A Bioenergetics Approach to Estimating Consumption of Zooplankton by Juvenile Pink Salmon in Prince William Sound, Alaska

Jennifer L. Boldt and Lewis J. Haldorson

Reprinted from the Alaska Fishery Research Bulletin
Vol. 9 No. 2, Winter 2002

The Alaska Fisheries Research Bulletin can be found on the World Wide Web at URL:
http://www.ak.gov/adfg/geninfo/pubs/afrb/afrbhome.htm

Alaska Fishery Research Bulletin 9(2):111–127. 2002.

A Bioenergetics Approach to Estimating Consumption of Zooplankton by Juvenile Pink Salmon in Prince William Sound, Alaska

Jennifer L. Boldt and Lewis J. Haldorson

ABSTRACT: Juvenile pink salmon *Oncorhynchus gorbuscha* were sampled through the summer and fall of 1998 in Prince William Sound, Alaska. Samples collected in the field and a bioenergetics model were used to estimate consumption of zooplankton by juvenile pink salmon during their first three months at sea. Based on an initial weight of 0.26 g and a growth rate of 4% body weight per day, a pink salmon would consume 27.9 g of wet weight in a 93 d residence time in Prince William Sound. A cohort of juvenile pink salmon would consume 5.53×10^{9} g wet weight or 0.05 g Carbon/m^2/year (g C/m^2/year) in PWS. Sensitivity analyses indicate that residence time, mortality, and diet strongly influence consumption estimates. Assuming a primary production of 100 to 300 g C/m^2/year, a transfer efficiency of 20%, and secondary production of 20 to 60 g C/m^2/year, consumption by juvenile pink salmon was about 0.06–0.45% of annual secondary production. This estimate would be higher (up to 8.28%) if only nearshore areas of Prince William Sound are considered. The average daily consumption of large calanoid copepods was 2.2×10^{-4} g C/m^2 or 1.5% of the large calanoid copepods available. If standing stocks were fixed over a 10-day period, pink salmon consumption would represent a large proportion of large calanoid copepods (15%) and amphipods (19%). Consumption by pink salmon and other planktivores needs to be considered along with geographic and interannual variability in zooplankton biomass and productivity when examining the carrying capacity of the Prince William Sound ecosystem.

INTRODUCTION

The amount of fish production a marine environment can support has been examined previously, but is inadequately understood (Sanger 1972; Brodeur et al. 1992; Cooney 1993). A period of high salmon production accompanied by decreasing salmon weight (Bigler et al. 1996) in Alaska during the mid-1970s to the late 1990s has been attributed to changes in atmospheric and oceanic conditions in the North Pacific (Beamish and Bouillon 1993; Coronado and Hilborn 1998; Mantua et al. 1997). A popular hypothesis states a regime shift (change in atmospheric and oceanic conditions) in the mid-1970s, as indicated by a positive Pacific Decadal Oscillation index, may have changed the production and carrying capacity of the ecosystem (Beamish et al. 1995; Mantua et al. 1997; Anderson and Piatt 1999). Additionally, hatchery production of salmon in Prince William Sound (PWS), Alaska increased in the mid-1970s to the 1990s, raising concerns over the ability of prey resources there to support the large numbers of hatchery fish (Hilborn and Eggers 2000).

The regime after the mid-1970s was characterized by an intensified Aleutian Low that increased precipitation and freshwater runoff into the Gulf of Alaska (GOA), resulting in increased stability of coastal north

Authors: JENNIFER L. BOLDT works at the Juneau Center School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 11120 Glacier Hwy, Juneau, AK 99801. Email: j.boldt@uaf.edu. LEWIS J. HALDORSON works at the Juneau Center School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 11120 Glacier Hwy, Juneau, AK 99801.
Aknowledgments: We thank Dave Reggiani, Tim Joyce, and the Prince William Sound Aquaculture Corporation for providing valuable information and samples of pink salmon fry upon release from hatcheries. We thank Ken Coyle and Tom Weingartner, University of Alaska Fairbanks, and Jennifer Purcell, University of Maryland Center for Environmental Science, for providing data and for reviewing this paper. Also, we thank Terrance Quinn II, University of Alaska Fairbanks, and Chris Rooper, National Marine Fisheries Service, for reviewing this paper. We thank Julia Mabry, Judy McDonald, Amy McKenzie, A. J. Paul, and Tom Shirley, University of Alaska Fairbanks, Jill Snyder, Crawford and Associates, as well as Jack Helle and Ed Farley, with the Ocean Carrying Capacity program, Auke Bay Laboratory, National Marine Fisheries Service, for help in collection of data. We thank Kris Munk, Pete Hagen, and the Alaska Department of Fish and Game Tag Laboratory for assistance with otolith analysis. We also thank the crews of F/V *Pagan*, F/V *Great Pacific*, University of Alaska R/V *Alpha Helix*, and Alaska Department of Fish and Game R/V *Pandalus* for help in collection of samples. This manuscript was improved with the suggestions of three anonymous reviewers. This study was part of the Global Ocean Ecosystem Dynamics (GLOBEC) project, funded by National Oceanic and Atmospheric Administration (NOAA) grant NA67RF0147, and part of the Apex Predator Ecosystem eXperiment (APEX), funded by NOAA grant 50ABNP-4-00092.

GOA waters (McLain 1984; Hollowed and Wooster 1992; Beamish 1993; Gargett 1997; Royer and Weingartner 1999). The stable water column may have retained the light-limited phytoplankton in the euphotic zone resulting in the observed increase in total chlorophyll *a* in the central North Pacific between 1968 and the mid-1980s (Venrick et al. 1987; Polovina et al. 1995; Bigler et al. 1996; McGowan et al. 1998). Zooplankton biomass increased significantly in the northeast Pacific between the early 1960s and 1980s, possibly benefiting from elevated primary production levels (Brodeur and Ware 1992). Zooplankton from the north GOA are transported into PWS in the westward-flowing Alaska Coastal Current or with an influx of deep water through Hinchinbrook Entrance (Kline 1999; Eslinger et al. 2001). Increased zooplankton may have positively affected zooplankton predators, such as pink salmon *Oncorhynchus gorbuscha*, in the north GOA and PWS, which experienced a higher abundance from 1976 to 1999 (Beamish et al. 1997; Sharp et al. 2000).

Increased pink salmon numbers in the north GOA and PWS may be linked to increased zooplankton biomass; however, the average body size of returning salmon decreased by about 20% between 1975 and 1993 (Ricker 1995; Bigler et al. 1996), and has remained lower than pre-1976 weights (Donaldson et al. 1995; Morstad et al. 1996, 1997, 1998, 1999; Sharp et al. 2000; Johnson et al. 2002; Gray et al. 2002). It is possible that planktivory by the historically large number of pink salmon is affecting zooplankton density. For example, pink salmon abundance is inversely related to macrozooplankton biomass and directly related to phytoplankton biomass in the subarctic North Pacific, suggesting top-down processes may be controlling zooplankton abundance (Shiomoto et al. 1997). Another hypothesis is that higher temperatures after the regime shift (Beamish 1993) increased metabolic and energetic demands reducing salmon weight, despite increased zooplankton biomass.

Alternatively, it is possible that the decrease in pink salmon weight may be due to food-limitation during pink salmon early life history, despite the increase in zooplankton biomass. PWS is a large estuary in the north GOA that supports large runs of both wild and hatchery pink salmon (Cooney 1993). Pink salmon year class strength is thought to be determined during their first few months at sea (Parker 1966; Peterman 1987; Karpenko 1998; Beamish and Mahnken 2001). Main determinants of survival and growth during these months include food availability, temperature, salinity, and predators (Gilhousen 1962; Peterman 1987; Blackbourn 1989; Cooney 1993; Mortensen et al. 2000). Pink salmon fry emerge or are released into PWS in spring and spend the first four months of their lives in PWS, initially occupying shallow nearshore habitats, before moving into deeper waters and eventually into the GOA (Cooney et al. 1981; Willette 2001). Competition for limited food during this time period may have negative effects on pink salmon growth and therefore, their ability to escape size-selective predators (Cooney et al. 1995).

The objective of this paper was to estimate zooplankton consumption by juvenile pink salmon in PWS. To accomplish this objective we: (1) estimated consumption of zooplankton by PWS juvenile pink salmon in their first three months at sea using a bioenergetics model, and (2) investigated the sensitivity of consumption estimates to variable temperatures, diets, mortality rates, energy content, and model duration. We also discussed the estimates of zooplankton consumption in relation to available estimates of zooplankton production and standing stock.

MATERIALS AND METHODS

Study Areas and Sampling Methods

The 1997 brood year of pink salmon was sampled on five occasions in 1998 with a variety of nets (Figure 1; Table 1): (1) In May the Prince William Sound Aquaculture Corporation provided hatchery fry at times of release, (2) in the northeast GOA in July, (3) in mid-July in PWS, (4) in the northeast GOA in early August samples were provided by the National Marine Fisheries Service, Ocean Carrying Capacity project, and (5) in the northeast GOA in October.

Hatchery releases, May 1998

Pink salmon fry were provided by PWS Aquaculture hatcheries at the time of release (Figure 1; Table 1). Samples from Cannery Creek Hatchery (CCH) were collected from the early (May 7) and late (May 29) release groups. Two samples were also collected from Armin F. Koernig Hatchery (AFK), one early (May 8) and one late (May 24). One sample was collected from the Wally Noerenberg Hatchery (WNH) early release group (May 1). All samples were frozen for later laboratory analyses.

Gulf of Alaska, July 1998

The Global Ocean Ecosystem Dynamics project conducted a fish sampling survey in the north GOA along the Seward hydrographic line July 10–15, 1998 (Figure

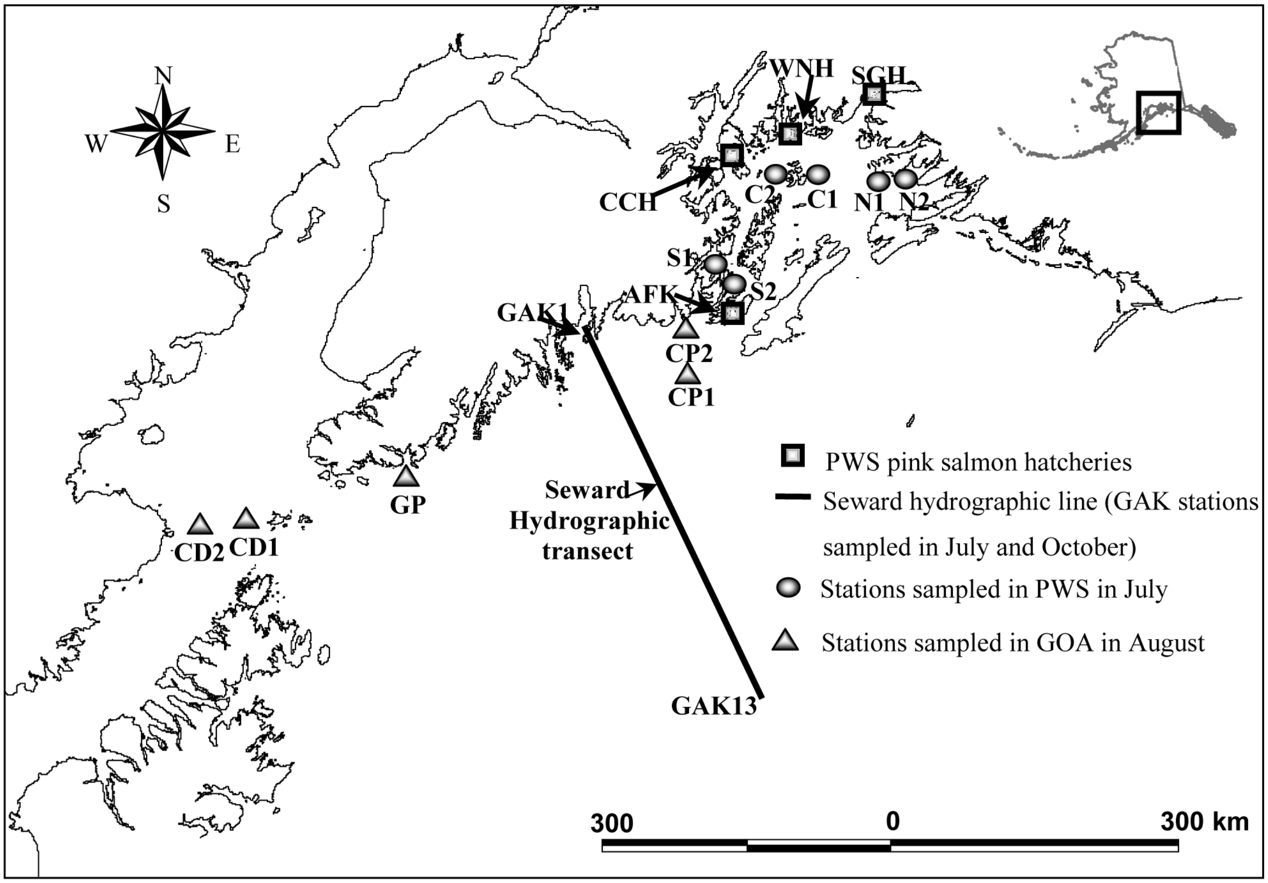

Figure 1. Sampling locations in PWS and the GOA in 1998. Samples were collected from three of the four pink salmon hatcheries in PWS, Solomon Gulch hatchery (SGH), Wally Noerenberg (WNH), Cannery Creek hatchery (CCH), and Armin F. Koernig hatchery (AFK). Six stations were sampled in PWS in July (N1, N2, C1, C2, S1, S2). Gulf of Alaska (GAK) stations along the Seward hydrographic transect were sampled in July and October. Main and intermediate stations (such as GAK1i, not shown) are located every 18.5 km and 9.25 km, respectively, along the Seward transect. Five stations were sampled in the GOA in August (CP1, CP2, GP, CD1, CP2).

1). A small number of pink salmon were collected on this cruise during daylight hours. These fish were sampled within 32 km of shore with variable-meshed gillnets. Gillnets used were 200 m in length, 3 m deep, and were comprised of four 50 m panels. The four panels had mesh sizes of 19 mm, 25 mm, 32 mm, and 38 mm stretched mesh. Two gillnets were tied together and soaked for about 2–4 hours. All pink salmon collected were measured and frozen for later laboratory analysis.

Prince William Sound, July 1998

The Apex Predator Ecosystem Experiment project conducted a survey of fish abundance and distribution in three areas of PWS from July 14 to 19, 1998. Salmon were collected at two stations in each of the three areas, Port Gravina in northeast PWS, Naked Island in central PWS, and Whale Bay-Bainbridge Passage in southwest PWS (Figure 1; Table 1). Blind sets were completed at each predetermined station during daylight hours with a purse seine (200 m long, 20 m deep, 25 mm stretched mesh). Pink salmon collected were measured and frozen for later laboratory analysis (Table 1). When there was a large catch of salmon, 10-15 pink salmon were preserved in 10% buffered formalin for diet analyses.

Gulf of Alaska, August 1998

The fourth sampling period was conducted in the northern GOA August 1–3, 1998 by the Ocean Carrying Capacity project. Fish were collected with a surface trawl that was 198 m long, the mouth opening was 25 m wide

Table 1. Pink salmon collection dates and station locations in 1998. Sample sizes (*n*) are the number of fish used for determining energy content, growth rate, and diet of fish in the model.

Area	Date	Station	Gear	Energy (*n*)	Growth (*n*)	Diet (*n*)
Prince William Sound	May 8	AFK early[a]	None	10		
	May 24	AFK late[b]	None	10		
	May 7	CCH early[c]	None	10		
	May 29	CCH late[d]	None	10		
	May 1	WNH early[e]	None	10		
Gulf of Alaska	July 15	GAK 1i	Gillnet	0		
	July 14	GAK 2	Gillnet	0		
	July 7, 14	GAK 2i	Gillnet	10		
Prince William Sound	July 15	N1	Purse seine	10	6	10
	July 15	N2	Purse seine	10	7	13
	July 16	C1	Purse seine	30	53	10
	July 17	C2	Purse seine	29	26	10
	July 18	S1	Purse seine	11	12	10
	July 19	S2	Purse seine	9	17	10
Gulf of Alaska	August 3	CD1	Surface trawl	16		
	August 3	CD2	Surface trawl	11		
	August 1	CP1	Surface trawl	14		
	August 1	CP2	Surface trawl	30	12	
	August 2	GP	Surface trawl	15	4	
Gulf of Alaska	October 4	GAK 1	Gillnet	5		
	October 8	GAK 2	Gillnet	6		
	October 8	GAK 4	Gillnet	8		
	October 8	GAK 5	Gillnet	12		
	October 6	GAK 6	Gillnet	10		
TOTAL:				286	137	63

[a] Armin F. Koernig hatchery early release date, May 8, 1998.
[b] Armin F. Koernig hatchery late release date, May 24, 1998.
[c] Cannery Creek hatchery early release date, May 7, 1998.
[d] Cannery Creek hatchery late release date, May 29, 1998.
[e] Wally Noerenberg hatchery early release date, May1, 1998.

and 35 m deep, and the cod end had a 1.2 cm mesh lining. Samples were collected during daylight hours at five stations (Figure 1; Table 1). Two stations were sampled off of Cape Puget, one nearshore (CP2) and one over the shelf (CP1). Another two stations were sampled off of Cape Douglas, CD1 and CD2. The fifth station was sampled nearshore off of Gore Point (GP). Fifty pink salmon were collected from each station and frozen for later laboratory analysis.

Gulf of Alaska, October 1998

The Global Ocean Ecosystem Dynamics project conducted sampling along the Seward hydrographic line in the north GOA from October 2–9, 1998. Fish were collected with the same variable mesh floating gillnets that were used on the Seward hydrographic line in July, 1998. Sampling was conducted at night and nets were soaked for approximately 2 to 3 hours at 10 stations (GAK stations) along the transect (Figure 1; Table 1). Fish sampled were identified, measured, and frozen for later laboratory analysis.

Bioenergetics Model

The Hewitt and Johnson/Wisconsin model (Kitchell et al. 1977; Hanson et al. 1997) was used to estimate consumption by pink salmon during their residence in PWS from May to August in 1998. The model estimates how much prey a fish would need to consume to achieve an observed growth rate while accounting for respiration, egestion, and excretion (Appendices A and B). Physiological parameters for adult pink salmon, provided in the software for this model (Fish Bioenergetics 3.0; Hanson et al. 1997), were used since information on juvenile pink salmon is limited (Appendices A and B). Field-generated model inputs include: diet, fish growth in weight, and fish energy content. Prey energy con-

Table 2. The proportions, based on percent weight, of prey items in juvenile pink salmon diets.

	Diet proportions					
Source for diet proportions	[a]	[a]	[a]	[a]	[b]	[b]
Model day	1	19	37	56	62	93
Date	May 1	May 19	June 6	June 25	July 1	August 1
Large calanoid copepods (≥2.5mm)	0.792	0.656	0.703	0.256	0.249	0.249
Small calanoid copepods (<2.5mm)	0.147	0.128	0.012	0	0.071	0.071
Harpacticoid copepods	0.046	0.048	0.006	0	0	0
Hyperiid amphipods	0	0	0	0	0.024	0.024
Euphausiids	0.004	0	0.001	0	0.016	0.016
Insects	0	0.164	0.014	0	0.043	0.043
Cladocerans	0	0	0	0	0.235	0.235
Larvaceans	0	0	0.264	0.739	0.195	0.195
Gastropods	0	0	0	0.004	0.011	0.011
Fish	0	0	0	0	0.011	0.011
Crab megalopae	0	0	0	0	0.006	0.006
Crab zoea	0.011	0.004	0	0	0.003	0.003
Barnacle nauplii	0	0	0	0	0.055	0.055
Barnacle cyprids	0	0	0	0	0.027	0.027
Bivalves	0	0	0	0	0.001	0.001
Ostracods	0	0	0	0	0.002	0.002
Other	0	0	0	0.001	0.051	0.051

[a] Cooney et al. 1978.
[b] Boldt and Haldorsen *In press*; Boldt 2001.

tent, temperature, population numbers, mortality, and residence time were estimated from literature values. The sources of each model input and values over which they were varied for sensitivity analyses are specifically addressed below.

Consumption was calculated as prey consumed (g) over a 93 day (d) residence in PWS. To convert consumption to grams of carbon (C) consumed per square meter of surface, consumption was divided by the area of PWS (8.8×10^9 m^2; Grant and Higgens 1910) and multiplied by 0.0844 g C/1.0 g wet weight (Omori 1969).

Diet

Prey weights were estimated in the laboratory, using values obtained from the literature (Cooney et al. 1981) and provided by K. Coyle (University of Alaska Fairbanks, personal communication; Boldt and Haldorson *In press*; Boldt 2001). The diet of pink salmon sampled in PWS during July 1998 was used for model days 62-93 (July) (Tables 1 and 2; Boldt and Haldorson *In press*; Boldt 2001). The diet of pink salmon prior to model day 62 was estimated from the literature (Cooney et al. 1978).

Prey energy content

Energy content of prey items utilized in the model were averaged from literature values and assumed to be constant for the months that were modeled (Table 3). Prey items comprising a small percentage of pink salmon diets (polychaetes, unidentified crustaceans, and invertebrate eggs) were grouped together and labeled as "other". The caloric content of this "other" category was calculated as an average of caloric values of the different prey items (Table 3). The proportion of each prey group that was indigestible was estimated from the literature where possible, otherwise, it was assumed that 10% of the prey was indigestible (Table 3). To examine the effect of variable prey energy density on consumption estimates, the model was run with a low calorie diet (consumption of only nauplii, 2,045 J/g wet weight) and a high calorie diet (consumption of only insects, 4,532 J/g wet weight) over the entire period of PWS residency (Table 4).

Weight of pink salmon

Initial (0.26 g) and final (9.60 g) pink salmon weights utilized in the bioenergetics model were based on wet weights and a growth rate of 4% as determined in the laboratory and in combination with literature values (Boldt 2001). Wild and hatchery pink salmon have been reported to weigh 0.2–0.3 g when they enter the sea (Pritchard 1944; LeBrasseur and Parker 1964; Cooney et al. 1978; Parker and Massa 1993). Previous growth estimates in PWS were primarily between 3% and 5% body weight per day (Willette et al. 1994). All hatchery

Table 3. Percent of prey that is indigestible and prey energy content as found in the literature.

Prey	Percent Indigestible	Energy content (J/g wet wt)	Literature sources
Large calanoid copepods (≥2.5mm)	9.04	3,810.7	Davis et al. 1998; Harris 1985; Kosobokova 1980
Small calanoid copepods (<2.5mm)	9.04	3,810.7	Davis et al. 1998; Harris 1985; Kosobokova 1980
Harpacticoid copepods	9.04	3,810.7	Davis et al. 1998; Harris 1985; Kosobokova 1980
Hyperiid amphipods	12.99	2,906.0	Davis et al. 1998; Harris 1985; Cooney et al. 1981
Euphausiids	10.35	3,454.8	Davis et al. 1998; Harris 1985
Insects	10.00	4,531.8	Griffiths 1977
Cladocerans	10.00	2,513.5	Cummins and Wuychek 1971
Larvaceans	10.00	3,287.8	Healey 1991; Cooney et al. 1981
Gastropods	8.50	2,619.8	Davis et al. 1998
Fish	8.98	5,353.4	Davis et al. 1998; Ciannelli et al. 1998
Crab megalopae	10.00	3,795.7	Dawirs et al. 1986 (at 9 °C assuming 30% dry wt)
Crab zoea	10.00	3,785.0	Dawirs et al. 1986 (at 9 °C assuming 30% dry wt)
Barnacle nauplii	10.00	2,045.3	Thayer et al. 1973
Barnacle cyprids	10.00	2,045.3	Thayer et al. 1973
Bivalves	10.00	1,787.4	Norrbin and Bamstedt 1984 (assume 10% dry wt as for pelecypoda); Thayer et al. 1973
Ostracods	10.00	2,585.7	Norrbin and Bamstedt 1984 (assume 10% dry wt)
Other	10.00	2,595.0	average value of other prey

pink salmon in PWS are thermally marked and their release size is known, therefore we calculated hatchery-specific growth rates based on weights at release in May and capture in July and August (Boldt 2001; Table 1). These results indicate juvenile pink salmon grew in body weight from 3.6% to 6.7% per day with a median value of 4.6% (Boldt 2001). The estimates of growth rates in this study do not take into account size-selective mortality or gear selectivity, however, they are within the range of values estimated by Willette et al. (1994) using coded wire tags.

Energetic content of pink salmon

An average energy content value of pink salmon sampled in 1998, 4.171 kJ/g wet weight, was utilized in the bioenergetic model (Table 1). Energy content values were estimated in the laboratory with a bomb calorimeter and were observed to vary significantly among stations within sampling periods and among sampling periods (Boldt 2001). The energy content was not varied over the 93 d in the original model; hatchery fish energy content was expected to be higher because of artificial feeding conditions. The average energy content of pink salmon measured upon release in May 1998 was 4.102 kJ/g wet weight, and in July 1998 was 3.883 kJ/g wet weight (Boldt 2001). In a sensitivity analysis these two values were used for days 1 and 93 in a variation of the original model to examine the effects of predator energy content on the consumption estimate (Table 4).

Temperature

The model was run using 6°C, 8°C, 10°C, and 12°C for days 1, 32, 62, and 93, respectively. Juvenile pink salmon are usually found near the surface, therefore estimates of water temperature in the upper 1 m of the water column were used for the model (Cooney et al. 1995; Vaughan et al. 2001). The water temperature in the upper 1 m of the water column of PWS is typically about 4°C in early April and warms to 12°C by August (Cooney et al. 1995; Vaughan et al. 2001) (Table 4). Within the bioenergetics model, temperature is incremented by linear interpolation. The model was also run with minimum (4°C, 6°C, 8°C, 10°C for days 1, 32, 62, 93) and maximum (8°C, 10°C, 12°C, 14°C for days 1, 32, 62, 93) temperature values to examine the effect of temperature variation on consumption estimates (Table 4). These temperatures were chosen because average sea surface temperatures in the north GOA from April to June vary by approximately ±2°C (Cooney et al. 1995). Daily water temperatures at 20 m depth were also available from mooring data at GAK 1 in 2000 (Figure 2; Royer and Weingartner 2002; T. Weingartner, University of Alaska Fairbanks, personal communication). This daily temperature data was utilized in the model to examine the effects of daily temperature variation on overall fish consumption.

Population numbers

The numbers of fry released from hatcheries have been documented (Sharp et al. 2000), but the numbers of wild

Table 4. Original model inputs, and the minimum and maximum values used in the model for sensitivity analyses. Sources of inputs are shown in the footnotes.

Model input	Original	Minimum	Maximum	Source
Duration (d)	93	83	120	a, b
Mortality first 40 d (%)	69.00	62.10	75.90	c
Mortality last 53 d (%)	26.87	24.54	29.13	c
Wild fish survival (%)	7.39	6.65	8.13	d
May temperature (°C)	6	4	8	e, f, g, h
June temperature (°C)	8	6	10	e, f, g, h
July temperature (°C)	10	8	12	e, f, g, h
August temperature (°C)	12	10	14	e, f, g, h
May fish energy content (kJ/g wet weight)	4.171	4.108		a
June fish energy content (kJ/g wet weight)	4.171			a
July fish energy content (kJ/g wet weight)	4.171	3.883		a
August fish energy content (kJ/g wet weight)	4.171			a
Diet energy content (kJ/g wet weight)	multispecies diet	2,045	4,532	see Table 3

[a] Boldt 2001
[b] Cooney and Brodeur 1998
[c] Parker 1966
[d] Sharp et al. 2000
[e] Cooney et al. 1995
[f] Vaughan et al. 2001
[g] T. Weingartner, University of Alaska Fairbanks, personal communication
[h] Royer and Weingartner 2001

fry entering PWS are not well known. To estimate the number of wild fry entering PWS in 1998, wild fish returns in 1999 (9,426,391; estimated using wild stock catch plus the aerial escapement index) were divided by the average survival rate of hatchery fish in that year (7.39%) (Morstad et al. 1996; T. Joyce, Alaska Department of Fish and Game, Cordova, personal communication). The number of wild fry (127,561,263) was added to hatchery fry release numbers (542,383,070) to estimate the total number of fry entering PWS in 1998 (669,944,333). To estimate a range of wild fry numbers that could enter PWS, the marine mortality of wild pink salmon was altered by ±10% to derive populations of 115,964,785 to 141,734,737 (Table 4).

Mortality

A total mortality of 69.00% was used for the first 40 d and 26.87% for the last 53 d. These values are based on mortality estimates from British Columbia (B.C.), since there are no available estimates for PWS. Bella Coola River pink salmon experienced 59.00%–77.00% loss of the initial population in their first 40 d at sea and then lost an average of 0.40%–0.80% of the population per day after that (Parker 1966). Fraser River and central B.C. coastal pink salmon experienced mortalities of 90.00% and 81.00% respectively in their first four months of life at sea (Parker 1966; Walters et al. 1978). Mortality rates of both hatchery and wild fish were varied by ±10% to examine the effects on consumption (Table 4).

Period modeled

The model was initially run for 93 d from May 1 to August 1, 1998. May 1 is the approximate median date that fish are released from PWS hatcheries. Pink salmon were found to move out onto the GOA shelf beginning at least in mid-July, but can still be found near PWS on the shelf in October (Boldt 2001); therefore, August 1 was chosen as an approximate end date of pink salmon residence in PWS. For sensitivity analyses, the number of days modeled was altered by ±10 d (83 and 103 d) to examine the effect on consumption (Table 4). The model was also run for 120 d, the number of days that has been previously reported as the residence time of pink salmon in PWS (Cooney and Brodeur 1998; Table 4). The values used for water temperature, diet of fish, prey energy density, and predator energy density for the three models were the same as those used on day 93 of the original model. The same growth rate utilized in the 93 d model was utilized to estimate a final fish weight for days 83, 103, and 120, as 6.5 g, 14.2 g, and 27.7 g, respectively. A mortality rate of 69.00% was utilized for the first 40 d modeled. A mortality rate of 0.60%/d was utilized after day 40, and resulted in mortality estimates of 22.4%, 31.1%, and 37.8% for days 83, 103, and 120, respectively.

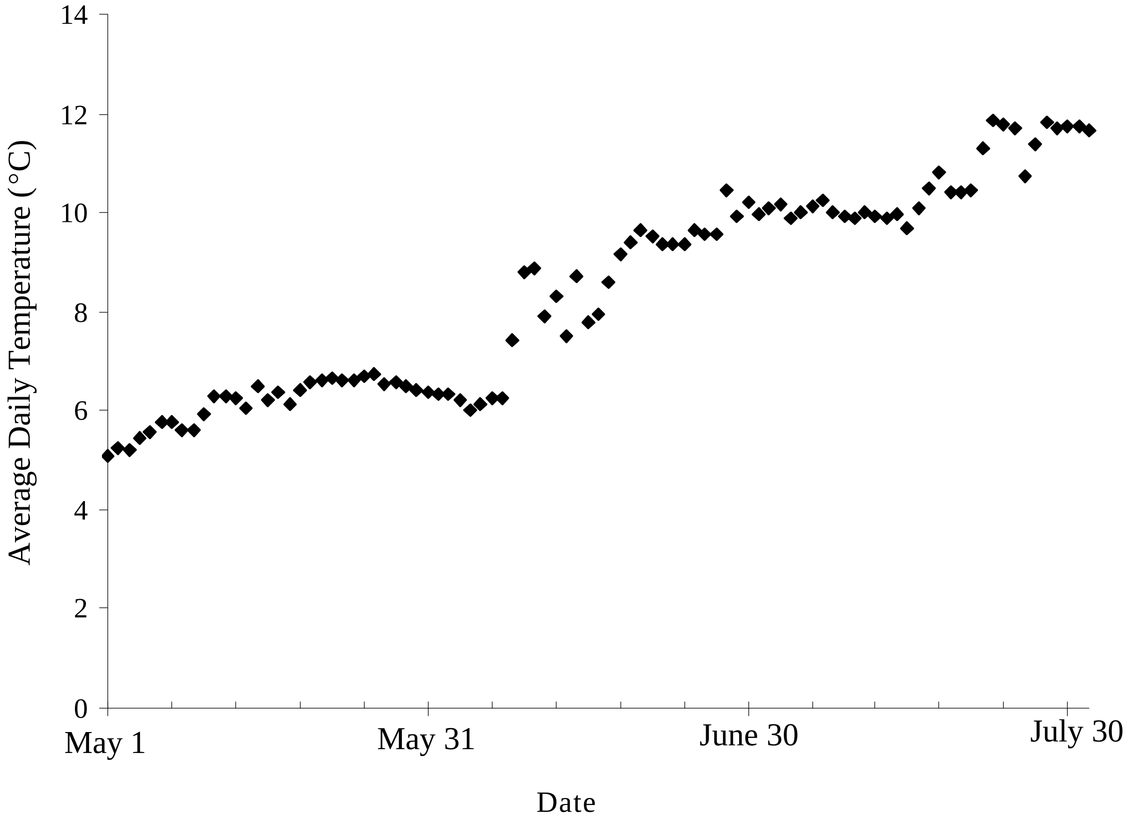

Figure 2. Average daily temperatures at 20 m depth at station GAK 1 in the mouth of Resurrection Bay, north Gulf of Alaska, from May 1 to August 1, 2000. Mooring data provided by T. Weingartner, University of Alaska Fairbanks, personal communication; Royer and Weingartner 2001. <http://www.ims.uaf.edu/gak1/>).

RESULTS

The estimated consumption by a juvenile pink salmon cohort during its first three months at sea was $5.5{\times}10^9$ g wet weight or 27.9 g wet weight of prey per individual fish (Table 5). Large calanoid copepods, larvaceans, and cladocerans comprised the majority of pink salmon prey, representing 40.1%, 24.3%, and 12.5 %, respectively, of the total prey biomass consumed.

The consumption estimate was affected differentially by varying fish diet and fish energy content (Table 5). If pink salmon consumed prey of low energy density, such as barnacle nauplii, consumption estimates increased by 68%, whereas, if pink salmon consumed high energy prey, such as insects, consumption estimates decreased by 28% (Table 5). If pink salmon energy content decreased from 4.1 to 3.9 kJ/g wet weight as was measured at the time of release and in mid-July, the consumption estimate was 4% lower (Table 5).

Varying the temperature regime by ±2°C altered the estimate of consumption. Compared to the original estimates, consumption estimates were 10% higher ($6.1{\times}10^9$ g) for warmer temperatures and 8% lower ($5.1{\times}10^9$ g) for cooler temperatures (Table 5). Utilization of the daily mooring temperature data from GAK 1 in the north GOA resulted in very little change in the original consumption estimate. The consumption estimate based on the mooring temperature data was 2% lower than that of the original model (Table 5). This estimate falls within the range of consumption estimates calculated using the minimum and maximum temperature regimes.

Wild pink salmon consumption represented 27.6% of the consumption in the original model. When wild pink salmon survival was altered by ±10%, the overall consumption in PWS changed by ± 2% (Table 5). Increased fry-to-adult survival rates of wild fish compared to hatchery fish resulted in fewer wild fry entering PWS. Overall consumption by juvenile pink salmon in PWS was, therefore, reduced when fewer wild pink salmon entered PWS (Table 5).

Consumption estimates were strongly affected by changes in the mortality rate of both hatchery and wild

Table 5. Consumption of zooplankton by juvenile pink salmon in Prince William Sound (PWS). Results of sensitivity analyses are shown with both the consumption estimate (*C*) and the percent difference (% D) from the original model. Consumption (*C*) is expressed in 1×10^9 g wet weight and in g C/m^2/yr (C^a and C^b).

Model input varied	Scenario	*C*	% D	C^a	C^b
None	original (93 days)	5.530		0.036	0.985
Duration	83 days	3.860	-30	0.025	0.688
Duration	103 days	7.184	30	0.047	1.280
Duration	120 days (final wt of 27 g)	14.511	162	0.094	2.585
Duration, growth rate	120 days (final wt of 9.6g)	5.615	2	0.036	1.000
Mortality rate	10% higher	4.369	-21	0.028	0.778
Mortality rate	10% lower	6.712	21	0.043	1.196
Wild fry numbers	10% higher	5.435	-2	0.035	0.968
Wild fry numbers	10% lower	5.647	2	0.037	1.006
Temperature	mooring data	5.419	-2	0.035	0.965
Temperature	high temperature regime	6.081	10	0.039	1.083
Temperature	low temperature regime	5.109	-8	0.033	0.910
Energy content	varied energy content	5.316	-4	0.034	0.947
Diet	high calorie diet	3.979	-28	0.026	0.709
Diet	low calorie diet	9.301	68	0.060	1.657

[a] Consumption over entire area of PWS (88×10^8 m^2)
[b] Consumption over a 100 m wide strip along shores of PWS (3.2×10^8 m^2).

pink salmon over the 93 d modeled. Varying the mortality rate of pink salmon by ±10% resulted in a ±21% change in the estimated consumption (Table 5).

Varying pink salmon residence time in PWS also affected consumption estimates. The model was run for 83 d, 103 d, and 120 d, assuming a constant growth rate of 4% body weight per day. Compared to the 93 d model, the consumption estimate for the 83 d model was 30% lower. If pink salmon residence time in PWS was 103 d or 120 d consumption would be 30% or 162% higher, respectively (Table 5).

DISCUSSION

The bioenergetics model has over 25 parameters and input values that could affect the estimates of consumption. In this study, sensitivity analyses on model inputs, such as prey and predator energy content, temperature, pink salmon numbers, mortality, diet, and model duration, resulted in consumption estimates that ranged from –30% to +162% of the original estimate. Altering fish diet, mortality rate, and model duration had the largest effects on the consumption estimates.

Pink salmon consumption estimates reflect seasonal changes in zooplankton composition. Large calanoid copepods were consumed in May whereas in June and July, larvaceans and cladocerans were major components of the diet. Small calanoid copepods comprise the majority of zooplankton numbers and biomass in the upper 50 m of PWS in all months (Cooney et al. 2001). The density and biomass of large calanoid copepods, such as *Neocalanus* spp. and *Calanus marshallae*, increase in May and June, and decrease by July and August, when pteropods, larvaceans, and cladocerans become more important components of the zooplankton (Cooney et al. 2001). Pink salmon diet is affected by these seasonal changes in zooplankton availability as well as by geographic location and year (Willette et al. 1997; Landingham et al. 1998; Boldt 2001) and this alters the estimated consumption of zooplankton. When pink salmon consume low calorie prey items, such as bivalves, barnacles, and amphipods, they must satisfy energetic demands by consuming more prey. When pink salmon consume high energy prey items, such as fish and insects, consumption estimates decrease. A low energy diet resulted in a 68% higher consumption estimate whereas a high energy diet resulted in a 28% lower consumption estimate.

The energy content and condition of juvenile pink salmon can vary geographically (Parker and Massa 1993; Perry et al. 1996; Paul 1997; Boldt 2001); however, there was not enough data available to examine spatial differences in consumption. We used an average pink salmon energy content of 4.171 kJ/g wet weight in the model, a value within the range (3.2–5.2 kJ/g wet weight) found for PWS pink salmon between May 31–June 2 (Paul 1997). Variables known to affect the condition and energy content of fish include temperature, salinity, interspecific and intraspecific competition, and the types of prey consumed (Brett et al. 1969; Smith et al. 1986; Parrish and Mallicoate 1995).

Pink salmon consumption is affected by water temperature (Brett et al. 1969) and zooplankton availability (Cooney et al. 1995). Temperature not only affects the amount of food salmon consume, it also affects their emigration timing from natal streams (Simenstad and Salo 1982; Cooney et al. 1995; Mortensen et al. 2000). During cold years, pink salmon fry emigrate later than in warmer years in PWS (Cooney et al. 1995). The earlier emigration of pink salmon fry in warmer years corresponds closely with the zooplankton peak, which typically occurs in May (Cooney et al. 1995); therefore, temperature determines whether pink salmon enter PWS at a time during peak or declining zooplankton biomass. Varying water temperature in the model changed consumption estimates by –8% to +10 %.

Currents may also affect pink salmon residence time in PWS and, therefore, the final weight of pink salmon and their consumption of zooplankton (Cooney et al. 1981). Longer residence times resulted in a larger final fish weight and an increased consumption by pink salmon. Part of the westward flowing Alaska Coastal Current (ACC) of the north GOA flows into Prince William Sound through Hinchinbrook Entrance and out the southwest part of the sound (Royer et al. 1990; Niebauer et al. 1994). The amount of the ACC entering PWS varies with year and season (Royer et al. 1990). Pink salmon are thought to follow the ACC current; therefore, the amount of flow into and out of PWS may affect pink salmon residence time.

The survival rates of wild pink salmon are difficult to determine, and are probably not the same as for hatchery fish. We back-calculated the number of wild fry entering PWS from the number of returning adults using hatchery survival rates. If wild salmon survival rates were actually higher than those of hatchery salmon, fewer wild salmon would have entered PWS, resulting in decreased consumption estimates. Similarly, changes in mortality within the 93 d model period would also change consumption estimates, with higher mortality rates decreasing consumption estimates.

The model indicates a pink salmon that grows from 0.26 to 9.60 g wet weight in 93 d in PWS would consume 27.9 g of wet weight in prey, an amount less than Cooney's (1993) estimate for pink salmon that reside in PWS for four months (36.4 g). The population consumption estimate in this study ranged from 3.9×10^9 (short residence time in PWS) to 9.3×10^9 (low calorie diet) g wet weight or 0.037–0.089 g C/m^2. Cooney (1993) estimated that consumption by 371 million surviving and 829 million non-surviving salmon would be about 45.9×10^9 g wet weight, which is about five times higher than the estimate in this study.

Disparities between consumption estimates in this study and Cooney's (1993) study are due to differing assumptions made about residence time, pink salmon numbers, mortality, and gross growth efficiencies. Cooney (1993) assumed that pink salmon reside in PWS for 4 months, whereas, in this study, the model was run for only 3 months (93 d). Increasing the residence time of pink salmon in PWS in the bioenergetics model resulted in an increased estimate of consumption, assuming that fish continue to grow at the same rate. If pink salmon resided in PWS for 120 d and grew to 27.67 g, they could potentially consume 162% (14.5×10^9 g wet weight) more zooplankton than if they resided there for 93 d and grew to 9.6 g. This estimate of consumption is 3.3 times lower than Cooney's (1993) estimate.

Cooney (1993) assumed there were 1.2 billion hatchery and wild salmon entering PWS, an estimate almost double the estimate utilized in this study (0.67 billion). Also, Cooney (1993) applied all the mortality at the halfway point of residence time, while the bioenergetics approach used in this study applied a daily mortality. Additionally, the mortality rate used in this study was higher than that of Cooney (1993); he estimated that 62.7% of hatchery fry and 78.0% of wild fry would be lost to predation. The bioenergetics model was run separately for hatchery and wild fish utilizing the same population numbers and mortality estimates as Cooney (1993). The resultant consumption estimate of wild and hatchery fish (initial weight of 0.25 g and final weight of 9.1 g) over 120 d was 17.2×10^9 g wet weight, which is much lower than Cooney's (1993) estimate of 45.9×10^9 g wet weight.

Another source of disparities between the two studies is that Cooney (1993) assumed a gross growth efficiency of 25%, whereas the model used in this study determines consumption based on data input. The advantages of the bioenergetics model over the use of a single gross growth efficiency are that estimates of consumption are calculated on a daily basis, while accounting for water temperature, metabolism, fish weight, prey energy density, fish diet, egestion, and excretion.

The importance of consumption estimates can be appreciated by comparing them to the amount of production that is available. Sanger (1972) estimated that throughout their life cycle, pink salmon consume 1.03% of the annual zooplankton production in the North Pacific. Primary production in a typical nontropical, coastal shelf area, such as PWS, is about 100 to 300 g C/m^2/year (Ryther 1969; Jones 1984; Pauly and Christensen 1995). Assuming a transfer efficiency of 20%, secondary production would be approximately 20 to 60 g C/m^2/year (Jones 1984). This range of values is consistent with estimates of zooplankton production on the GOA shelf and coastal areas of 30–60 g C/m^2/year (Cooney 1988). Consumption by juvenile pink salmon would represent about 0.06 to 0.45% of this gross es-

Table 6. Estimates of zooplankton density (Purcell 2000), standing stock, and pink salmon consumption, assuming the area of Prince William Sound (PWS) is 8.8×10^9 m^2 (Grant and Higgens 1910), and a carbon to wet weight conversion factor of 0.0898 for large calanoid copepods, 0.0949 for amphipods, and 0.0844 for other prey (Omori 1969). Large copepod, amphipod, cladoceran (Boldt 2001), and larvacean (K. Coyle, University of Alaska Fairbanks, personal communication) weights are shown.

Prey	Density (#/m^2)	Wet weight ($\times 10^{-3}$g)	Standing stock (g C/m^2)	Pink salmon consumption (% of standing stock)
Large copepods	265.3928	0.6160	0.0093	1.51
Amphipods	31.8471	0.3910	0.0007	1.90
Cladocerans	7,452.2293	0.0700	0.0297	0.45
Larvaceans	2,813.1635	1.4870	0.2384	0.05

timate of secondary production, depending on residence time and diet in PWS.

A more detailed examination of zooplankton consumption indicates that pink salmon are consuming a small proportion of the available standing stock of cladocerans and larvaceans, but a substantial proportion of the standing stock of large calanoid copepods. Data from vertically hauled bongo net (20 cm diameter, 243 mm mesh) stations where pink salmon were captured were available from July 14–20, 1998 (Purcell 2000; Table 6). Assuming that these plankton samples are representative of typical plankton composition available to the pink salmon, comparisons to the consumption estimates can be made. The average daily consumption of large calanoid copepods during this period was 2.22×10^{-4} g C/m^2, or 1.51% of the large calanoid copepods available (Table 6). If it is assumed the standing stock of large calanoid copepods remains fixed for 10 d, pink salmon could consume about 15% of the available copepods. The average daily consumption was 0.23, 1.97, and 1.63×10^{-4} g C/m^2, representing 1.90%, 0.45%, and 0.05% of the amphipods, cladocerans, and larvaceans, respectively (Table 6). If the standing stocks of these prey groups were fixed over a 10-day period, pink salmon would consume up to 19.10 % of the amphipods, 4.50% of the cladocerans, and 0.46% of the larvaceans. Juvenile coho and chinook salmon on the Washington and Oregon shelf also consumed high percentages of individual prey, such as fish and pteropods (Brodeur et al. 1992).

The estimates of consumption derived here for PWS assume that primary and secondary production and pink salmon are distributed evenly throughout PWS and the time period modeled. However, juvenile pink salmon only reside in PWS for 3 to 4 months and they may not be using the entire sound since aggregations of juveniles are found in bays and nearshore areas (Cooney et al. 1978). The concentration of fish in nearshore areas may result in localized depletion of food resources, and alter the amount of energy consumed by pink salmon (Cooney et al. 1978; Paul 1997). The zooplankton samples taken in PWS were integrated from 60 m depth to the surface and collected at night, whereas, the pink salmon were collected in the day. It is likely that not all zooplankton were available to the juvenile pink salmon since juvenile salmon are thought to occupy surface waters (Moulton 1997). Water column structure may also determine the availability of zooplankton to pink salmon. In areas of strong stratification, zooplankton may be concentrated in the upper layer and, therefore, be available to pink salmon. In areas of weak stratification, zooplankton may be more evenly distributed in the water column and hence less available to pink salmon juveniles. If pink salmon reside in only a 100 m wide area along the shorelines of PWS, an area of 3.2×10^8 m^2 (Cooney et al. 1978), the proportion of zooplankton they consume would be considerably higher, 1.15% to 8.28% of the secondary production within that area.

To determine if pink salmon have reached the carrying capacity of PWS, local processes that affect zooplankton and fish distribution, as well as the presence of potential competitors would need to be considered. For example, other zooplanktivores, such as sand lance, herring, juvenile walleye pollock, juvenile chum and sockeye salmon, and jellyfish in PWS occupy the same areas at comparable times and consume similar prey as juvenile pink salmon (Boldt 1997; Landingham et al. 1998; Mabry 2000; Purcell and Sturdevant 2001; Cooney et al. 2001). The energy content of both herring and pink salmon can vary among locations within PWS, indicating that growth conditions vary geographically (Boldt 2001; Norcross et al. 2001). Fish planktivory, zooplankton availability, and water column structure may result in food limitation in local bays reducing the growth and survival of pink salmon resulting in poor fish condition and low energy content (Cooney et al. 1981; Paul 1997).

Planktivory in the open ocean rather than in coastal areas could have resulted in the observed decrease in salmon body weight after the mid-1970s regime shift. Cooney and Brodeur (1998) estimated that pink salmon consumption increased three-fold after 1988 (from pre-1976 conditions) and most consumption took place in the open ocean. There is some evidence that planktivory by pink salmon can affect zooplankton abundance in the subarctic North Pacific (Shiomoto et al. 1997). Additionally, Russian sockeye salmon were smaller in years when pink salmon were abundant, suggesting competition for zooplankton resources can occur in the open ocean (Bugaev et al. 2001). Also, decreased food availability in combination with the higher sea surface temperatures of this period may have affected the growth rate of the salmon. Brett et al. (1969) observed that optimal sockeye salmon growth occurred at lower temperatures combined with lower food rations. Higher temperatures after the regime shift may have caused increased metabolism and energy requirements of salmon and, therefore, decreased weight of the salmon, despite increased zooplankton biomass.

This study indicates that juvenile pink salmon did not consume a large proportion of zooplankton biomass or production in PWS. Even when the model input data was varied, pink salmon consumption represented only a minor proportion of the available zooplankton. If standing stocks of zooplankton are assumed to be fixed over periods of 10 days, however, consumption by juvenile pink salmon could represent a substantial portion (up to 19%) of some zooplankton, such as large calanoid copepods and amphipods. When examining carrying capacity, consumption by pink salmon needs to be considered along with other planktivores and geographic and interannual variability in zooplankton biomass and productivity, since pink salmon represent only one, albeit important, component of the PWS ecosystem.

LITERATURE CITED

Anderson, P. J., and J. F. Piatt. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Marine Ecological Progress Series 189:117–123.

Beamish, R. J. 1993. Climate and exceptional fish production off the west coast of North America. Canadian Journal of Fisheries and Aquatic Sciences 50:2270–2291.

Beamish, R. J., and D. R. Bouillon. 1993. Pacific salmon production trends in relation to climate. Canadian Journal of Fisheries and Aquatic Sciences 50:1002–1016.

Beamish, R. J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Progress in Oceanography 49:423–437.

Beamish, R. J., C. Mahnken, and C. M. Neville. 1997. Hatchery and wild production of Pacific salmon in relation to large-scale, natural shifts in the productivity of the marine environment. International Council for the Exploration of the Sea Journal of Marine Science 54:1200–1215.

Beamish, R. J., B. E. Riddell, C. M. Neville, B. L. Thomson, and Z. Zhang. 1995. Declines in chinook salmon catches in the Strait of Georgia in relation to shifts in the marine environment. Fisheries Oceanography 4(3):243–256.

Bigler, B. S., D. W. Welch, and J. H. Helle. 1996. A review of size trends among North Pacific salmon (*Oncorhynchus* spp.). Canadian Journal of Fisheries and Aquatic Sciences 53:455–465.

Blackbourn, D. J. 1989. Comparison of release size and environmental data with the marine survival rates of some wild and enhanced stocks of pink and chum salmon in British Columbia and Washington State. Pages 82–87 *in* P. A. Knudsen, editor. 14th Northeast Pacific Pink and Chum Salmon Workshop. February 22–24 1989, Port Ludlow Resort, Washington State Department of Fisheries.

Boldt, J. L. 1997. Condition and distribution of forage fish in Prince William Sound, Alaska. Master's thesis, University of Alaska Fairbanks.

Boldt, J. L. 2001. Ecology of juvenile pink salmon in the North Gulf of Alaska and Prince William Sound. Doctoral dissertation, University of Alaska Fairbanks.

Boldt, J. L., and L. J. Haldorson. *In press*. Seasonal and geographic variation of juvenile pink salmon diets in the North Gulf of Alaska and Prince William Sound. Transactions of the American Fisheries Society.

Brett, J. R., J. E. Shelbourn, and C. T. Shoop. 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncoryhnchus nerka*, in relation to temperature and ration size. Journal of Fisheries Research Board of Canada 26:2363–2394.

Brodeur, R. D., R. C. Francis, and W. G. Pearcy. 1992. Food consumption of juvenile coho (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) on the continental shelf off Washington and Oregon. Canadian Journal of Fisheries and Aquatic Sciences 49:1670–1685.

Brodeur, R. D., and D. M. Ware. 1992. Long-term variability in zooplankton biomass in the subarctic Pacific Ocean. Fisheries Oceanography 1(1):32–37.

Bugaev, V. F., D. W. Welch, M. M. Selifonov, L. E. Grachev, and J. P. Eveson. 2001. Influence of the marine abundance of pink (*Oncorhynchus gorbuscha*) and sockeye salmon (*O. nerka*) on growth of Ozernaya River sockeye. Fisheries Oceanography 10(1):26–32.

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

Cooney, R. T. 1988. Distribution and ecology of zooplankton in the Gulf of Alaska: A synopsis. Pages 27–41 *in* T. Nemoto and W. G. Pearcy, editors. The Biology of the subarctic Pacific—Part I. No. 26. Ocean Research Institute, University of Tokyo, Japan.

Cooney, R. T. 1993. A theoretical evaluation of the carrying capacity of Prince William Sound, Alaska, for juvenile Pacific salmon. Fisheries Research 18:77–87.

Cooney, R. T., J. R. Allen, M. A. Bishop, D. L. Eslinger, T. Kline, B. L. Norcross, C. P. McRoy, J. Milton, J. Olsen, V. Patrick, A. J. Paul, D. Salmon, D. Scheel, G. L. Thomas, S. L. Vaughan, and T. M. Willette. 2001. Ecosystem controls of juvenile pink salmon (*Oncorhynchus gorbuscha*) and Pacific herring (*Clupea pallasi*) populations in Prince William Sound, Alaska. Fisheries Oceanography 10 (Suppl. 1):1–13.

Cooney, R. T., and R. D. Brodeur. 1998. Carrying capacity and North Pacific salmon production: stock-enhancement implications. Bulletin of Marine Science 62(2):443–464.

Cooney, R. T., K. O. Coyle, E. Stockmar, and C. Stark. 2001. Seasonality in surface-layer net zooplankton communities in Prince William Sound, Alaska. Fisheries Oceanography 10 (Suppl. 1):97–109.

Cooney, R. T., D. Urquhart, and D. Barnard. 1981. The behaviour, feeding biology, and growth of hatchery released pink and chum salmon fry in Prince William Sound, Alaska. Alaska Sea Grant College Program, Report 81-5, University of Alaska Fairbanks.

Cooney, R. T., D. Urquhart, R. Neve, J. Hilsinger, R. Clasby, and D. Barnard. 1978. Some aspects of the carrying capacity of Prince William Sound, Alaska for hatchery released pink and chum salmon fry. Alaska Sea Grant College Program, Report 78-4, University of Alaska Fairbanks.

Cooney, R. T., T. M. Willette, S. Sharr, D. Sharp, and J. Olsen. 1995. The effect of climate on North Pacific pink salmon (*Oncorhynchus gorbuscha*) production: examining some details of a natural experiment. Pages 475–482 *in* R. J. Beamish, editor. Climate change and northern fish populations. Canadian Special Publication of Fisheries and Aquatic Sciences 121.

Coronado, C., and R. Hilborn. 1998. Spatial and temporal factors affecting survival in coho and fall chinook salmon in the Pacific Northwest. Bulletin of Marine Science 62(2):409–125.

Cummins, K. W., and J. C. Wuychek. 1971. Caloric equivalents for investigations in ecological energetics. Mitteilungen–Internationale Vereinigung für Theoretische und Angewandte Limnologie 18:1–158.

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. North Pacific Anadromous Fish Commission Bulletin No. 1:146–162.

Dawirs, R. R., C. Puschel, and F. Schorn. 1986. Temperature and growth in *Carcinus maenas* L. (Decapoda: Portunidae) larvae reared in the laboratory from hatching through metamorphosis. Journal of Experimental Marine Biology and Ecology 100:47–74.

Donaldson, W., S. Morstad, D. Sharp, J. Wilcock, and S. Sharr. 1995. Prince William Sound management area 1994 annual finfish management report. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report No. 2A95-47, Anchorage.

Eslinger, D. L., R. T. Cooney, C. P. McRoy, A. Ward, T. C. Kline Jr., E. P. Simpson, J. Wang, and J. R. Allen. 2001. Plankton dynamics: observed and modeled responses to physical conditions in Prince William Sound, Alaska. Fisheries Oceanography 10(Suppl. 1):81–96.

Gargett, A. E. 1997. The optimal stability 'window': a mechanism underlying decadal fluctuations in North Pacific salmon stocks? Fisheries Oceanography 6(2):109–117.

Gilhousen, P. 1962. Marine factors affecting the survival of Fraser River pink salmon. Pages 203–210 *in* N. J. Wilimovsky, editor. Symposium on pink salmon. Institute of Fisheries, University of British Columbia, Vancouver.

Grant, U. S., and D. F. Higgens. 1910. Reconnaissance of the geology and mineral resources of Prince William Sound, Alaska. U.S. Geological Survey Bulletin B0443.

Gray, D., D. Ashe, J. Johnson, R. Merizon, and S. Moffit. 2002. Prince William Sound management area 2001 annual finfish management report. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report No. 2A02-20, Anchorage.

Griffiths, D. 1977. Caloric variation in animals. Journal of Animal Ecology 46:593–605.

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

Harris, R. K. 1985. Body composition (carbon, nitrogen, and calories) and energetics of immature walleye pollock, *Theragra chalcogramma* (Pallas), in the southeast Bering Sea. Master's thesis, University of Alaska Fairbanks.

Healey, M. C. 1991. Diets and feeding rates of juvenile pink, chum, and sockeye salmon in Hecate Strait, British Columbia. Transactions of the American Fisheries Society 120:303–318.

Hilborn, R., and D. Eggers. 2000. A review of the hatchery programs for pink salmon in Prince William Sound and Kodiak Island, Alaska. Transactions of the American Fisheries Society 129:333–350.

Hollowed, A. B., and W. S. Wooster. 1992. Variability of winter ocean conditions and strong year classes of Northeast Pacific groundfish. International Council for the Exploration of the Sea Marine Science Symposium 195:433–444.

Johnson, J., D. Sharp, T. Joyce, and S. Moffit. 2002. Prince William Sound management area 2000 annual finfish management report. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report No. 2A02-02, Anchorage.

Jones, R. 1984. Some observations on energy transfer through the North Sea and Georges Bank food webs. Rapports et procès-verbaux des réunions/Commission internationale pour l'exploration scientifique de la Mer méditerranée 183:204–217.

Karpenko, V. I. 1998. Ocean mortality of Northeast Kamchatka pink salmon and influencing factors. North Pacific Anadromous Fish Commission Bulletin 1:251–261.

Kitchell, J. F., D. J. Stewart, and D. Weininger. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). Journal of Fisheries Research Board of Canada 34:1922–1935.

Kline, T. C. Jr. 1999. Temporal and spatial variability of 13C/12C and 15N/14N in pelagic biota of Prince William Sound, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 56(Suppl. 1):94–117.

Kosobokova, K. N. 1980. Caloric values of some zooplankton representatives from the Central Arctic Basin and the White Sea. Oceanology 20:84–89.

Landingham, J. H., M. V. Sturdevant, and R. D. Brodeur. 1998. Feeding habits of juvenile Pacific salmon in marine waters of southeastern Alaska and northern British Columbia. Fishery Bulletin 96:285–302.

LeBrasseur, R. J., and R. R. Parker. 1964. Growth rate of central British Columbia pink salmon (*Oncorhynchus gorbuscha*). Journal of Fisheries Research Board of Canada 21(5):1101–1128.

Mabry, J. 2000. Condition and food availability to Pacific sand lance (*Ammodytes hexapterus*) in Prince William Sound, Alaska. Master's thesis, University of Alaska Fairbanks.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78:1069–1079.

McLain, D. R. 1984. Coastal ocean warming in the Northeast Pacific, 1976–83. Pages 61–85 *in* W. G. Pearcy, editor. The influence of ocean conditions on the production of salmonids of the North Pacific. Oregon State University Sea Grant College Program ORESU-W-83-001.

McGowan, J. A., D. R. Cayan, and L. M. Dorman. 1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. Science 281:210–217.

Morstad, S., D. Sharp, J. Wilcock, and J. Johnson. 1996. Prince William Sound management area 1995 annual finfish management report. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report No. 2A96-25, Anchorage.

Morstad, S., D. Sharp, J. Wilcock, and J. Johnson. 1997. Prince William Sound management area 1996 annual finfish management report. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report No. 2A97-17, Anchorage.

Morstad, S., D. Sharp, J. Wilcock, T. Joyce, and J. Johnson. 1998. Prince William Sound management area 1997 annual finfish management report. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report No. 2A98-05, Anchorage.

Morstad, S., D. Sharp, J. Wilcock, T. Joyce, and J. Johnson. 1999. Prince William Sound management area 1998 annual finfish management report. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report No. 2A99-20, Anchorage.

Mortensen, D., A. Wertheimer, S. Taylor, J. Landingham. 2000. The relation between early marine growth of pink salmon, *Oncorhynchus gorbuscha*, and marine water temperature, secondary production, and survival to adulthood. Fishery Bulletin 98:319–335.

Moulton, L. L. 1997. Early marine residence, growth, and feeding by juvenile salmon in Northern Cook Inlet, Alaska. Alaska Fishery Research Bulletin 4(2):154–177.

Niebauer, H. J., T. C. Royer, and T. J. Weingartner. 1994. Circulation of Prince William Sound, Alaska. Journal of Geophysical Research 99(C7):14,113–14,126.

Norcross, B. L., E. D. Brown, R. J. Foy, M. Frandsen, S. M. Gay, T. C. Kline Jr., D. M. Mason, E. V. Patrick, A. J. Paul, and K. D. E. Stokesbury. 2001. A synthesis of the life history and ecology of juvenile Pacific herring in Prince William Sound, Alaska. Fisheries Oceanography 10 (Suppl.1):42–57.

Norrbin, F., and U. Bamstedt. 1984. Energy contents in benthic and planktonic invertebrates of Kosterfjorden, Sweden. A comparison of energetic strategies in marine organism groups. Ophelia 23(1):47–64.

Omori, M. 1969. Weight and chemical composition of some important oceanic zooplankton in the North Pacific Ocean. Marine Biology 3:4–10.

Parker, R. R. 1966. Marine mortality schedules of pink salmon of the Bella Coola River, central British Columbia. Journal of Fisheries Research Board of Canada 25(4):757–794.

Parker, D., and J. Massa. 1993. A comparison of diets and apparent growth rates for juvenile pink and chum salmon collected in Prince William Sound, Alaska. Pages 1–16 *in* Proceedings of the 16th Northeast Pacific pink and chum salmon workshop, Juneau, Alaska, February 24–26, 1993. Alaska Sea Grant College Program, Report 94-02, University of Alaska Fairbanks.

Parrish, R. H., and D. L. Mallicoate. 1995. Variation in the condition factors of California pelagic fishes and associated environmental factors. Fisheries Oceanography 4(2):171–190.

Paul, A. J. 1997. The use of bioenergetic measurements to estimate prey consumption, nutritional status and thermal habitat requirements for marine organisms reared in the sea. Bulletin of the National Research Institute of Aquaculture, Supplement 3:59–68.

Pauly, D., and V. Christensen. 1995. Primary production required to sustain global fisheries. Nature 374:255–257.

Perry, R. I., N. B. Hargreaves, B. J. Waddell, and D. L. Mackas. 1996. Spatial variations in feeding and condition of juvenile pink and chum salmon off Vancouver Island, British Columbia. Fisheries Oceanography 5(2):73–88.

Peterman, R. M. 1987. Review of the components of recruitment of Pacific salmon. American Fisheries Society Symposium 1:417–429.

Polovina, J. J., G. T. Mitchum, and G. T. Evans. 1995. Decadal and basin-scale variation in mixed layer depth and the impact on biological production in the Central and North Pacific, 1960–88. Deep Sea Research 42(10):1701–1716.

Pritchard, A. L. 1944. Physical characteristics and behaviour of pink salmon fry at McClinton Creek, B.C. Journal of Fisheries Research Board of Canada 6(3):217–227.

Purcell, J. E. 2000. Jellyfish as competitors and predators of fishes. *Exxon Valdez* Oil Spill Restoration Project Final Report, Restoration project 99163S, Anchorage.

Purcell, J. E., and M. V. Sturdevant. 2001. Prey selection and dietary overlap among zooplanktivorous jellyfish and juvenile fishes in Prince William Sound, Alaska. Marine Ecology Progress Series 210:67–83.

Ricker, W. E. 1995. Trends in the average size of Pacific salmon in Canadian catches. Pages 593–602 *in* R. J. Beamish, editor. Climate change and northern fish populations. Canadian Special Publication of Fisheries and Aquatic Sciences 121.

Royer, T. C., and T. Weingartner. 1999. Coastal hydrographic responses in the northern Gulf of Alaska to the 1997–98 ENSO event *in* H. Freeland, J. Peterson, W. Thornton, and A. Tyler (editors). Proceedings of the 1998 science board symposium on the impacts of the 1997/98 El Nino event on the North Pacific Ocean and its marginal seas. North Pacific Marine Science Organization (PICES) Scientific Report No. 10:89–92.

Royer, T. C., J. A. Vermersch, T. J. Weingartner, H. J. Niebauer, and R. D. Muench. 1990. Ocean circulation influencing the *Exxon Valdez* oil spill. Oceanography, November 1990:3–10.

Royer, T. C., and T. J. Weingartner. 2001. University of Alaska Fairbanks GAK1 Time series. <http://www.ims.uaf.edu/gak1/>. Accessed August 15, 2001.

Ryther, J. H. 1969. Photosynthesis and fish production in the sea. Science 166:72–76.

Sanger, G. A. 1972. Fishery potentials and estimated biological productivity of the subarctic Pacific region. Pages 561–574 *in* A. Y. Takenouti, editor. Biological oceanography of the northern Pacific Ocean. Idemitsu Shoten, Tokyo, Japan.

Sharp, D., T. Joyce, J. Johnson, S. Moffitt, and M. Willette. 2000. Prince William Sound management area 1999 annual finfish management report. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report No. 2A00-32, Anchorage.

Shiomoto, A., K. Tadokoro, K. Nagasawa, and Y. Ishida. 1997. Trophic relations in the subarctic North Pacific ecosystem: possible feeding effect from pink salmon. Marine Ecology Progress Series 150:75–85.

Simenstad, C. A., and E. O. Salo. 1982. Foraging success as a determinant of estuarine and nearshore carrying capacity of juvenile chum salmon (*Oncorhynchus keta*) in Hood Canal, Washington. Pages 21–37 *in* G. R. Melteff and R. A. Neve, editors. Proceedings of the North Pacific Aquaculture Symposium, Alaska Sea Grant Report 82-2, University of Alaska Fairbanks.

Smith, R. L., A. J. Paul, and J. M. Paul. 1986. Effect of food intake and temperature on growth and conversion efficiency of juvenile pollock (*Theragra chalcogramma* (Pallas)): a laboratory study. Journal du conseil/Conseil international pour l'exploration de la mer 42:2412–53.

Thayer, G. W., W. E. Schaaf, J.W. Angelovic, and M. W. LaCroix. 1973. Caloric measurements of some estuarine organisms. Fishery Bulletin 71(1):289–296.

Vaughan, S. L., C. N. K. Mooers, S. M. Gay III. 2001. Physical variability in Prince William Sound during the SEA Study (1994–98). Fisheries Oceanography 10(Suppl. 1):58–80.

Venrick, E. L., J. A. McGowan, D. R. Cayan, and T. L. Hayward. 1987. Climate and chlorophyll a: long-term trends in the Central North Pacific Ocean. Science 238:70–72.

Walters, C. J., R. Hilborn, R. M. Peterman, and M. J. Staley. 1978. Model for examining early ocean limitation of Pacific salmon production. Journal of Fisheries Research Board of Canada 35:1303–1315.

Willette, T. M. 2001. Foraging behaviour of juvenile pink salmon (*Oncorhynchus gorbuscha*) and size-dependent predation risk. Fisheries Oceanography 10(Suppl. 1):110–131.

Willette, T. M., G. Carpenter, P. Shields, and S. R. Carlson. 1994. Early marine salmon injury assessment in Prince William Sound, *Exxon Valdez* Oil Spill state/federal natural resource damage assessment final report (Fish/Shellfish Study Number 4A), Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, Cordova.

Willette, T. M., M. V. Sturdevant, and S. Jewett. 1997. Prey resource partitioning among several species of forage fishes in Prince William Sound. Alaska Sea Grant College Program, Report 97-01, University of Alaska Fairbanks.

Appendix A. Model equations and notations as written in the Fish Bioenergetics 3.0 for Windows manual (Hanson et al. 1997). The parameter values, notations, and definitions are described in Appendix B.

The basic bioenergetics formula is:

$$C = (R + A + S) + (F + U) + (\Delta B + G)$$

$\Delta B =$ somatic growth

The formulae for consumption are:

$$C = C_{\max} \times p \times f(T)$$
$$C_{\max} = CA \times W^{CB}$$
$$f(T) = K_A \times K_B$$
$$K_A = (CK1 \times L1)/(1 + CK1(L1 - 1))$$
$$L1 = e^{[G1(T - CQ)]}$$
$$G1 = (1/(CTO - CQ)) \times \ln\left((0.98 \times (1 - CK1))/(CK1 \times 0.02)\right)$$
$$K_B = (CK4 \times L2)/(1 + CK4(L2 - 1))$$
$$L2 = e^{[G2(CTL - T)]}$$
$$G2 = (1/(CTL - CTM)) \times \ln\left((0.98 \times (1 - CK4))/(CK4 \times 0.02)\right)$$

The formulae for respiration are:

$$R = RA \times W^{RB} \times f(T) \times ACTIVITY$$
$$S = SDA(C - F)$$
$$f(T) = e^{(RQ \times T)}$$
$$ACTIVITY = e^{(RTO \times VEL)}$$
$$VEL = Act \times W^{RK4} \times e^{(BACT \times T)},$$
$$\text{when}$$
$$T \le RTL$$

The formulae for egestion and excretion are:

$$F = PF \times C$$
$$U = UA \times T^{UB} \times e^{(UG \times p)} \times (C - F)$$
$$PF = ((PE - 0.1)/0.9) \times (1 - PFF) + PFF$$
$$PE = FA \times T^{FB} \times e^{FG \times p}$$
$$PFF = \sum (PREY[n] \times DIET[n])$$

Appendix B. Values of parameters used in the bioenergetics model. The notation, definitions, and values are presented as in the Fish Bioenergetics 3.0 for Windows manual (Hanson et al. 1997).

Symbol	Definition	Value
	CONSUMPTION	
C	specific consumption rate (g/g/d)	
C_{max}	maximum specific feeding rate (g/g/d)	
p	proportion of maximum consumption	
f(T)	temperature dependence function	
T	water temperature (°C)	
W	fish weight (g)	
CA	intercept of the allometric mass function	0.303
CB	slope of the allometric mass function	-0.275
CQ	temperature corresponding to a small fraction of maximum consumption rate	3
CTO	temperature corresponding to 0.98 of maximum consumption rate	20
CTM	temperature (>*CTO*) corresponding to 0.98 of maximum consumption rate	20
CTL	temperature corresponding to reduced fraction of maximum consumption rate	24
*CK*1	proportion of maximum consumption at *CQ*	0.58
*CK*4	proportion of maximum consumption at *CTL*	0.5
	RESPIRATION	
R	specific rate of respiration (g/g/d)	
RA	intercept of the allometric mass function (g/g/d)	0.00143
RB	slope of the allometric mass function	-0.209
RQ	approximation of Q10	0.086
RTO	coefficient of R as a function of swimming speed	0.0234
RTL	temperature, above which activity relationship changes	25
*RK*4	coefficient of swimming speed as a function of weight	0.13
ACT	activity multiplier (intercept cm/s)	9.9
BACT	coefficient of swimming speed as a function of temperature	0.0405
S	proportion of assimilated energy lost to specific dynamic action	
SDA	specific dynamic action	0.172
	EGESTION/EXCRETION	
F	specific egestion rate (g/g/d)	
FA	intercept of proportion egested as a function of temperature and ration	0.212
FB	coefficient of water temperature dependence of egestion	-0.222
FG	coefficient of *p*-value as a function of egestion	0.631
UA	intercept of proportion excreted as a function of temperature and ration	0.0314
UB	coefficient of water temperature dependence of excretion	0.58
UG	coefficient of *p*-value as a function of excretion	-0.299
PREY[n]	proportion of indigestible nth prey	
DIET[n]	proportion of *n*th prey in diet	