Using Temperatures from Data Storage Tags in Bioenergetic Models of High-Seas Salmon Growth

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Abstract: Data storage tags provide a new technology for acquiring environmental data on salmon movements at sea. In 1998 and 1999, temperature-recording data tags were recovered in Alaska and Japan from salmonids tagged in the Gulf of Alaska and Bering Sea. One use of temperature data records is to improve bioenergetic models of salmon growth in the ocean. Recent bioenergetic models of salmon growth have often used constant, fixed temperatures, because information on actual daily temperature regimes for salmon was lacking. We used actual temperatures in a bioenergetic model to estimate daily ration. We compared simulated salmon marine growth under two temperature conditions: a constant temperature close to sea surface temperature (SST) at the point of release, and actual temperatures. Estimated daily rations were 1.30–1.72% of body weight/day for three chum salmon over migrations of 62 to 98 days from the Bering Sea to Hokkaido. Over a 30-day simulation, final weights of fish at actual temperatures differed from weights of fish at a constant temperature SST by 0.15%–3.46%. Differences were usually negative, because fish migrated from cooler waters, where the constant temperatures used in our analyses were taken, to warmer coastal waters.

INTRODUCTION

Data storage tags (DSTs) provide a new technology for acquiring environmental data from salmon migrating at sea. In 1998 and 1999, DSTs were recovered in Alaska and Japan from Pacific salmonids (*Oncorhynchus* spp.) tagged in the North Pacific Ocean and Bering Sea (Fukuwaka et al. 1999; Wada and Ueno 1999; Walker et al. 1999, 2000). These tags provide the first detailed records of ambient sea water temperatures encountered by Pacific salmonids. One potential use of these temperature data is to improve bioenergetic models of salmon growth in the ocean. Recent bioenergetic models of ocean salmon growth have often used fixed (Davis et al. 1998) or monthly average (Hinch et al. 1995) sea surface temperatures, as information on actual daily temperature regimes for salmon was lacking. The diel behavior pattern indicated by the DST data, with frequent descents to cooler water during the day, could be feeding behavior, or an indication of a strategy to conserve energy, as proposed by Bevelhimer and Adams (1993) for kokanee salmon (*O. nerka*). Such a strategy might be detectable as an increase in growth rate (Brett 1971).

We have employed a commonly-used bioenergetic model and data on actual temperatures experienced by migrating salmon for two objectives: 1) to estimate the daily ration or consumption rate of migrating chum salmon, and 2) to evaluate possible differences in growth with respect to temperature by comparing simulated salmon marine growth using actual temperatures and using constant temperatures based on sea surface temperatures.

MATERIALS AND METHODS

Fish growth was calculated using a published model, Fish Bioenergetics 3.0 for Windows (Hanson et al. 1997). This model uses a balanced energy equation where energy consumed equals energy expended in metabolism, waste elimination, and growth. Users enter data for several factors that affect the energy budget: water temperature, predator

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and prey energy density, diet composition, and initial predator weight.

The physiological parameter values provided with the software included values for pink (*O. gorbuscha*) and sockeye (*O. nerka*) salmon (identical values), coho salmon (*O. kisutch*), and steelhead trout (*O. mykiss*; Appendix Table 1). These parameters were taken from studies on juvenile and adult Pacific salmonids in freshwater lakes. Because no parameter values are given for chum salmon (*O. keta*), we followed the example of Davis et al. (1998) and used the same values as those for pink and sockeye, modifying the intercept for weight dependence of maximum consumption (CA) to accommodate the larger stomach and faster digestion rate of chum (Azuma 1995; Welch 1997).

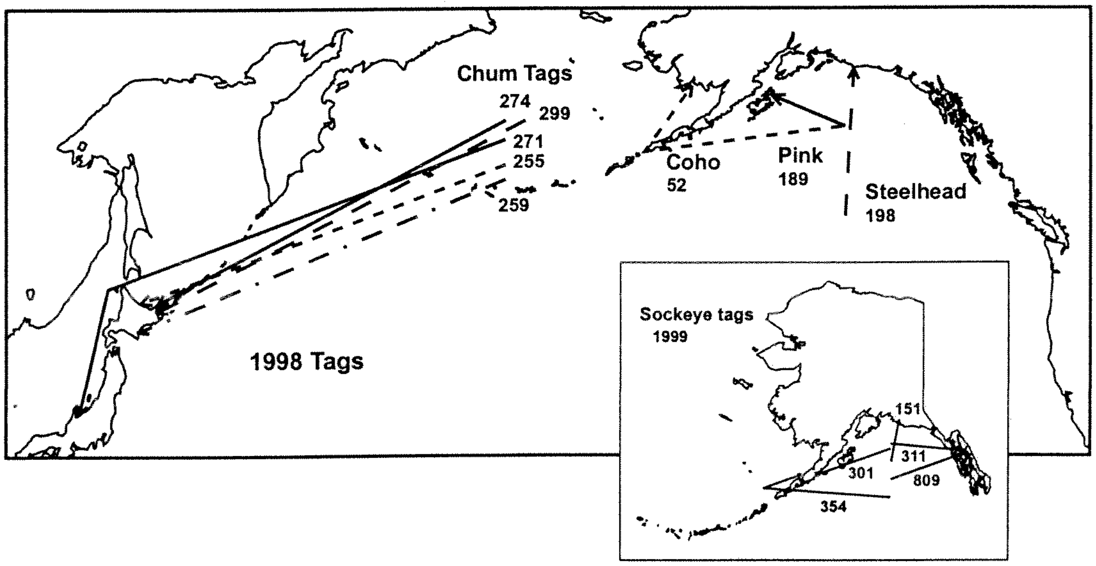
For initial predator weight and diet composition, we used average values for each species from catches in the regions where the tagged fish were released (Table 1; Fig. 1). When data from several ocean age classes were available for a species, these parameters were taken from the same age group as the fish in the model, and in the case of chum salmon, weights were calculated from age- and maturity-specific regressions of length and weight of chum caught in the region of tagging. Caloric values for prey were taken from Davis (1993) and Davis et al. (1998). The model allows entry of the fraction of each prey type that is indigestible; these values were also taken from the compilations in Davis et al. (1998). Predator caloric density is a function of body mass for all species except chum salmon. For chum salmon, a value determined by Davis et al. (1998) was used (1376 cal/g).

Table 1. Diet composition and prey caloric values used in bioenergetic simulations of salmon tagged with data storage tags. EU, euphausiids; CO, copepods; AM, amphipods; SQ, squid; PT, pteropods; FI, fish; GE, gelatinous zooplankton; PO, polychaetes; AP, appendicularians; CH, chaetognaths. Caloric values taken from Davis et al. (1998).

Species	Data Tag No.	Region	Age		Prey									
					EU	CO	AM	SQ	PT	FI	GE	PO	AP	CH
				caloric value: (cal/g wet wt.)	743	627	589	1550, 775*	624	1185	169	814	759	455
					Proportions									
Sockeye	151,301,311	Gulf of Alaska	-.3		56	12			11		8		8	5
	354		2.2		33	16	5		21	12	5		5	3
	809		1.3		19	24	20	11	14	5	2	5		
Chum	255,259,271, 274,299	Bering Sea			20	10	15	5*	20	8	12	10		
Pink	189	Gulf of Alaska	0.1			9	10	52	29					
Coho	52	Gulf of Alaska	1.1		5		5	85	5					
Steelhead	198	Gulf of Alaska	2.3				2	55	10	33				

* lower caloric value (775) used for larval squid consumed in Bering Sea

Fig. 1. Release and recovery locations of thirteen data storage tags placed on Pacific salmonids in the Gulf of Alaska and Bering Sea in 1998 and 1999. Lines connect release and recovery sites and do not indicate actual routes traveled.



Temperature data were taken from thirteen data storage tags placed on five sockeye, five chum, one pink, and one coho salmon and one steelhead trout (Table 2; Fig. 1). Tags were manufactured by Conservation Devices, Inc., and are described more fully in Walker et al. (2000). Temperature data were recorded over a range of -5°C to 30°C with an accuracy of ±0.2°C at intervals of 1.875 to 30 minutes. Fish for tagging were caught by surface longline (chum, pink, coho, steelhead, and sockeye tag 809) or trawl (remaining four sockeye).

Table 2. Release and recovery information for 13 salmonids tagged with data storage tags in the North Pacific Ocean and Bering Sea in 1998 and 1999 and recovered in Alaska and Japan. Age determined from scale sample taken at release. Days = number of days fish was at large after tagging. Distance = great circle distance between release and recovery points (for tags 354 and 52, two segments via Unimak Pass; for Tag 271, two segments via Soya Strait). Data points = total temperature data points recorded while the fish was at large and do not include data before release or after recovery.

		Release				Recovery								
Species	Tag No.	Date	Location	Length (FL; mm)	Age	Date	Days	Location	Distance (km)	Data Points	Data Interval	Length (mm)	Weight (kg)	Sex
Sockeye	151	5/21/99	Gulf of Alaska 57°37'N 145°00'W	525	2.3	7/9/99	50	Copper R. 61°29'N 144°27'W	431	4,697	15"			M
Sockeye	301	5/22/99	Gulf of Alaska 58°26'N 145°00'W	640	1.3	6/16/99	26	Chignik Lagoon 56°20'N 158°29'W	839	4,857	7.5"			
Sockeye	311	5/22/99	Gulf of Alaska 58°58'N 145°00'W	635	1.3	7/4/99	44	Taku Inlet 58°12'N 134°06'W	636	4,150	15"	652		M
Sockeye	354	5/20/99	Gulf of Alaska 54°45'N 145°00'W	490	2.2	7/11/99	53	Port Moller 56°31'N 159°53'W	1,670	4,976	15"			
Sockeye	809	7/14/99	Gulf of Alaska 56°10'N 145°04'W	635	1.3	8/3/99	21	Taku Inlet 58°07'N 134°04'W	697	10,837	1.875" & 3.45"			
Chum	255	7/4/98	Bering Sea 53°30'N 179°30'W	560	0.3	10/10/98	98	Yubetsu, Okhotsk 44°13'N 143°40'E	2,845	4,680	30"	610	2.1	M
Chum	259	7/3/98	Bering Sea 52°30'N 179°30'W	622	0.3	9/4/98	62	Tokachi R. mouth 42°39'N 143°37'E	2,942	6,011	15"	650	3.0	M
Chum	271	7/6/98	Bering Sea 55°30'N 179°30'W	592	0.3	10/31/98	117	Sho R., Hon., J.Sea 36°47'N 137°05'E	3,997	5,607	30"	610	1.8	M
Chum	274	7/7/98	Bering Sea 56°30'N 179°30'W	680	0.4	9/24/98	79	Shiretoko Peninsula 44°19'N 145°21'E	2,779	3,782	30"	716		M
Chum	299	7/12/98	Bering Sea 56°30'N 177°30'W	577	0.3	10/5/98	85	Shibetsu, Nem. Strt 43°41'N 145°09'E	2,969	4,059	30"	590	2.4	F
Pink	189	7/3/98	Gulf of Alaska 55°59'N 145°00'W	495	0.1	7/24/98	21	Afognak Island 58°06'N 152°20'W	501	4,063	7.5"		1.4	
Coho	52	7/3/98	Gulf of Alaska 55°59'N 145°00'W	592	1.1	8/24/98	52	Togiak Bay 59°02'N 160°20'W	1,858	5,857	15"			M
Steelhead	198	7/9/98	Gulf of Alaska 49°58'N 144°58'W	690	2.3	8/14/98	36	Copper R. Delta 60°13'N 144°40'W	931	6,909	7.5"		3.4	M

Daily Ration

To estimate daily ration, we used initial weights estimated from release lengths and weight-length regressions of appropriate age and maturity classes of chum salmon in the area of release, final weights as reported by fishermen, average diet of chum salmon in the release area, and temperature data recorded from release to recovery. Tagged fish were not weighed prior to release, to avoid additional trauma. Data returned by fishermen with recovered tags usually did not include weight, and when included, weight was often estimated or approximate. We received weights at recovery for six salmon. For two fish (a pink salmon and one chum salmon), initial weights as estimated by length-weight regressions were larger than the final reported weights. For a steelhead trout, there were insufficient data to estimate initial weight. For the remaining three fish, all chum salmon, initial weight estimates were less than recovery weights, and estimation of daily ration was possible.

Temperature Comparison

For each fish in Table 2, a simulation was run at a constant temperature approximating the sea surface temperature (SST) at the release site of the tagged fish, rounded to the nearest integer. A second simulation was run using data from the data storage tags for the first 30 days following recuperation from tagging trauma (Fig. 2). (The recuperation period was defined as ending when relatively frequent temperature changes began, indicating resumption of diving behavior. The period ranged from 0 to 21 days in the thirteen salmon in this study.) A uniform simulation period of 30 days was chosen to allow comparison between different fish; most fish had at least 30 days of post-recuperation data (for three fish lacking 30 days of data, data were resampled). Final salmon body weights from simulations using temperature data from DSTs were compared to the final weights from simulations using the constant SSTs from the release site.

The model allows two approaches: fit to end weight (which was used in the daily ration estimates) and fit to consumption. As we had no accurate measures of end weight for most fish, we used the fit to consumption method. Prey weights from stomachs of salmon caught at the same times and places as tagged fish were in the range of 0.6%–1.2% of body weight. These are values from one period of the day and are likely very conservative estimates of daily consumption because no corrections were made for digestion. They are also below the range of estimates derived by Davis et al. (1998) to match observed summer growth of immature salmon (2.6–4.1%) and by Aydin (unpublished data) based on prey consumption (2.7–3.3%), but are closer to the daily rations estimated for three chum salmon (1.3–1.72%; see Results below). We chose uniform values of 2% and 3% for our simulations and fit the model to 30 days of consumption at rates of 2% and 3% of body weight per day. The value of 2% was in the range of

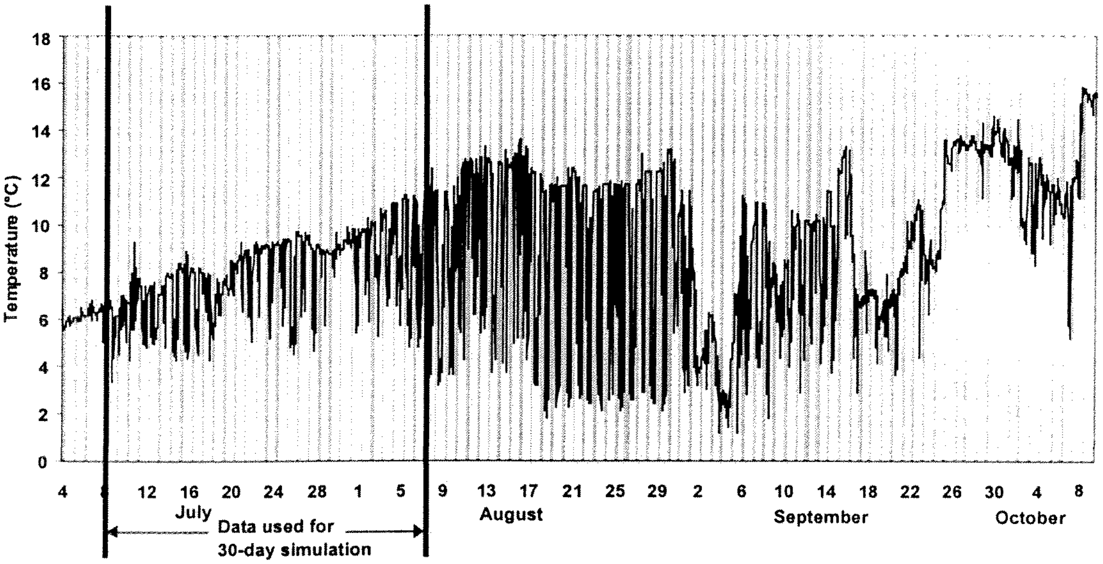


Fig. 2. Temperature data from chum salmon tagged with data storage tag 255 in the Bering Sea and recovered on the Sea of Okhotsk coast of Hokkaido. Data used for 30-day simulation are indicated between dark vertical lines. Entire data set used for daily ration estimation. Light grey bars indicate hours of darkness.

0.44–0.81 of maximum feeding rate, while 3% was close to or exceeded the maximum rate for sockeye and coho (0.94–1.2 of maximum rate). The 3% rate was 0.64–0.93 of the maximum rate for chum, pink and steelhead.

Computations are based on specific rates and a "daily" time step: grams of oxygen per gram of body weight per day and grams of food per gram of body weight per day at a single temperature. To accommodate simulations using actual temperatures, the model parameters implicitly based on 24 hr (only three: CA, RA, and the daily consumption rate) were divided by 48, 96, or 192, to accommodate data intervals of 30, 15, and 7.5 minutes, respectively.

RESULTS

Estimated daily rations were 1.30–1.72% of body weight/day for three chum salmon over migrations of 62 to 98 days from the Bering Sea to Hokkaido (Table 3). Weight gains between estimated initial and final weights were 60 to 279 g. Consumption rates were 35% to 48% of possible maximum rates. When the same weight-length regression used to calculate initial weights from initial lengths was applied to lengths reported at recovery, the estimated final weights were close to reported weights for two fish (3058 cf. 3000 g; 2365 cf. 2400 g; Table 3). For the other fish (tag 255), the estimated final weight was much larger than the reported weight (2584 g vs. 2100 g), which suggests the regression may not have provided an accurate estimate for the initial weight.

Final weights from 30-day simulations using actual temperatures differed from weights of fish at a constant temperature by 0.15%–3.46% (Table 4). The average difference was -1.23%, and the average magnitude of difference was 1.42%. Differences were usually negative.

DISCUSSION

The estimated daily rations for three chum salmon are lower than some other estimates of consumption for salmon. Model simulations by Davis et al. (1998) showed that observed size changes in sockeye, chum, pink, and coho in the Bering Sea and North Pacific in early summer indicated salmon were feeding at rates close to their physiological maxima. Brett (1983) also found that sockeye feeding rates probably approximated maximum intake. There could be several reasons for our lower values. The chum salmon in our study were on homeward migrations. While they may have fed at maximal rates in the Bering Sea, feeding rates probably declined during directed movement toward spawning streams. In warm coastal waters, salmon may not have been feeding at all, and may have lost weight. This could have been especially true for the chum carrying tag 271. After 117 days, including six weeks near the end of its migration where surface temperatures were between 19°C and 22°C, the reported weight at capture for this fish was only 1.8 kg, less than the weight we estimated from the length at tagging.

Our simulations were based on estimated initial values, since the tagged fish were not weighed. If the estimations were not accurate, the daily ration estimates would also be in error. However, when the same method was used to estimate the final weights, for two fish the estimated final weights differed from the observed final weights by less than 2%. For the other fish, the estimated weight differed by 23% from the reported weight.

The differences in simulated salmon growth using actual data and one constant temperature were not large over the short 30-day simulation period, but the differences are not negligible. The fish are actually spending a large portion of the day at the surface (most of the night, and moving between the surface

Table 3. Daily rations estimated from estimated initial weights and reported final weights for three chum salmon tagged in the Bering Sea and recovered in Hokkaido, Japan. Daily rations were estimated using average diets of chum salmon in the area of release and actual data storage tag temperature data in Fish Bioenergetics Model 3.0. Initial weights were estimated from age- and maturity-specific regressions of data from chum salmon caught in the region of release. Weights estimated from lengths reported at recovery are provided for comparison with actual reported weight. Days = number of days fish was at large after tagging. FL, fork length; BW, body weight.

			Release		Recovery				
Species	Tag No.	Age	Length (FL; mm)	Est. Weight (g)	Days	Actual Weight (g)	Est. Daily Ration (% BW/day)	Length (mm)	Est. Weight (g)
Chum	255	0.3	560	2060	98	2100	1.30	610	2584
Chum	259	0.3	622	2721	62	3000	1.72	650	3058
Chum	299	0.3	577	2230	85	2400	1.56	590	2365

Table 4. Results of 30-day bioenergetic simulations of salmon growth using data from data storage tags (DST). Actual SST = sea surface temperature at release site. Actual DST = actual temperatures as recorded by DSTs (minimum and maximum of range are indicated). % difference = difference from final weight using constant temperature.

Species	Data Tag No.	Actual SST (°C)	Type of temperature data	Temperature used (°C)	Initial wt. (g)	2% consumption		3% consumption	
						Final Wt. (g)	% difference	Final Wt. (g)	% difference
Sockeye	151	5.1	Constant	5	2435	2613.36		2659.92	
			Actual DST	4.0–17.2	2435	2562.90	-1.93	2666.46	0.25
	301	7.2	Constant	7	2435	2586.41		2674.76	
			Actual DST	4.4–10.11	2435	2593.30	0.27	2670.81	-0.15
	311	7.3	Constant	7	2435	2586.43		2674.76	
			Actual DST	5.5–11.9	2435	2552.90	-1.30	2668.02	-0.25
	354	4.9	Constant	5	1802	1959.43		2021.00	
			Actual DST	4.3–11.5	1802	1951.82	-0.39	2030.07	0.45
	809	10.2	Constant	10	3059	3228.35		3386.56	
			Actual DST	7.2–17.3	3059	3173.83	-1.69	3345.87	-1.20
Chum	255	5.9	Constant	6	2060	2290.64		2478.17	
			Actual DST	3.3–11.4	2060	2241.28	-2.15	2432.37	-1.85
	259	7.4	Constant	7	2721	3002.42		3249.02	
			Actual DST	1.6–14.8	2721	2916.29	-2.87	3152.06	-2.98
	271	6.3	Constant	6	2387	2655.74		2869.79	
			Actual DST	1.2–13.6	2387	2563.73	-3.46	2773.13	-3.37
	274	6.9	Constant	7	3363	4046.36		4368.07	
			Actual DST	0.04–11.8	3363	4021.26	-0.62	4275.21	-2.13
	299	7.1	Constant	7	2230	2458.36		2664.05	
			Actual DST	2.1–12.5	2230	2403.53	-2.23	2605.04	-2.22
Pink	189	11.0	Constant	11	1331	1490.03		1649.64	
			Actual DST	5.7–14.4	1331	1500.88	0.73	1659.42	0.59
Coho	52	11.0	Constant	11	3170	3572.64		3913.73	
			Actual DST	6.6–14.4	3170	3578.38	0.16	3885.11	-0.73
Steelhead	198	10.9	Constant	11	3200	3534.50		3898.77	
			Actual DST	6.4–15.6	3200	3482.07	-1.48	3839.93	-1.51

and deeper, cooler waters during the day). The percent of time in cooler waters may be too small to have a major effect on simulated growth. The fact that differences were usually negative was perhaps because fish migrated from cooler waters where the constant temperatures used in our analyses were taken, to warmer coastal waters.

The differences are of a similar magnitude to those found by Cianelli et al. (1998), who used the same fish bioenergetics model to study juvenile walleye pollock (*Theragra chalcogramma*). Over a one month simulation period, they found a 1.16% difference in final weights between fish modeled at a constant temperature and fish modeled at two different temperatures, simulating vertical migration, on a daily basis. They also found that the model was much more sensitive to consumption parameters than to temperature. In this case, the differences in temperature that salmon experience may have less effect on their growth than availability of food.

Further uses and analyses of the DST data are planned. For example, the DST data help to clarify some features of 24-hr experiments on salmon feeding (Davis et al. this volume). Sampling with surface gillnets over a 24-hour period indicated that fish may be feeding throughout the day (though on different prey). While fish were found with food in their stomachs throughout the day, it was not clear if all fish were from a population that fed at the same time, or if successive groups of fish were feeding at different times of the day and becoming successively vulnerable to surface gillnets. DST data indicate that all fish recovered so far are moving vertically during the day, so it is likely one population of fish and many of them are feeding throughout the day.

CONCLUSIONS

Data storage tags are a useful new tool for investigating salmon marine life. Their use and development have been endorsed by the NPAFC Committee on Scientific Research and Statistics, which identified five areas for future research. Our study is a beginning in one area: swimming behavior and bioenergetics relating to carrying capacity. The data from DSTs have great potential for improving our ability to model more accurately salmon behavior and growth at sea.

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REFERENCES

Azuma, T. 1995. Biological mechanisms enabling sympatry between salmonids with special reference to sockeye and chum salmon in oceanic waters. Fish. Res. 24: 291–300.

Bevelhimer, M.S., and S.M. Adams. 1993. A bioenergetics analysis of diel vertical migration by kokanee salmon, *Oncorhynchus nerka*. Can. J. Fish. Aquat. Sci. 50: 2336–2349.

Brett, J.R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). Am. Zool. 11: 99–113.

Brett, J.R. 1983. Life energetics of sockeye salmon, *Oncorhynchus nerka*. *In* Behavioral energetics: the cost of survival in vertebrates. *Edited by* W.P. Aspey and S.I. Lustik. Ohio State University Press, Columbus, Ohio.

Cianelli, L., R.D. Brodeur, and T.W. Buckley. 1998. Development and application of a bioenergetics model for juvenile walleye pollock. J. Fish Biol. 52: 879–898.

Davis, N.D. 1993. Caloric content of oceanic zooplankton and fishes for studies of salmonid food habits and their ecologically related species. (NPAFC Doc. 15) 10p. University of Washington, U.S.A.

Davis, N.D., K.W. Myers, and Y. Ishida. 1998. Caloric value of high-seas salmon prey organisms and simulated salmon ocean growth and prey consumption. N. Pac. Anadr. Fish. Comm. Bull. No. 1: 146–162.

Davis, N.D., K.Y. Aydin, and Y. Ishida. This volume. Diel catches and food habits of sockeye, pink, and chum salmon in the central Bering Sea in summer. N. Pac. Anadr. Fish. Comm. Bull. No. 2.

Fukuwaka, M., S. Urawa, I. Ono, K. Umeda, M. Kawana, and R.V. Walker. 1999. Recoveries of high-seas tags in Japan, 1998, and 1999 tag releases and recoveries of fin-clipped salmon collected by Japanese research vessels in the North Pacific Ocean. (NPAFC Doc. 416) 11p. Hokkaido National Fisheries Research Institute, Japan.

Hanson, P.C., T.B. Johnson, D.E. Schindler, and J.F. Kitchell. 1997. Fish Bioenergetics 3.0 for Windows. Center for Limnology, Univ. of Wisconsin and Univ. of Wisconsin Sea Grant Institute.

Hinch, S.G., M.C. Healey, R.E. Diewert, and M.A. Henderson. 1995. Climate change and ocean energetics of Fraser River sockeye (*Oncorhynchus nerka*). *In* Climate change and northern fish populations. *Edited by* R.J. Beamish. Can. Sp. Pub. Can. Fish. Aquat. Sci. 121: 439–445.

Wada, K., and Y. Ueno. 1999. Homing behavior of chum salmon determined by an archival tag. (NPAFC Doc. 425) 29p. Hokkaido National Fisheries Research Institute, Japan.

Walker, R.V., K.W. Myers, N.D. Davis, H.R. Carlson, and K.D. Friedland. 1999. U.S. releases and recoveries of salmonid data storage tags and disk tags in the North Pacific Ocean and Bering Sea, 1999. (NPAFC Doc. 412) 20p. FRI-UW-9910. University of Washington, U.S.A.

Walker, R.V., K.W. Myers, N.D. Davis, K.Y. Aydin, K.D. Friedland, H.R. Carlson, G.W. Boehlert, S. Urawa, Y. Ueno, and G. Anma. 2000. Diurnal variation in thermal environment experienced by salmonids in the North Pacific as indicated by data storage tags. Fish. Oceanogr. 9: 171–186.

Welch, D.W. 1997. Anatomical specialization in the gut of Pacific salmon (*Oncorhynchus*): Evidence for oceanic limits to salmon production. Can. J. Zool. 75: 936–942.

Appendix

Appendix Table 1. Parameter values used to estimate growth and prey consumption by sockeye, pink, chum, and coho salmon and steelhead trout given a constant daily food ration. Parameters are published in Fish Bioenergetics Model 3.0 (Hanson et al. 1997), and are taken from values in the literature derived from studies of Pacific salmonids in lakes. Value for CA for chum salmon was estimated by Davis et al. (1998).

Symbol	Physiological Parameter	Nominal Value			
		Sockeye/ Pink	Chum	Coho	Steelhead
	CONSUMPTION (CON)				
CA	Intercept for weight dependence of CON	0.303	0.394	0.303	0.628
CB	Slope for weight dependence of CON	-0.275	-0.275	-0.275	-0.3
CQ	Lower temperature where dependence is CK1	3	3	5	5
CTO	Higher temperature where dependence is 0.98 of max	20	20	15	20
CTM	Temp≥CTO where dependence is still .98 of max	20	20	18	20
CTL	Temperature where dependence is CK4	24	24	24	24
CK1	Temperature dependence at CQ	0.58	0.58	0.36	0.33
CK4	Temperature dependence at CTL	0.50	0.50	0.01	0.2
	RESPIRATION (RES)				
RA	Intercept for std. metabolism vs weight, temperature, and swimming speed	0.00143	0.00143	0.00264	0.00264
RB	Slope for weight dependence of standard metabolism	-0.209	-0.209	-0.217	-0.217
RQ	Coefficient for temperature dependence of metabolism	0.086	0.086	0.06818	0.06818
RTO	Coefficient for swimming speed dependence of metabolism	0.0234	0.0234	0.0234	0.0234
RTM	Coefficient for swim speed dependence of temperature	0	0	0	0
RTL	Cut-off temp	25	25	25	25
RK1	Intercept for weight dependence of swimming speed when temperatures >RTL	1	1	1	1
RK4	Slope for weight dependence of swimming speed at all temperatures	0.13	0.13	0.13	0.13
ACT	Intercept for swimming speed vs temperature and weight (cm/sec/1-g fish at 0°), when temperature <RTL	9.9	9.9	9.7	9.7
BACT	Coefficient for temperature dependence of swimming speed when temperature <RTL	0.0405	0.0405	0.0405	0.0405
SDA	Proportion of assimilated energy lost to specific dynamic action	0.172	0.172	0.172	0.172
	EGESTION (EGES)				
FA	Intercept for proportion of consumption EGES vs temperature and ration	0.212	0.212	0.212	0.212
FB	Slope for temperature dependence of EGES	-0.222	-0.222	-0.222	-0.222
FG	Coefficient for feeding level dependence of EGES	0.631	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	0.0314
UB	Slope for temperature dependence of EXCR	0.58	0.58	0.58	0.58
UG	Coefficient for feeding level dependence of EXCR	-0.299	-0.299	-0.299	-0.299