; M; mat; gw=85	July	GOA
<i>O. kisutch</i>	1287	5046	74.5	fl=630; bw=2134; M; mat; gw=13	July	GOA

juveniles ranged from 1000 to 1300 cal/g ww. Larger sticklebacks (> 50mm sl) and Pacific saury (*Cololabis saira*) were approximately 1530 cal/g ww, and herring (*Clupea harengus pallasii*) and northern lampfish (*Stenobrachius leucopsarus*) were the most calorically dense fish prey category (> 1900 cal/g ww; Table 3).

The mean whole body caloric value for immature chum salmon was generally lower than for the other salmon species examined (mean=1375 cal/g ww; Table 3). Caloric density was higher for immature sockeye and maturing pink salmon (mean=1864 and 1790; Table 3). The two estimates for coho salmon were widely separated, from 1287 to 2083 cal/g ww (Table 3). The wide disparity between these values

for coho salmon could have occurred because the higher caloric value came from a mature fish with a significantly higher gonad weight, and, therefore may have contained a higher lipid content, or as the result of using a non-representative subsample of the whole body for bomb calorimetry.

Bioenergetics Modeling

Sockeye salmon

The estimated maintenance ration for an immature ocean age .1 sockeye in the Bering Sea in June and July ranged from 0.8 to 1.3% bw/day at 5-9°C (Table 4). The maintenance ration increased

Table 4. Estimated sockeye salmon growth and prey consumption over a range of temperatures and daily rations resulting from a 60-day simulation. Model input values represent conditions for an ocean age .1 immature sockeye salmon in the Bering Sea in June and July and an initial weight of 361 g. Maint=daily maintenance ration, max=daily physiological maximum consumption. Grams are wet weights. Temp=water temperature, Gross Conversion Efficiency (%)=total growth (g)/total weight of prey consumed (g) after 60 days. Prey consumption rate=total prey consumed (g)/ 60 days. Wt=weight (g), BW=body weight, EU=euphausiids, CO=copepods, AM=hyperiid amphipods, SQ=squid, PT=pteropods, FI=fish.

Sockeye Salmon

Temp (°C)	Daily Ration (% BW/day)	Final Wt (g)	Net Production (g)	Gross Conversion Efficiency	Consumption Rate (g/day)	Total Prey Consumption (g)							Total kcal
						EU	CO	AM	SQ	PT	FI	Total	
5	maint (0.8%)	361	0	0.0	3.0	25	23	43	44	14	28	177	133
	1.0% BW	372	11	5.0	3.7	31	29	53	55	18	35	221	165
	2.0% BW	439	78	16.4	8.0	67	62	115	119	38	76	477	358
	3.0% BW	518	157	20.1	13.0	109	101	187	195	62	125	779	585
	3.57% BW	568	207 *	21.2	16.2	136	127	234	244	78	156	975	731
	max (3.6-4.1%)	589	228	21.5	17.7	148	138	254	265	85	170	1060	794
6	maint (0.9%)	361	0	0.0	3.3	28	26	48	50	16	32	200	149
	1.0% BW	366	5	2.2	3.6	31	28	52	55	17	35	218	163
	2.0% BW	432	71	15.0	7.9	66	62	114	118	38	76	474	355
	3.0% BW	509	148	19.1	12.9	108	101	186	193	62	124	774	580
	3.68% BW	568	207 *	20.6	16.8	141	131	241	251	80	161	1005	753
	max (3.8-4.3%)	602	241	21.1	19.0	159	148	273	285	91	182	1138	853
7	maint (1.0%)	361	0	0.0	3.7	31	29	54	56	18	36	224	167
	2.0% BW	424	63	13.4	7.8	66	61	113	117	38	75	470	352
	3.0% BW	499	138	18.1	12.8	107	100	184	191	61	122	765	574
	3.8% BW	568	207 *	20.0	17.3	145	135	249	260	83	166	1038	778
	4.0% BW	587	226	20.3	18.5	156	145	267	278	89	178	1113	833
	max (4.0-4.6%)	611	250	20.7	20.2	169	157	290	302	97	193	1208	906
8	maint (1.2%)	361	0	0.0	4.2	35	33	60	63	20	40	251	189
	2.0% BW	415	54	11.6	7.7	65	60	111	116	37	74	463	348
	3.0% BW	488	127	16.8	12.6	106	98	182	189	61	121	757	567
	3.94% BW	568	207 *	19.3	17.9	151	140	258	269	86	172	1076	807
	4.0% BW	574	213	19.4	18.3	154	143	264	275	88	176	1100	823
	max (4.1-4.8%)	616	255	20.1	21.2	178	165	305	318	102	203	1271	953
9	maint (1.3%)	361	0	0.0	4.7	40	37	68	71	23	45	284	213
	2.0% BW	405	44	9.5	7.6	64	60	110	115	37	73	459	344
	3.0% BW	476	115	15.4	12.5	105	97	179	187	60	120	748	560
	4.0% BW	560	199	18.3	18.1	152	141	260	271	87	173	1084	812
	4.09% BW	567	206 *	18.5	18.6	156	145	268	279	89	179	1116	837
	max (4.3-5.0%)	618	257	19.4	22.1	185	172	318	331	106	212	1324	992

* net production estimated for June through July from Japanese research vessel data.

with temperature as the energetic costs of metabolism increased. Likewise, the physiological maximum ration increased from 3.6 to 5.0% bw/day over the 5-9°C temperature range considered. Net production at each ration level decreased as the temperature increased. For example, at a constant ration of 2% bw/day, the net production decreased by 43% between 5-9°C (Table 4). Gross conversion efficiency was highest at the maximum ration and the lowest temperature (21.5%, 5°C; Table 4). An ocean age .1 sockeye growing from 361 to 568 g would therefore consume an average of 16-19 g of prey/day, the equivalent of 3.57 to 4.09% bw/day (27-31 cal/g-predator/day), depending on temperature. To achieve this net production (207 g), the sockeye would have

to feed at 88 to 93% of its physiological maximum rate. Over two months, the total prey consumption was estimated as 0.975-1.116 kg, the equivalent of 731-837 kcal (Table 4).

Chum salmon

The estimated maintenance ration for an immature ocean age .2 chum salmon in the Bering Sea ranged from 0.9 to 1.4% bw/day and the maximum ration ranged from 3.5 to 4.8% bw/day at 5-9°C (Table 5). At a daily ration of 2% bw/day, net production decreased by 52% from 5° to 9°C. To grow from 1042 to 1547 g, a mean ration of 3.28-3.86% bw/day (20-24 cal/g-predator/day) was

Table 5. Estimated chum salmon growth and prey consumption over a range of temperatures and daily rations resulting from a 60-day simulation. Model input values represent conditions for an ocean age .2 immature chum salmon in the Bering Sea in June and July and an initial weight of 1042 g. Maint=daily maintenance ration, max=daily physiological maximum consumption. Grams are wet weights. Temp=water temperature, Gross Conversion Efficiency (%)=total growth (g)/total weight of prey consumed (g) after 60 days. Prey consumption rate=total prey consumed (g)/ 60 days. Wt=weight (g), BW=body weight, EU=euphausiids, AM=hyperiid amphipods, PT=pteropods, FI=fish, GE=medusae, AP=appendicularians.

Temp (°C)	Daily Ration (% BW/day)	Final Wt (g)	Net Pro- duction (g)	Gross Con- version Effi- ciency	Cons- ump- tion Rate (g/day)	Total Prey Consumption (g)							Total kcal
						EU	AM	PT	FI	GE	AP	Total	
5	maint (0.9%)	1042	0	0.0	9.2	144	66	61	66	149	66	552	338
	1% BW	1061	19	3.0	10.5	164	76	69	76	170	76	631	386
	2% BW	1252	210	15.3	22.8	356	164	151	164	370	164	1369	838
	3% BW	1477	435	19.4	37.3	581	268	246	268	604	268	2235	1367
	3.28% BW	1546	504 *	20.1	41.7	651	301	276	301	676	301	2506	1531
	max (3.5-3.9%)	1659	617	21.0	49.0	764	353	323	353	794	353	2940	1798
6	maint (1%)	1042	0	0.0	10.4	162	75	68	75	168	75	623	381
	2% BW	1229	187	13.8	22.6	353	163	149	163	366	162	1356	830
	3% BW	1449	407	18.4	36.9	576	266	244	266	598	266	2216	1354
	3.4% BW	1548	506 *	19.5	43.3	675	312	286	312	701	312	2598	1588
	max (3.7-4.2%)	1690	648	20.5	52.6	820	379	347	379	852	379	3156	1929
7	maint (1.1%)	1042	0	0.0	11.7	183	84	77	84	190	84	702	430
	2% BW	1203	161	12.0	22.4	349	161	148	161	363	161	1343	821
	3% BW	1418	376	17.2	36.5	569	263	241	263	591	263	2190	1339
	3.53% BW	1547	505 *	18.7	44.9	701	324	297	324	728	324	2698	1648
	max (3.9-4.4%)	1712	670	20.0	55.8	871	402	368	402	904	402	3349	2047
8	maint (1.3%)	1042	0	0.0	13.2	207	95	87	95	215	95	794	486
	2% BW	1174	132	10.0	22.1	345	159	146	159	358	159	1326	811
	3% BW	1383	341	15.8	36.0	562	259	238	259	584	259	2161	1322
	3.68% BW	1546	504 *	17.9	46.8	731	337	309	337	759	337	2810	1718
	4.0% BW	1629	587	18.7	52.3	816	377	345	377	848	377	3140	1919
	max (4.1-4.7%)	1722	680	19.4	58.6	914	422	387	422	949	422	3516	2149
9	maint (1.4%)	1042	0	0.0	15.0	234	108	99	108	243	108	900	551
	2% BW	1142	100	7.7	21.8	340	157	144	157	353	157	1308	800
	3% BW	1345	303	14.2	35.5	554	256	234	256	575	256	2131	1303
	3.86% BW	1547	505 *	17.1	49.1	767	354	324	354	796	354	2949	1803
	4.0% BW	1583	541	17.5	51.5	804	371	340	371	835	371	3092	1890
	max (4.2-4.8%)	1721	679	18.6	60.9	810	374	343	374	842	374	3117	1906

* net production estimated for June through July from Japanese research vessel data.

required, which was a daily consumption rate of 42 to 49 g-prey/day, or 85 to 89% of its physiological maximum consumption rate per day, depending on temperature. Estimated chum salmon cumulative consumption was 2.506-2.949 kg or 1531-1803 kcal (Table 5).

Pink salmon

The estimated maintenance ration for a maturing ocean age .1 pink salmon in the Bering Sea ranged from 0.6 to 1.0% bw/day, and the physiological

maximum ration ranged from 2.8 to 3.9% bw/day at 5-9°C (Table 6). At a daily ration of 2% bw/day, net production decreased by 31% from 5° to 9°C. If a maturing pink salmon grew from 912 to 1313 g, the required ration was estimated as 2.73-3.14% bw/day (24-27 cal/g-predator/day) and a daily prey consumption of 30-35 g/day, or 86 to 94% of its physiological maximum consumption rate per day, depending on temperature. Over 60 days, 1,800-2,068 kg of prey, or 1552-1783 kcal were estimated to be consumed (Table 6).

Table 6. Estimated pink salmon growth and prey consumption over a range of temperatures and daily rations resulting from a 60-day simulation. Model input values represent conditions for an ocean age .1 maturing pink salmon in the Bering Sea in June and July and an initial weight of 912 g. Maint=daily maintenance ration, max=daily physiological maximum consumption. Grams are wet weights. Temp=water temperature, Gross Conversion Efficiency (%)=total growth (g)/total weight of prey consumed (g) after 60 days. Prey consumption rate=total prey consumed (g)/ 60 days. Wt=weight (g), BW=body weight, EU=euphausiids, CO=copepods, AM=hyperiid amphipods, SQ=squid, PT=pteropods, FI=fish.

Pink Salmon

Temp (°C)	Daily Ration (% BW/day)	Final Wt (g)	Net Production (g)	Gross Conversion Efficiency	Consumption Rate (g/day)	Total Prey Consumption (g)							Total kcal
						EU	CO	AM	SQ	PT	FI	Total	
5	maint (0.6%)	912	0	0.0	5.7	52	28	31	103	14	117	345	296
	1.0% BW	974	62	10.9	9.4	85	45	51	170	23	192	566	487
	2.0% BW	1160	248	20.1	20.6	185	99	111	371	49	420	1235	1065
	2.73% BW	1314	402 *	22.3	30.0	270	144	162	540	72	612	1800	1552
	max (2.8-3.0%)	1363	451	22.7	33.1	298	159	179	595	79	674	1984	1710
6	maint (0.7%)	912	0	0.0	6.5	58	31	35	116	15	132	387	334
	1.0% BW	960	48	8.6	9.4	84	45	51	168	22	191	561	484
	2.0% BW	1144	232	18.9	20.4	184	98	110	368	49	417	1226	1057
	2.81% BW	1313	401 *	21.7	30.9	278	148	167	556	74	630	1853	1597
	3.0% BW	1356	444	22.1	33.5	302	161	181	603	80	684	2011	1734
max (3.0-3.4%)	1394	482	22.3	33.9	323	172	194	647	86	733	2155	1858	
7	maint (0.8%)	912	0	0.0	7.3	66	35	39	131	17	149	437	377
	1.0% BW	945	33	5.9	9.3	84	45	50	167	22	189	557	480
	2.0% BW	1125	213	17.6	20.3	182	97	109	365	49	413	1215	1048
	2.91% BW	1314	402 *	21.0	32.0	288	153	173	576	77	652	1919	1654
	3.0% BW	1334	422	21.2	33.2	299	159	179	598	80	678	1993	1719
max (3.1-3.5%)	1410	498	21.8	38.1	343	183	206	686	91	777	2286	1971	
8	maint (0.9%)	912	0	0.0	8.2	74	40	44	148	20	168	494	426
	1.0% BW	928	16	2.8	9.2	83	44	50	166	22	188	553	476
	2.0% BW	1105	193	16.0	20.1	181	96	108	361	48	410	1204	1039
	3.0% BW	1310	398	20.1	32.9	296	158	178	592	79	671	1974	1702
	3.02% BW	1314	402 *	20.2	33.2	299	159	179	597	80	677	1991	1716
max (3.3-3.7%)	1420	508	21.2	40.0	360	192	216	720	96	816	2401	2070	
9	maint (1.0%)	912	0	0.0	9.3	84	45	50	168	22	190	559	482
	2.0% BW	1082	170	14.3	19.9	179	95	107	358	48	405	1192	1027
	3.0% BW	1282	370	19.0	32.5	293	156	176	586	78	664	1953	1683
	3.14% BW	1313	401 *	19.4	34.5	310	165	186	621	83	703	2068	1783
	max (3.4-3.9%)	1423	511	20.4	41.6	375	200	225	750	100	850	2500	2154

* net production estimated for June through July from Japanese research vessel data.

Coho salmon

The estimated maintenance ration for a maturing ocean age .1 coho salmon in the central North Pacific Ocean ranged between 0.7 and 1.1% bw/day, and the physiological maximum consumption ranged from 2.0 to 3.4% bw/day at 7-11°C (Table 7). At a daily ration of 2% bw/day, net production decreased by 33% from 7° to 11°C. A maturing coho salmon growing from 1909 to 2975 g would consume 2.64-2.86% bw/day (37-40 cal/g-predator/day) and a daily prey consumption of 63-68 g-prey/day at 9° to 11°C, or 91 to 96% of its physiological maximum consumption rate. Over two months, 3.785-4.105 kg of prey, or 5248-5693 kcal of energy would be consumed (Table 7).

DISCUSSION

The specific energy requirements for the smaller (361-568 g) immature sockeye salmon found in this study were lower (27-31 cal/g-predator/day) than the ration required for large (2211 and 2546 g) maturing sockeye returning to Bristol Bay reported by Nishiyama (1970; 39 cal/g-predator/day for females; 54 cal/g-predator/day for males). This is reasonable because of the large difference in weight, maturity, and age of the sockeye salmon investigated. The specific consumption increases and the ration as a percentage of body weight gradually decreases as the fish grow. Sockeye salmon gross conversion efficiency in this study was estimated at 18.5-21.2%, slightly less than the lifetime conversion efficiency

Table 7. Estimated coho salmon growth and prey consumption over a range of temperatures and daily rations resulting from a 60-day simulation. Model input values represent conditions for an ocean age .1 maturing coho salmon in the central North Pacific Ocean in June and July and an initial weight of 1909 g. Maint=daily maintenance ration, max=daily physiological maximum consumption. Grams are wet weights. Temp=water temperature, Gross Conversion Efficiency (%)=total growth (g)/total weight of prey consumed (g) after 60 days. Prey consumption rate=total prey consumed (g)/ 60 days. Wt=weight (g), BW=body weight, SQ=squid, AM=hyperiid amphipods.

Coho Salmon									
Temp (°C)	Daily Ration (%BW/day)	Final Wt (g)	Net Production (g)	Gross Conversion Efficiency	Consumption Rate (g/day)	Total Prey Consumption (g)			Total kcal
						SQ	AM	Total	
7	maint (0.7%)	1909	0	0.0	13.2	657	135	792	1098
	1.0% BW	2064	155	13.0	19.8	988	202	1190	1650
	2.0% BW	2652	743	27.5	45.1	2244	460	2704	3749
	max (2.0-2.2%)	2715	806	28.1	47.8	2381	488	2869	3977
8	maint (0.8%)	1909	0	0.0	14.6	728	149	877	1217
	1.0% BW	2024	115	9.7	19.6	978	200	1178	1635
	2.0% BW	2599	690	25.8	44.6	2221	455	2676	3710
	max (2.3-2.6%)	2905	996	28.7	57.9	2881	590	3471	4813
9	maint (0.9%)	1909	0	0.0	16.3	810	166	976	1354
	1.0% BW	1980	71	6.1	19.4	968	198	1166	1617
	2.0% BW	2541	632	23.9	44.1	2195	450	2645	3667
	2.64%BW	2976	1067 *	28.2	63.1	3142	643	3785	5248
	max (2.6-2.9%)	3055	1146	28.7	66.6	3319	680	3999	5545
10	maint (1.0%)	1909	0	0.0	18.2	904	185	1089	1511
	1.0% BW	1932	23	2.0	19.2	956	196	1152	1598
	2.0% BW	2477	568	21.8	43.5	2166	444	2610	3619
	2.74% BW	2975	1066 *	27.1	65.5	3264	669	3933	5453
	max (2.8-3.0%)	3126	1217	28.1	72.3	3599	737	4336	6013
11	maint (1.1%)	1909	0	0.0	20.3	1011	207	1218	1689
	2.0% BW	2407	498	19.4	42.9	2135	437	2572	3567
	2.86% BW	2976	1067 *	26.0	68.4	3407	698	4105	5693
	3.0% BW	3080	1171	26.7	73.1	3638	745	4383	6078
	max (2.9-3.4%)	3197	1288	27.3	78.5	3911	801	4712	6533

* net production estimated for June through July from Japanese research vessel data.

(26%) estimated for Babine Lake sockeye salmon (Table 4; Brett 1986). The conversion efficiency will likely be higher for older, larger fish, thereby raising the lifetime efficiency for sockeye with two to three years at sea above that determined for the ocean age .1 sockeye salmon in this study. Brett (1983, 1986) hypothesized that high conversion efficiencies such as these are the result of a strategy whereby juvenile sockeye salmon feed heavily in coastal areas, quickly attaining a large size and reducing size-dependent mortality, and that sockeye sustain a high growth rate throughout their ocean residence until they move into freshwater for spawning. In comparisons of our results with those of other studies, it must be taken into consideration that our growth data are pooled and are not from a single stock or ocean production area. There may be considerable variation in growth rates among stocks and oceanic production areas (Brett 1986).

Our estimates of daily ration for an immature ocean age .2 chum salmon (3.3-3.9% bw; 20-24 cal/g-predator/day) and a maturing pink salmon (2.7-3.1% bw; 24-27 cal/g-predator/day; Tables 5, 6) in the Bering Sea were smaller than the estimates of daily ration that Gorbatenko and Chuchukalo (1989) obtained for pre-spawning adult chum (7% bw) and pink salmon (5.8-6.4%) caught on the West Kamchatka shelf in summer. They estimated ration from the amount of food consumed and the digestion rate. Perhaps our estimates of daily ration were lower because we assumed a higher prey caloric density and prey digestibility than Gorbatenko and Chuchukalo (1989).

Our estimate of 2.6-2.9% bw (37-40 cal/g-predator/day) daily ration for maturing coho salmon is the first published for adult coho in offshore marine habitats (Table 7). Brodeur and Percy (1987) determined daily ration for juvenile coho at 2.4-3.7% bw for temperatures slightly warmer than those used in this study. At 7° and 8°C, our coho salmon simulations were not able to attain the 1066 g net production indicated from the mean monthly values from the high-seas salmon research vessel data. This indicates either that the model consumption parameters were too low for a maturing offshore coho salmon, or that the mean monthly size values were too large. Consumption would have to increase by 18% (increase CA from 0.303 to 0.359; Appendix Table 1) in order for simulated net production to equal 1066 g under conditions of a constant 7° or 8° C thermal habitat. Coho salmon have been caught at 7° and 8° C, so it is not likely that the thermal conditions were unrealistic. Examination of coho salmon stock- and location-specific ocean growth deserves further study.

Chum salmon feed upon a wide range of prey organisms. In addition to the prey organisms

(euphausiids, amphipods, and fish) commonly eaten by sockeye, pink, and chum salmon, chum salmon also can eat gelatinous zooplankton (cnidarians, ctenophores, and salps) not common in the stomachs of other salmon (Andrievskaya 1957, 1966; Ito 1964; Brodeur 1990; Davis et al. 1996; Tadokoro et al. 1996). By utilizing gelatinous zooplankton in their diet, chum salmon may reduce direct trophic competition with other salmon (Welch and Parsons 1993). Chum salmon have been shown to have higher stomach acidity and larger stomach capacity as a proportion of body size than other salmon (Azuma 1995; Welch 1997). The esophageal villi and extensive vascularization in the stomach wall observed by Welch (1997) may increase surface area and perhaps speed digestion of prey. This could be particularly helpful for efficient digestion of prey, such as gelatinous zooplankton, that contain a large amount of water (Table 3). However, it is unlikely that chum salmon could grow, particularly at summertime temperatures, on a diet composed mostly of gelatinous zooplankton because the caloric value of gelatinous prey is too low (approximately 20% of the caloric value of crustaceans; Table 3). When chum or pink salmon abundance is high and chum salmon increase the portion of gelatinous zooplankton in their diet, the results may be a reduction or cessation of growth as observed on chum salmon scales by Ishida et al. (1993).

Tadokoro et al. (1996) suggested that micro-nekton, such as fish and squid, were the most efficient prey group for salmon to feed upon because of their relatively large size when compared to the small-sized crustaceans such as amphipods and copepods frequently found in salmon stomach contents. Fish and squid were the most calorically dense salmon prey organisms among those we analyzed (Table 3). Micro-nekton are active swimmers making them more demanding for salmon to catch, but the energetic cost of pursuing and capturing fish and squid is probably offset by the consumption of this energy-rich prey. However, when fish and squid abundance is low, and the time and energy required to search for and capture these prey increases, a smaller proportion of ingested energy is available for salmon growth.

The balance between growth and metabolism is affected by temperature (Jobling 1994). As temperature increases, prey consumption and metabolism increase, but the energetic requirements of metabolism increase faster than the energy gained through increasing consumption, and this reduces growth (Brett et al. 1969). Assuming prey is abundant and that salmon reside in summertime temperatures similar to those used in our simulations (5-9°C in the Bering Sea and 7-11°C in the central North Pacific Ocean), we speculate that as the energy requirements of metabolism increase with temperature, prey

consumption increases and provides sufficient energy for substantial growth. In this temperature range, prey availability rather than metabolic efficiency governs how much the salmon will grow. Welch et al. (1995) observed a step-function response in salmon catch data to upper sea surface temperatures in the northeastern Pacific Ocean in the spring. Perhaps the upper thermal limits Welch et al. (1995) described represent the temperature where energy demands of metabolism begin to rapidly exceed the energy supplied by consumption, even when prey is readily available and consumption rate is at a maximum. We suggest that there may be lower thermal limits below which, although the energy conversion efficiency for salmon is high because metabolic demands are low, consumption rates are also low, and therefore growth is reduced. For example, hydroacoustic data from a winter trans-Pacific survey showed that salmon were not in sub-surface waters colder than 4°C (Sakai et al. 1996). If true, when salmon prey is abundant, an upper thermal limit favorable for salmon growth may be bounded by metabolic requirements, and a lower limit may be bounded by the capacity for prey consumption at low temperatures. The three dimensional aspect of ocean salmon thermal habitat is difficult to characterize. Movements of salmon during their summer ocean residence have been detected using transmitters mounted on salmon and used in conjunction with oceanographic temperature probes to provide a detailed record of individual salmon movements (Ogura and Ishida 1992, 1995; Ogura 1994). However, these data have not been analyzed with respect to salmon feeding habits and bioenergetics. Changes in temperatures can have a large effect on the conversion efficiencies and therefore growth of salmon. Clarification of changes in ocean salmon thermal habitats and changes in diurnal feeding are an important area of continuing research.

CONCLUSIONS

If our estimates of monthly growth during June and July are reasonable, then our simulations indicate that salmon are feeding at a rate close to their physiological maximum (85 to 93% of the maximum for immature sockeye and chum, and 86 to 96% of the maximum for maturing pink and coho salmon). In addition, our estimates indicate that small decreases in the daily ration can cause significant decreases in growth over a time as short as two months during the summer when feeding and growth opportunities are generally thought to be at a maximum. The growth estimates used in these simulations are from pooled data which may not represent growth rates of a particular stock or growth

conditions in a specific ocean production area. Therefore, stock- and ocean region-specific growth data for particular stocks and time periods are needed for further bioenergetics modeling and to evaluate the recently observed decrease in fish size observed in many Pacific Rim salmon stocks.

The bioenergetics approach was helpful in making estimates of consumption and growth using ship-board observations on salmon feeding habits and environmental conditions. The bioenergetics Model 2 developed by Hewitt and Johnson (1992) has been used in previous studies to estimate consumption by juvenile sockeye and coho in freshwater and juvenile coho and chinook in coastal waters, and in those cases, the model was in close agreement with laboratory experiments (Beauchamp et al. 1989; Brodeur et al. 1992; Ruggerone and Rogers 1992). Because the model is constrained by the balanced energy equation, it limits error propagation from the numerous parameters used in the model (Hansen et al. 1993). Model parameter estimates could be improved by additional laboratory experiments measuring the metabolic cost of activity at several levels of swimming effort. Additional observations from field studies of salmon thermal habitats would be useful improvements to model parameters. These data may be easier to measure *in situ* with recent advances in more economical archival tags capable of recording temperature profiles as the fish moves through its ocean habitat.

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Appendix

Appendix 1. Equations used to calculate consumption, respiration, egestion, and excretion rates of salmon. Symbols and equations are those of Hewett and Johnson (1992).

(1) Consumption

$$C = CA * W^{CB} * P * f(T)$$

where

$$f(T) = K_A * K_B$$

$$K_A = (CK1 * L1) / (1 + CK1 * (L1 - 1))$$

$$L1 = e^{(G1 * (T - CQ))}$$

$$G1 = (1 / (CTO - CQ)) * LN((0.98 * (1 - CK1)) / (CK1 * 0.02))$$

$$K_B = (CK4 * L2) / (1 + CK4 * (L2 - 1))$$

$$L2 = e^{(G2 * (CTL - T))}$$

$$G2 = (1 / (CTL - CTM)) * LN((0.98 * (1 - CK4)) / (CK4 * 0.02))$$

(2) Respiration

$$R = (RA * W^{RB} * f(T) * Activity) + (SDA * (C - F))$$

where

$$f(T) = e^{(RO * T)}$$

$$Activity = e^{((RTO - (RTM * T)) * VEL)}$$

$$VEL = ACT * e^{(BACT * T)} * W^{(RK4)}$$

when temperature is $\leq 25^\circ\text{C}$

(3) Egestion

$$F = PF * C$$

where

$$PF = ((PE - 0.1) / (1 - 0.1)) * (1 - PFF) + PFF$$

$$PE = FA * T^{FB} * e^{(FG * P)}$$

$$PFF = \sum (PREYK[n] * DIET[n], \text{ for } n = 1 \text{ to number of prey categories})$$

PREYK[n] = indigestible proportion of the nth prey category

DIET[n] = proportion of nth prey category in the diet

(4) Excretion

$$U = UA * T^{(UB)} * e^{(UG * P)} * (C - F)$$

Appendix (continued)

Appendix Table 1. Fish bioenergetics Model 2 parameter values used to estimate growth and prey consumption by sockeye, chum, pink, and coho salmon given a constant daily food ration (Hewett and Johnson 1992).

Symbol	Physiological Parameter Value	Nominal Value		
		Pink/Sockeye	Chum	Coho
CONSUMPTION (CON)				
C	Specific feeding rate (g/g/day)			
P	Constant proportion of maximum feeding rate			
W	Fish weight (g)			
CA	Intercept for weight dependence of CON	0.303	0.394	0.303
CB	Slope for weight dependence is CON	-0.275	-0.275	-0.275
CQ	Lower temperature where dependence is CK1	3	3	5
CTO	Higher temperature where dependence is 0.98 of max	20	20	15
CTM	Temp \geq CTO where dependence is still .98 of max	20	20	18
CTL	Temperature where dependence is CK4	24	24	24
CK1	Temperature dependence at CQ	0.58	0.58	0.36
CK4	Temperature dependence at CTL	0.50	0.50	0.01
RESPIRATION (RES)				
R	Specific rate of respiration (g-O ₂ /g/day)			
RA	Intercept for std. metabolism vs weight, temperature, and swimming speed	0.00143	0.00143	0.00264
RB	Slope for weight dependence of standard metabolism	-0.209	-0.209	-0.217
RQ	Coefficient for temperature dependence of metabolism	0.086	0.086	0.06818
RTO	Coefficient for swimming speed dependence of metabolism	0.0234	0.0234	0.0234
RTM	Coefficient for swim speed dependence of temperature	0	0	0
RTL	Cut-off temp	25	25	25
RK1	Intercept for weight dependence of swimming speed when temperatures >RTL	1	1	1
RK4	Slope for weight dependence of swimming speed at all temperatures	0.13	0.13	0.13
ACT	Intercept for swimming speed vs temperature and weight	9.9	9.9	9.7
BAC	(cm/sec/1-g fish at 0°), when temperature <RTL	0.0405	0.0405	0.0405
T	Coefficient for temperature dependence of swimming speed when temperature <RTL	0.172	0.172	0.172
SDA	Proportion of assimilated energy lost to specific dynamic action			
EGESTION (EGES)				
F	Specific rate of egestion (g/g/day)			
FA	Intercept for proportion of consumption EGES vs temperature and ration	0.212	0.212	0.212
FB	Slope for temperature dependence of EGES	-0.222	-0.222	-0.222
FG	Coefficient for feeding level dependence of EGES	0.631	0.631	0.631
EXCRETION (EXCR)				
UA	Intercept for proportion of assimilated consumption EXCR vs temperature and ration	0.0314	0.0314	0.0314
UB	Slope for temperature dependence of EXCR	0.58	0.58	0.58
UG	Coefficient for feeding level dependence of EXCR	-0.299	-0.299	-0.299