

## Juvenile chum salmon consumption of zooplankton in marine waters of southeastern Alaska: a bioenergetics approach to implications of hatchery stock interactions

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*Key words:* bioenergetics, hatchery interactions, juvenile chum salmon, southeastern Alaska, zooplankton consumption

### Abstract

Bioenergetics modeling was used to estimate zooplankton prey consumption of hatchery and unmarked stocks of juvenile chum salmon (*Oncorhynchus keta*) migrating seaward in littoral (nearshore) and neritic (epipelagic offshore) marine habitats of southeastern Alaska. A series of model runs were completed using biophysical data collected in Icy Strait, a regional salmon migration corridor, in May, June, July, August, and September of 2001. These data included: temperature (1-m surface versus surface to 20-m average), zooplankton standing crop (surface to 20-m depth versus entire water column), chum salmon diet (percent weight of prey type consumed), energy densities, and weight. Known numbers of hatchery releases were used in a cohort reconstruction model to estimate total abundance of hatchery and wild chum salmon in the northern

region of southeastern Alaska, given average survival to adults and for two different (low and high) early marine littoral mortality rate assumptions. Total prey consumption was relatively insensitive to temperature differences associated with the depths potentially utilized by juvenile chum salmon. However, the magnitudes and temporal patterns of total prey consumed differed dramatically between the low and high mortality rate assumptions. Daily consumption rates from the bioenergetics model and CPUE abundance from sampling in Icy Strait were used to estimate amount and percentage of zooplankton standing crop consumed by mixed stocks of chum salmon. We estimated that only a small percentage of the available zooplankton was consumed by juvenile chum salmon, even during peak abundances of marked hatchery and unmarked mixed stocks in July. Total daily consumption of zooplankton by all stock groups of juvenile chum salmon was estimated to be between 330 and 1764 g/km<sup>2</sup> d<sup>-1</sup> from June to September in the neritic habitat of Icy Strait. As with any modeling exercise, model outputs can be misleading if input parameters and underlying assumptions are not valid; therefore, additional studies are warranted, especially to determine physiological input parameters, and to improve abundance and mortality estimates specific to juvenile chum salmon. Future bioenergetics modeling is also needed to evaluate consumption by the highly abundant, vertically migrating planktivorous that co-occurred in our study; we suggest that these fishes have a greater impact on the zooplankton standing crop in Icy Strait than do hatchery stock groups of juvenile chum salmon.

## Introduction

Interactions between hatchery and other stocks of Pacific salmon (*Oncorhynchus* spp.) in marine environs are important to identify, particularly when regional salmon production approaches historically high levels. Hatchery production of chum salmon (*O. keta*), a principal salmon species in southeastern Alaska, reached record levels in the 1990s (McNair, 2002), nearly doubling the historic highs within the past century (Hienl et al., 2003). In recent years (1994–2002), commercial chum salmon harvests in southeastern Alaska have averaged 12.3 million fish that are valued at more than 27 million; hatchery fish comprised 77% of this harvest (ADFG, 2003). Despite increased hatchery production of chum salmon in the past decade, information on the degree of competitive or other interactions among marked hatchery and mixed stocks (including wild and unmarked hatchery) of juvenile salmon is rare, and consequently, estimation of the actual marine carrying capacity of salmon in specific habitats is not possible.

Understanding marine carrying capacity for salmon requires an assessment of biophysical parameters important to the fish within a particular habitat, and the incorporation of these parameters into production estimates in the context of energetics. An energetics-based approach focuses on the processes that regulate fish growth (Kitchell et al., 1977). For every organism, energy

acquired through ingestion must be used in metabolic processes, lost into wastes, or synthesized into new tissue (Adams and Breck, 1990). Bioenergetic modeling incorporates the rates of energy intake, transformation, loss, and use as functions of an organism (Brett and Groves, 1979) and provides a means of relating growth and feeding rates to environmental conditions, thus giving insight to causal relationships among variables (Allen and Wootton, 1982).

Bioenergetics modeling is a mass balance approach to an energy budget that provides a useful framework for identifying how consumption, growth, and physiological parameters of an organism relate to the biophysical parameters of its environment. The bioenergetics approach has primarily been used to estimate prey consumption by an entire predator population, usually under a variety of different biophysical scenarios to determine model sensitivity. In fisheries, a common usage of this bioenergetics approach is to quantify predator trophic demand on the prey resource (Ney, 1990). Studies using the bioenergetics model have focused on prey consumption by salmonids in Alaska lakes (Ruggerone and Rodgers, 1992; Cartwright et al., 1998) or estuarine and oceanic habitats (Brodeur et al., 1992; Boldt and Haldorson, 2002). In this paper, we use the bioenergetics approach to examine zooplankton consumption by juvenile chum salmon stock groups in the context of hatchery interactions.

In order to help identify stock groups of salmon, an otolith marking technique was recently developed by varying incubation water temperature over time, thereby inducing a series of unique banding patterns on the otoliths of the developing fish (Brothers, 1990; Volk et al., 1990). Implementation of this marking technique, and its application on a mass-marking scale, has enabled individual hatchery stock groups to be marked in southeastern Alaska (Munk et al., 1993). Otolith thermal marking affords an unprecedented opportunity to examine stock-specific characteristics of hatchery juvenile salmon as they interact with other stocks during their early marine life history. For example, two hatcheries in southeastern Alaska each uniquely thermally marked 100% of their juvenile chum salmon in 2001, which represented half of the total hatchery production for this species in the entire region (McNair, 2002). Consequently, stock-specific occurrence and growth of marked hatchery stocks that are recovered can be combined with a bioenergetics approach to assess the demands of increased hatchery production on the total carrying capacity of the marine ecosystem.

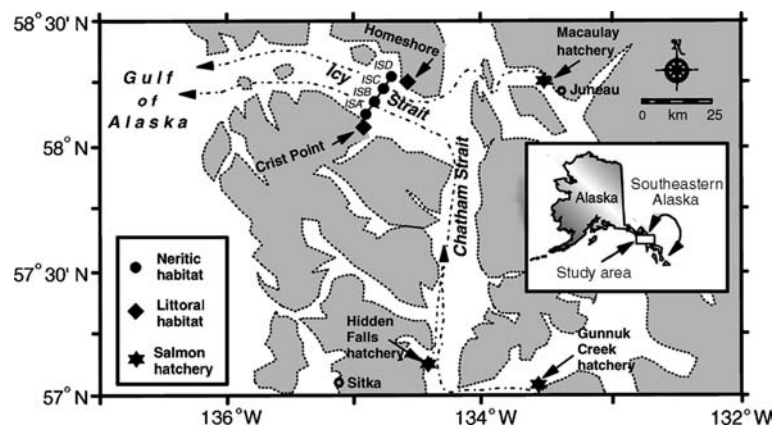
We used the Wisconsin Bioenergetics Model 3.0 (Hanson et al., 1997) to estimate zooplankton consumption by juvenile chum salmon stocks during their early marine residency period in the marine waters of the northern region of southeastern Alaska. Our study has two main objectives: (1) to determine total zooplankton consumption by hatchery and wild chum salmon

using abundance estimates derived from cohort reconstruction under two different initial marine mortality rates and two thermal regimes, and across littoral and neritic habitats during the salmon's first 5 months in the entire northern region, and (2) to apply the maximum zooplankton consumption estimates of three chum salmon stock groups (two hatchery and an unmarked mixed stock group) from the neritic habitat at four monthly time periods to determine the percentage of the available standing crop of zooplankton consumed in the upper 20-m depth versus the entire water column of Icy Strait.

## Materials and methods

### *Study locality and time frame*

Juvenile chum salmon and associated biophysical data were collected in marine waters of Icy Strait, located in the northern region of southeastern Alaska, from May to September in 2001 (Figure 1). This strait is the sole seaward migration corridor for juvenile salmonids within the northern region. Upon migration, juvenile salmon from the inside waters of the northern region funnel from Chatham Strait westward through Icy Strait and out into the Gulf of Alaska. Icy Strait is relatively shallow marine habitat (depths to 250 m) compared to Chatham Strait (depths to 700 m) to the east or to the Gulf of Alaska (depths >1000 m) to the west. Icy Strait extends 80 km between these two



*Figure 1.* Habitats sampled within the Icy Strait study area of the marine waters of the northern region of southeastern Alaska, May, June, July, August, and September 2001. Three primary chum salmon hatcheries in the region are identified (Macaulay, Hidden Falls, and Gunnuk Creek). Principal migration routes to the Gulf of Alaska are indicated with dashed lines.

hydrographic regimes, averages about 12–13 km in width, and covers an area of approximately 1000 km<sup>2</sup>.

We set up a transect line across Icy Strait to representatively sample two marine habitats, littoral and neritic. The littoral habitat was defined as the nearshore waters over the beach between low and high tide. This habitat was located at the opposing shorelines of the transect line; chum salmon were caught with beach seines in the littoral habitat off of Crist Point and Homeshore during late May. The neritic habitat was defined as the shallow epipelagic zone overlying the continental shelf (waters <200 m in depth) associated with the coast. This habitat was represented by four sampling stations along the transect line; chum salmon were caught in a surface trawl at stations ISA, ISB, ISC, ISD during four near-monthly intervals from late June to late September. Each trawling station was 3.2 or 6.4 km offshore and over water depths of 128–234 m.

#### *Hatchery chum salmon releases and marine distribution*

We chose three stock groups of chum salmon to represent the hatchery stock component migrating through the northern region of southeastern Alaska in 2001 (Figure 1). These three hatchery

stocks represent more than 99% of the hatchery chum released within 200 km of Icy Strait. Of these hatchery stock groups, two were 100% marked (Macaulay: MC and Hidden Falls: HF) and one was unmarked (Gunnuk Creek: GC) (Table 1). In relation to Icy Strait, the MC hatchery is 85 km east, the HF hatchery is 135 km south, and the GC hatchery is 200 km southeast. All three hatcheries are located within northern and central Inside Passage localities of southeastern Alaska and represent more than 62% of the 372 million juvenile chum salmon released from the region's hatcheries in 2001 (McNair, 2002). Other hatchery stock groups released from within southeastern Alaska are 230–525 km distant from Icy Strait. These stocks are largely unmarked and are released in the central outside and southern waters of southeastern Alaska. We assumed these stocks represented a small component of the unmarked stocks of juvenile chum migrating from the northern region out the Icy Strait migration corridor. Our rationale for this assumption are 2-fold: first, compared to Icy Strait, these stock groups have four, more proximate seaward entry points to the Gulf of Alaska (Sitka Sound, Chatham Strait, Sumner Strait, and Clarence Strait); and second, in order for these stocks to enter into the Icy Strait corridor, they would need to migrate inland and northward through an extensive network of inside channels.

Table 1. Juvenile chum salmon hatchery releases and percent marked in southeastern Alaska in 2001, with marine distance from each hatchery to the Icy Strait study area

Hatchery	Millions released	(% of release)	Percent marked	Marine distance to Icy Strait (km)	Surviving to $S_3$ (%)
<i>Northern and central inside release localities of southeastern Alaska</i>					
Macaulay	103.9	(28)	100.0	85	2.5
Hidden Falls	81.9	(22)	100.0	135	6.9
Gunnuk Creek	46.2	(13)	0.0	200	1.5
Other	1.7	(0)	0.0	160	–
<i>Central outside and southern release localities of southeastern Alaska</i>					
Medvejie	40.9	(11)	32.2	230	–
Whitman Lake	26.9	(7)	0.2	520	–
Neets Bay	66.7	(18)	0.2	525	–
Other	4.1	(1)	0.0	230+	–
Total	372.3	(100)	–	–	–

The percent surviving to age 3 ( $S_3$ ) for three hatchery stocks in the inside waters of the northern and central regions is also indicated. Release data and recovery data for calculating  $S_3$  is from McNair (2002) and hatchery operators. Average survivals are based on 1990–1996 brood year (BY) returns for Macaulay (MC) and Hidden Falls (HF) and BY 1996 for Gunnuk Creek.

Previous data on the marine distribution of chum salmon stock groups indicate that more distant stocks arrive in Icy Strait at a later time. This data is only available from hatchery marked stocks because no wild chum salmon stocks are currently marked in the region. Historical sampling in Icy Strait has shown that MC and HF stocks occur from June–September; however, MC fish predominate in June, and HF fish predominate in July (Orsi et al., 2000a, b, 2001a, b, 2002). The sequential arrival and departure of known hatchery stock groups over time in Icy Strait suggests a pulsing of the stock groups through Icy Strait. Although the GC stock is not marked, limited recoveries of otolith marked juvenile chum salmon from Port Camden, an adjacent stock, have documented that this stock occurs in the inside waters of the northern region of southeastern Alaska in August (Courtney et al., 2000). This was our rationale for including the GC stock in the hatchery component migrating through the northern region of southeastern Alaska.

We acknowledge that because some hatchery stocks are marked at a low rate or are not marked, that the discrimination of wild chum salmon stocks is not precise. However, we maintain that the unmarked fish captured in Icy Strait inshore in late May and further offshore in June and July do represent wild fish. Because marked and unmarked juvenile chum salmon are released by hatcheries from several locations throughout southeastern Alaska in May, local stocks of wild chum salmon are isolated from hatchery stocks in Icy Strait. At this time, the principal unmarked stocks released by hatcheries come from no closer than 200 km away at Gunnuk Creek in central Southeast Alaska inside waters, to 525 km away at locations near Ketchikan in southern Southeast Alaska (Table 1). The pulsing of known 100% marked groups in June (MC) and July (HF) allows good precision in identifying the hatchery component at this time. Later, in August and September, unknown and unmarked hatchery stocks are most likely to occur, based on historical information and by virtue of their distant release localities.

#### *Bioenergetics model and input parameters*

We used the Wisconsin Bioenergetics Model 3.0 (Hanson et al., 1997) to estimate zooplankton consumption by hatchery and unmarked juvenile

chum salmon stocks as they utilized littoral and neritic marine habitats in the northern region of southeastern Alaska. We estimated consumption for two different scenarios: (1) total consumption in inside waters of the northern region of southeastern Alaska, and (2) daily consumption at four time periods in relation to standing crop of zooplankton in the Icy Strait neritic habitat (Table 2). In our first scenario, we estimated the effects on consumption of two thermal regimes and two levels of initial littoral mortality experienced by salmon. In our second modeling scenario, we estimated the percent of the available standing crop of zooplankton from the surface to 20-m depth versus the entire water column within Icy Strait that was consumed by hatchery and unmarked mixed stocks of juvenile chum salmon.

For the simulations, we used the following input parameters: calendar date, thermal exposure, zooplankton standing crop, salmon abundance, salmon weights (initial and final), salmon diet, energy densities (prey and predator), standard physiological model values, and natural salmon mortality rates. In most cases, data parameters were averaged from all the Icy Strait stations. However, salmon diet was represented from one station in Icy Strait (ISC), at which we conducted intensive diel sampling to characterize diel feeding habits of the juvenile salmon each month. Juvenile chum salmon used for predator energy densities were sampled from one littoral habitat site and from the MC hatchery net pens in late May and from the ISC station in June, July, August, and September.

#### *Temperatures by habitat*

Temperatures were taken in the littoral habitat in May and in the neritic habitat monthly from June until September (Table 3). Surface temperature in the littoral habitat was taken with a bucket thermometer and averaged from the Crist Point and Homeshore beaches in late May. Additional surface temperatures off the Auke Bay Laboratory dock (B.L. Wing, personal communication) were used to represent temperatures encountered by wild fish in early May, prior to our sampling of littoral habitats. The Auke Bay Laboratory dock is located 12 km west of the MC hatchery. In the neritic habitat in Icy Strait, temperature profiles

Table 2. Variables used under two scenarios with a bioenergetics model to estimate zooplankton consumption by hatchery and wild or unmarked stocks of juvenile chum salmon in marine waters of southeastern Alaska, 2001

Locality	Marine habitat (s)	Time period (s)	Model input variables	Chum stock comparison
<i>Scenario 1: Total zooplankton consumption</i>				
<i>General</i>	<i>Two</i>	<i>One continuous</i>	<i>Two varied</i>	<i>Four groups</i>
Inside waters of the northern region of southeastern Alaska	Littoral and neritic	May–September	Temperature Surface (1 m) Integrated (20 m) Littoral mortality Low High	Hatchery (3) and wild
<i>Scenario 2: Percent of available zooplankton consumed</i>				
<i>Specific</i>	<i>One</i>	<i>Four individual</i>	<i>Two fixed</i>	<i>Three groups</i>
Icy Strait, within inside waters of the northern region of southeastern Alaska	Neritic	June, July, August, and September	Temperature Surface (1 m) Trawl CPUE of chum salmon	Hatchery (2) and unmarked

Scenario 1 tested the effects of temperature and mortality on total zooplankton consumption by all hatchery and wild stocks originating from the inside waters of southeastern Alaska from May–September. Scenario 2 estimated the percent of the available zooplankton standing crop consumed by juvenile chum salmon captured in trawls in correspondence with measures of standing crop of zooplankton in the top 20 m and over the entire water column in Icy Strait, Alaska at four different time periods.

were taken with a Sea-bird<sup>1</sup> SBE-19 Seacat profiler and converted to readings per 1-m depth intervals (reference to trade names does not imply endorsement by the National Marine Fisheries Service). Monthly surface (1-m) and surface to 20-m average temperatures were calculated from the four stations in the neritic habitat.

For modeling scenario 1 (total zooplankton consumption in the northern region of southeastern Alaska), we used two thermal regimes based on the spatial and temporal occurrence of juvenile chum salmon during their early marine life from May until September. Marine residence in littoral habitats was assumed to occur from 01 May until 09 June (littoral phase), followed by a more epipelagic residence period in neritic habitats from 10 June until 28 September (neritic phase). We characterized the littoral phase only by the warmer surface temperatures and the neritic phase by both a high and a low temperature exposure (Table 3). Thus, the first series of model runs was made with surface (<1 m) warm temperatures in both littoral and neritic phases, while the second series of model runs was made (a) with the warmer surface temperatures in the littoral phase, and (b) with cooler temperatures averaged from the surface to 20-m depth in the neritic phase. The effects of these temperature regimes on zooplankton consumption

by juvenile salmon were computed with the Wisconsin Bioenergetics Model. The cooler, 20-m average temperature exposure was chosen to represent thermal conditions that fish might encounter if they were not entirely surface oriented, and this was the stratum sampled by both the salmon trawl and the shallow zooplankton nets.

For scenario 2 (percent consumption of available zooplankton standing crop in Icy Strait), we used the warmer surface temperatures at four monthly time periods in the neritic habitat only, from late June to late September. These surface temperatures were used in order to maximize zooplankton consumption estimates by the salmon.

#### *Zooplankton sampling and standing crop estimation*

Zooplankton was sampled at the Icy Strait stations using BONGO nets. The BONGO nets are two conical nets mounted inside a tandem 0.6-m diameter frame, with 333- and 505- $\Phi$ m mesh sizes. Only samples from the 333- $\Phi$ m mesh were processed and used in this analysis. A General Oceanics model 2031 flow meter was suspended inside each BONGO net to record the sampling distance, and a Bendix/Marine Advisors Model T-1 Bathymograph was attached to the BONGO frame to

Table 3. Two thermal regimes used to estimate prey consumption by juvenile chum salmon in southeastern Alaska from May–September, 2001

Date	Calendar day	Locality	Surface temperature < 1 m	
<i>Littoral habitat</i>				
01 May	121	Auke Bay Laboratory dock	7.6	
12 May	132	Auke Bay Laboratory dock	7.9	
22 May	142	Crist Point and Homeshore beaches	7.9	
31 May	151	Auke Bay Laboratory dock	11.5	
09 June	160	Auke Bay Laboratory dock	13.8	
<i>Neritic habitat</i>				
			1 m	Average 20 m
28 June	179	Icy Strait	12.5	10.0
29 July	210	Icy Strait	12.2	10.1
27 August	239	Icy Strait	12.2	10.4
27 September	270	Icy Strait	9.1	8.8

The first thermal regime assumed juvenile chum salmon remained entirely surface oriented from May until September, whereas the second thermal experience assumed juvenile chum salmon initially were surface oriented in the littoral habitat then shifted to a more epipelagic distribution (top 20 m) in the neritic habitat. Temperatures (°C) taken in neritic habitat were averaged from the four stations sampled along the Icy Strait transect.

validate the maximum deployment depth. The BONGO was deployed and retrieved at a 45° wire angle obliquely to two depths at each station: “shallow” (to 20-m depth), and “deep” (to 200-m depth or within 20 m of the bottom where depth was less than 220 m). The shallow sampling was done to estimate the standing crop of zooplankton in the surface to 20-m depth, in contrast to the deep sampling that was done to estimate the standing crop of zooplankton within the entire integrated water column, presumably encompassing the scattering layer. The descent rate of the

BONGO was 1.0 m/s and the ascent rate was 0.5 m/s, with a 30-s pause at maximum depth prior to ascent of the deep BONGO. All zooplankton collections were made during daylight hours (0700–2000).

Zooplankton standing crop ( $\text{g}/\text{m}^2$ ) was estimated from the displacement volume (DV) of each BONGO net sample. One ml of DV was assumed to be equivalent to 1 g of wet weight. Standing crop of zooplankton was determined by dividing the DV by the surface cross section area of the net opening and the distance traveled ( $0.283 \text{ m}^2 \cdot \text{flow meter count (m)}$ ) to obtain  $\text{g}/\text{m}^3$ , and then multiplying the resulting amount by the maximum depth (m) sampled to obtain  $\text{g}/\text{m}^2$ . For the shallow and deep BONGO sampling, zooplankton standing crop was averaged over the four Icy Strait stations each month, with the exception of the August shallow zooplankton sample that was represented by three samples taken only at the ISC station (Table 4). Detailed species composition of zooplankton samples was not determined for this paper.

#### Salmon collections

Samples of juvenile chum salmon were collected in littoral habitats in May during the day and in the neritic habitats from June to September during day and night. Salmon in the littoral habitat were sampled with a 37-m long beach seine. Also during this time, fish samples were obtained from the MC hatchery as they were being released from a seawater net pen. Fish were sampled in neritic habitat with a 24-m (wide) by 18-m (deep) rope trawl at the four stations on the Icy Strait transect line. Most neritic fish samples were collected during the day (0700–1900); however, additional samples were collected during crepuscular/night periods (2200–0400) at the ISC station to examine diel feeding periodicity of salmon and to document the presence of associated fish competitors that undergo diel vertical migrations. The rope trawl was fished at a speed of 4.63 km/h (2.5 knots) for 20 min, covering a distance of about 1500 m and a surface area of 36,000  $\text{m}^2$ . Trawling was accomplished with the NOAA ship *John N. Cobb*, a 28.3-m research vessel. For more information on rope trawl methodology see Orsi et al. (2000a, b).

Juvenile chum salmon and associated fishes were identified, counted, and measured (nearest

Table 4. Average zooplankton standing crop sampled with 333- $\Phi$ m BONGO nets in the upper and integrated water column of Icy Strait, southeastern Alaska from May to September, 2001

Date	Calendar day	Upper water column				Integrated water column			
		Hauls	Depth <sub>max</sub> (m)	(g/m <sup>3</sup> )	(g/m <sup>2</sup> )	Hauls	Depth <sub>max</sub> (m)	(g/m <sup>3</sup> )	(g/m <sup>2</sup> )
20 May	140	4	20	1.05 (0.13)	21.05 (2.64)	4	55–200	1.29 (0.06)	192.43 (42.32)
28 June	179	4	20	0.83 (0.12)	16.57 (2.41)	4	65–200	1.12 (0.14)	189.53 (50.87)
29 July	210	4	20	0.24 (0.05)	4.70 (0.99)	4	80–210	0.64 (0.11)	112.52 (34.25)
27–28 Aug.	239	3	20	0.08 (0.04)	2.50 (0.86)	4	110–210	0.60 (0.12)	97.81 (21.47)
27 Sept.	270	4	20	0.04 (0.01)	0.89 (0.18)	4	70–220	0.32 (0.08)	59.60 (17.05)

Monthly standing crops were based on samples from stations ISA, ISB, ISC, and ISD, except for August, where standing crop in the upper water column was averaged from three hauls at station ISC. One milliliter displaced volume of zooplankton was assumed to equal to 1 g of zooplankton wet weight. Volumes of zooplankton (g/m<sup>3</sup>) were multiplied by the maximum BONGO depth sampled to obtain g/m<sup>2</sup>. Standard errors of the means are shown in parenthesis.

1.0 mm fork length) at sea, and samples of juvenile chum salmon were frozen for later determination of weight (nearest 0.1 g), stock identification, and whole body energy content (WBEC) in the laboratory. A subset of samples was also preserved in 10% formalin and seawater solution for diet analysis. Otoliths were examined from a subset of the frozen juvenile chum salmon to determine the presence or absence of thermal marks used for stock identification. Stock composition of the juvenile chum salmon caught was derived from the proportions of thermal otolith marks detected in the subsample and allocated to either MC, HF, or unmarked chum stock groups. As explained previously, wild fish were assumed to be the majority of fish in the unmarked component in June and July, although unmarked GC or more distant chum salmon stock groups may have been included among fish of the unmarked component after July. The average monthly proportion of

each stock group was determined from sample sizes ranging from 31 to 354 fish at the four Icy Strait stations (Table 5).

#### Diet analysis

Proportions of prey in juvenile chum salmon diet used in the model were determined from fish captured in the littoral habitat in May and in the neritic habitat from June to September. We used juvenile chum salmon caught during 22 May with beach seines to represent the modeled littoral residence period of 01 May to 09 June, and juvenile chum salmon caught on 29–30 June, 30–31 July, 29–30 August, and 28–30 September during sampling at station ISC to represent the modeled neritic residence period of 10 June to 28 September. Details of these data are reported in Sturdevant et al. (2002). Diel sampling was conducted at

Table 5. Monthly stock composition (proportion) of juvenile chum salmon sampled for diurnal sampling periods at four stations (ISA, ISB, ISC, ISD) on the Icy Strait transect in marine waters of southeastern Alaska, June–September, 2001

Dates	Median calendar date	Number of hauls	Number of fish	Chum salmon stock composition		
				Unmarked	Macaulay	Hidden Falls
28 June–01 July	180	9	239	0.45	0.55	0.00
29–31 July	211	9	354	0.71	0.04	0.25
27–30 August	240	12	106	0.90	0.04	0.06
27–30 September	271	9	31	0.97	0.00	0.03



station ISC at seven, 3-h intervals (D1–D7) beginning at 0400, 0700, 1000, 1300, 1600, 1900, and 2200. Whenever possible, samples of up to 10 fish in each of the seven diel periods were taken each month ( $n=27$ –68 fish). Ten major prey taxa were identified by stomach analysis in the laboratory. The average weight proportions of these taxa were computed for each diel period within a month, and then the grand averages per month were computed and used as input values for the model (Table 6).

*Prey and predator energy densities and physiological parameters*

Prey WBEC (J/g wet wt) and the indigestible percentage of each prey type used in the model were derived from literature values. Prey energy densities were used from seven sources: Slobodkin and Richman (1961), Laurence (1976), Musayeva and Sokolova (1979), Percy and Fife (1983), Norrbirn and Bamstedt (1984), Wacasey and Atkinson (1987), and Yerokhin and Shershneva

(2000). Prey energy densities were varied in the model seasonally for euphausiids and calanoid copepods, the only taxa for which seasonal values were available (Musayeva and Sokolova, 1979; Yerokhin and Shershneva, 2000). Energy densities originally presented in cal/g dry wt were converted to cal/g wet wt by multiplying by a factor of 1.21. The indigestible percentages of prey were assumed to be 10%, except values for euphausiids, calanoid copepods, hyperiid amphipods, and fish larvae, which were taken from Griffiths (1977) and Davis et al. (1998).

The WBEC (J/g wet wt) of juvenile chum salmon used in the model was estimated by bomb calorimetry from frozen samples each month. In most cases, these samples were taken at the same time fish were collected for diet analysis. Juvenile chum salmon were combusted in a Parr 1425 Semimicro Bomb Calorimeter, including 20 fish from the littoral habitat in late May and 10 fish each from the neritic habitat in late June, July, August and September. For bomb calorimetry, individual whole fish minus their otoliths and stomach contents were dried to constant weight, homogenized in a grinder, and subsamples were generally pressed into 0.15-g pellets for combustion. However, the small size of the wild fish in May often required using the entire fish to obtain a pellet weight between 0.06 and 0.15 g. We used an average percentage moisture content of 19% to convert from dry weight to wet weight.

For juvenile chum salmon within the littoral habitat, we used a two-sample *t*-test to compare WBEC values of 10 unmarked fish sampled on the beach in Icy Strait with 10 hatchery fish released in May. The unmarked fry were collected on 22 May with beach seines at Crist Point; the marked hatchery fry were collected upon release on 21 May at the MC hatchery site. The unmarked fry were assumed to represent wild fish, by virtue of the distance of our sampling site from the nearest hatchery releasing unmarked chum salmon (GC, 200 km; Table 1). The size of these unmarked fish collected on the beaches was only 0.7 g compared to the 1.3 g size of unmarked fish released from GC 10 days prior to sampling. No significant differences in WBEC were detected between the marked and unmarked stock groups ( $p=0.87$ ,  $DF=18$ ). At these sample sizes and this observed sample standard deviation, the power ( $1-\beta$ ) of the test was 0.95 for detecting a 10% difference in

Table 6. Estimated proportion (wt) of each prey type eaten by juvenile chum salmon based on diet analysis of stomachs collected in Icy Strait, southeastern Alaska in May, June, July, August, and September 2001

Prey taxon	(142)	(180)	(211)	(241)	(272)
	22 May	19–30 June	28–30 July	28–30 Aug.	28–30 Sept.
Euphausiids	0.075	0.605	0.058	0.051	0.246
Calanoid copepods	0.631	0.026	0.191	0.036	0.002
Hyperiid amphipods	0.038	0.011	0.318	0.718	0.400
Oikopleurans	0.013	0.166	0.326	0.156	0.352
Haracticoid copepods	0.046	0.000	0.000	0.000	0.000
Barnacle larvae	0.004	0.035	0.004	0.001	0.000
Fish larvae	0.059	0.124	0.010	0.023	0.000
Crab larvae	0.012	0.024	0.093	0.014	0.000
Insects	0.110	0.006	0.000	0.001	0.000
Other	0.012	0.003	0.000	0.000	0.000
Total proportion	1.000	1.000	1.000	1.000	1.000

Calendar dates are shown in parentheses. Initial period of diet analysis was done on 22 May but was assumed to represent the initial littoral residence period of 01 May until 09 June.

sample means. The probability of making a type 2 error (accepting the  $H_0$  when false) is  $\exists$ . We therefore applied this result to samples from June to September and assumed that WBEC values were similar between unmarked stocks and hatchery stocks, because recoveries were not sufficient to test for stock-specific differences in WBEC each month.

We also tested for monthly differences in WBEC values of juvenile chum salmon. We compared values using one-way ANOVA from a mixed stock sample of 10 juvenile chum salmon collected each month (May–September) and detected significant differences ( $p=0.00$ ,  $DF=4$ ). We therefore used the individual monthly mean WBEC values (J/g wet wt) for juvenile chum salmon as follows: (May=4104.2; June=3802.3; July=3795.4; August=3826.8; and September=4175.3).

No standard physiological parameters were available for juvenile chum salmon in the bioenergetics model (Hanson et al., 1997), nor have any been reported in recent literature (Trudel and Welch, 2002). However, the model software (Fish Bioenergetics 3.0) provides physiological parameters for adults of some salmonid species. Therefore, we selected the fish physiological parameters listed for adult sockeye salmon (*O. nerka*) and pink salmon (*O. gorbuscha*) listed in the model reference material (Beauchamp et al., 1989 in Hanson et al., 1997).

#### *Salmon timing, size, and growth*

After emigration to seawater, chum salmon spend several weeks in littoral estuarine areas before moving further offshore to neritic habitats (Healy, 1982; Salo, 1991). For our simulations, we assumed estuarine arrival of wild juvenile chum salmon was 01 May (calendar day 121), the date of peak outmigration timing for Taku River chum salmon, a major chum salmon-producing river in the northern region of southeastern Alaska (Meehan and Siniff, 1962; Murphy et al., 1988). Initial weight of wild juvenile chum salmon at this time was assumed to be 0.40 g (Salo, 1991). For hatchery stocks, initial entry times of 13–21 May (calendar days 133–141) and average weights of hatchery chum salmon at release (1.32–2.00 g) were provided by hatchery operators (Table 7). Both wild and hatchery stocks were assumed to transition from the littoral to neritic habitat on 09

June (calendar day 160). Therefore, we used initial size at release and the size at the first neritic sample date of 29 June (calendar day 180) with an exponential growth model (Everhart and Youngs, 1981) to back-calculate size at calendar day 160. The exponential growth model used was:

$$r = \text{Ln}(W_{180}/W_i)/(180 - t_i),$$

where  $r$  is the daily growth rate,  $W_{180}$  is the weight at calendar day 180,  $W_i$  is the weight at emigration or release, and  $t_i$  is the calendar day of emigration or release between initial release and 29 June (calendar day 180). This growth model was used because juvenile fish were examined during their rapid growth phase over a relatively short time interval. For subsequent neritic samples, size was generally based on stock-specific sample estimates at 29 June, 30 July, 30 August, and 30 September (calendar days 180, 211, 242, and 273) (Table 7). Because GC stocks were unmarked, their size in the neritic habitat was assumed to be the average of the MC and HF hatchery stocks when both were present. Sizes were substituted for the hatchery fish where recoveries were insufficient; first, the size of MC fish in June was used to represent HF fish, and second, the size of HF fish in September was used to represent MC fish. Recoveries of MC fish in August and HF fish in September were also limited; therefore to improve sample size for stock-specific weight estimates, we included recoveries of these stocks from the Icy Strait area for the years 1997–2002.

Residency was estimated for the four stock groups of juvenile chum salmon in five sequential time periods from May to September (Table 8). The first time period encompassed the littoral residency phase. Wild chum salmon were assumed to remain in the littoral phase for 40 days, from 01 May until 09 June, because hatchery chum salmon, which are held captive in marine net pens and fed for several weeks of their littoral residence prior to release, were assumed to remain in the littoral phase from the average release dates in late May until 09 June. Thus, total littoral residence was assumed to be 40 days for wild chum salmon and 20–28 days for hatchery chum salmon. Residence within the neritic habitat was broken down into four time periods: one 20-day period followed by three 31-day periods (Table 8). Total neritic

Table 7. Size (g) and temporal occurrence of wild and hatchery stock groups of juvenile chum salmon used in bioenergetics model based on release information and at-sea recoveries in Icy Strait, southeastern Alaska, May–September 2001

Event (number of fish)	Date	Calendar day	Wild and hatchery salmon stock groups			
			Wild	Gunnuk Creek	Macaulay	Hidden falls
<i>Littoral habitat</i>						
Estuarine migration (328,377,109 <sub>low littoral mortality scenario</sub> ; 438,425,362 <sub>high littoral mortality scenario</sub> )	01 May	121	0.40	–	–	–
Gunnuk release (46,200,000)	13 May	133	–	1.32	–	–
Macaulay release (103,923,907)	18 May	138	–	–	1.65	–
Hidden Falls release (80,844,732)	21 May	141	–	–	–	2.00
Leave near shore	09 June	160	(2.83)	(4.20)	(4.24)	(4.40)
<i>Neritic habitat</i>						
First neritic sample	29 June	160	7.71	(9.59)	9.59	(9.59)
Number of fish			$n = 17$		$n = 24$	
Second neritic sample	30 July	211	15.54	(20.34)	23.16	17.51
Number of fish			$n = 67$		$n = 25$	$n = 26$
Third neritic sample	30 August	242	35.83	(52.05)	54.82	49.29
Number of fish			$n = 28$		$n = 42$	$n = 55$
Fourth neritic sample	30 September	273	89.15	(121.46)	(121.46)	121.46
Number of fish			$n = 22$			$n = 7$

The weight of each stock group on 09 June was estimated using the initial migration or release weight, the corresponding weight at first neritic sample, and an exponential growth model. Parentheses denote an estimated weight from either an exponential growth model (calendar day 160) or from values averaged between hatchery stock groups to represent the unmarked Gunnuk Creek stock group.

residence for all stock groups was 113 days (10 June until 30 September).

#### *Estimation of chum salmon numbers and mortality in northern inside SEAK*

To estimate total consumption by juvenile chum salmon in the northern inside waters of southeastern Alaska, we needed to estimate both initial numbers of the stock groups and their daily mortality rates to estimate the numbers of fish alive throughout the modeling period. For hatchery stocks, initial numbers were provided by the hatchery operators. We used literature values and marine survival data from hatchery operators to estimate marine mortality rates for the hatchery fish. In southeastern Alaska, chum salmon return from age 3 to 6. Because age composition of hatchery returns varies inter-annually between and within hatcheries, we standardized the survival rates to  $S_{i3}$ , the survival of brood year (BY)  $i$ , prior to fishing mortality:

$$S_{i3} = N_{i3}/F_{i3},$$

where  $N_{i3}$  is the number of age 3 survivors on 01 May (an arbitrarily chosen date prior to fishing), and  $F_{i3}$  is the number of fry released for BY  $i$ . To calculate  $N_{i3}$ , we used backward virtual population analysis (Hilborn and Walters, 1992):

$$N_{i3} = R_{i3} + R_{i4}/S + R_{i5}/(S \cdot S) + R_{i6}/(S \cdot S \cdot S),$$

where  $R_{ij,j=3,4,5}$  is the estimated return (catch and hatchery recoveries) for a given year class for BY  $i$ , and  $S$  is the estimated annual survival rate for age 3 and older chum salmon. We used an annual survival rate of 0.856 (85.6%), based on the monthly mortality rate for these age classes reported in Ricker (1976).

We computed  $S_{i3}$  for the three hatchery stocks using return data provided by the hatcheries. For MC and HF chum salmon, we computed  $S_3$  for each of BY 1990–1996, and used the average value to represent these stocks. For GC chum salmon, we computed  $S_3$  for BY 1996, the only year for which we had complete age-structured return data. Estimates of  $S_3$  varied among hatcheries from

Table 8. Early marine mortality estimates for wild and hatchery stocks of juvenile chum salmon for low and high survival years

Calendar dates	Calendar dates	Days of residence		% Dying per time interval	
		Littoral habitat	Neritic habitat	Low littoral mortality	High littoral mortality
<i>Wild unmarked stocks</i>					
01 May–09 June	121–160	40	0	86.3	93.1
10 June–29 June	161–180	0	20	6.4	5.3
30 June–30 July	181–211	0	31	9.7	8.1
31 July–30 August	212–242	0	31	9.7	8.1
31 August–30 September	243–273	0	31	9.7	8.1
<i>Macaulay stock</i>					
18 May–09 June	138–160	23	0	75.4	83.5
10 June–29 June	161–180	0	20	6.4	5.3
30 June–30 July	181–211	0	31	9.7	8.1
31 July–30 August	212–242	0	31	9.7	8.1
31 August–30 September	243–273	0	31	9.7	8.1
<i>Hidden Falls stock</i>					
21 May–09 June	141–160	20	0	33.0	55.1
10 June–29 June	161–180	0	20	6.4	5.3
30 June–30 July	181–211	0	31	9.7	8.1
31 July–30 August	212–242	0	31	9.7	8.1
31 August–30 September	243–273	0	31	9.7	8.1
<i>Gunnuk stock</i>					
13 May–09 June	133–160	28	0	85.2	90.1
10 June–29 June	161–180	0	20	6.4	5.3
30 June–30 July	181–211	0	31	9.7	8.1
31 July–30 August	212–242	0	31	9.7	8.1
31 August–30 September	243–273	0	31	9.7	8.1

Mortality rates are expressed as the percent dying for a given time interval for each marine survival scenario.

1.5% for Gunnuk Creek to 6.9% for Hidden Falls (Table 1).

For all Pacific salmon, mortality during initial marine residency is generally considered to be high and a key determinant of year-class strength (see reviews in Groot and Margolis, 1991). During their littoral phase, stocks are segregated by virtue of their different release areas and are therefore exposed to different local conditions. In contrast, as fish disperse offshore into more neritic and pelagic habitats, they converge and intermingle in migration corridors; as a result they encounter more homogeneous conditions, and therefore are affected by mortality on a more regional scale. Consequently, in our simulations we assumed the differences in survival rates among hatchery stocks were entirely due to differences in their survival rates during the initial littoral period. We assumed a daily mortality rate for the hatchery stock with the highest survival (HF), scaled the other hatch-

ery stocks to this rate to account for survival differences, and calculated a daily mortality rate as an average rate from the end of the littoral period to age 3+.

Several studies have estimated initial marine mortality rates for juvenile chum salmon. Over a 2–4 day period, Bax (1983) estimated mortality rates of 0.31–0.46 per day. Whitmas (1985, cited in Salo, 1991) estimated mortality of 0.44 per day for the first 2 days following release. Fukuwaka and Suzuki (2002) estimated daily mortality rates of 0.033–0.268 (average 14.6%) in the first 14–43 days after release of Japanese chum salmon. These rates are not sustainable over the duration of the littoral period for juvenile chum salmon. The proportion surviving is reduced below 0.06 after 8 days at a daily mortality rate of 0.46, and after 20 days at a rate of 0.146; HF chum salmon have an estimated 0.069 survival at  $S_3$ , more than 700 days after release. Fukuwaka and Suzuki

(2002) note that high estimates of initial mortality may be due to underestimating mark effects or emigration from the study area, or may simply reflect very intense initial mortality that rapidly declines. Parker (1968) estimated the daily mortality of juvenile pink salmon at 0.02–0.04 per day during their first 40 days at sea. Chum salmon, like pink salmon, emigrate to sea as newly emerged fry and initially utilize nearshore habitats. These rates bracket the lower end of Fukuwaka and Suzuki (2002) estimates for chum salmon. In our simulations, we used the end points of the range for daily mortality from Parker (1968) to represent initial littoral mortality rates encountered by HF chum salmon under low (0.02) and high (0.04) mortality.

Next, we scaled the initial mortality rates during the littoral phase for the other two hatchery facilities, assuming that differences in  $S_3$  (Table 1) were due entirely to differences in these initial rates. Then

$$r_{1a} = -(\text{Ln}(e^{r_{1\text{HF}} \cdot t_{1\text{HF}}} \cdot (S_{3a}/S_{3\text{HF}})))/t_{1a},$$

where  $r_{1a}$  is the daily mortality rate during the littoral phase,  $t_{1a}$  is the time in days spent in the littoral phase,  $a$  is the hatchery being scaled to HF, and HF indicates the parameters for Hidden Falls. Resulting estimates of daily mortality rates for MC and GC releases for low and high littoral mortality assumptions are shown in Table 9.

Mortality rates following the littoral phase were assumed to be similar for all stocks. No lit-

erature estimates exist for mortality rates between the littoral phase and age 3. We could calculate a rate for this period directly, given our assumptions for calculating  $S_3$  and rates for  $t_1$ , because for a given stock:

$$S_3 = e^{-r_1 t_1} \cdot e^{-r_2 t_2},$$

where  $r_1$  is the daily mortality rate during the littoral phase,  $r_2$  is the daily mortality rate during the juvenile neritic and pelagic phase from the end of the littoral phase until age 3+,  $t_1$  is the days the fish are in the littoral phase, and  $t_2$  is the days in the juvenile neritic and pelagic phase. The rate during this second phase can then be calculated as:

$$r_2 = -(\text{Ln}(S_3) + r_1 t_1)/t_2.$$

We defined  $t_2$  as 690 days, based on our temporal definition of the littoral phase and age 3+. Because  $S_3$  is the same under either assumption, mortality rates in the second phase must be higher for the low littoral mortality assumption than for the high littoral mortality assumption. The calculated daily rates for  $t_2$  were 0.0033 for low littoral mortality, and 0.0027 for high littoral mortality (Table 9).

The number of hatchery fish alive at the end of the littoral period for each hatchery stock can now be calculated as:

$$N_{1a} = N_{0a} \cdot e^{-(r_{1a} t_{1a})},$$

Table 9. Numbers of chum salmon fry entering the marine environment, entry dates, days in littoral phase, and phase-specific instantaneous daily mortality rates at low and high littoral mortality assumptions for simulations of consumption by BY 2000 hatchery and wild juvenile chum salmon entering the inside waters of the northern region of southeastern Alaska in spring, 2001

Stock	Initial numbers (millions)	Average seawater entry (calendar day)	Days in littoral phase	Instantaneous daily mortality rates			
				Littoral phase		Neritic phase	
				Low <sub>littoral</sub>	High <sub>littoral</sub>	Low <sub>littoral</sub>	High <sub>littoral</sub>
Hidden Falls Hatchery	81.85	May 20 (141)	20	0.020	0.040	0.0033	0.0027
Macaulay Hatchery	103.91	May 17 (138)	23	0.061	0.078	0.0033	0.0027
Gunnuk Creek Hatchery	46.22	May 12 (133)	28	0.068	0.082	0.0033	0.0027
Wild	328.38	May 1 (121)	40	0.050	–	0.0033	–
Low <sub>littoral</sub> mortality assumption							
Wild	438.43	May 1 (121)	40	–	0.067	–	0.0027
High <sub>littoral</sub> mortality assumption							

See Methods for details on data sources and assumptions for estimating initial numbers of wild fry and mortality rates for hatchery and wild fry.

where  $a$  is the hatchery, and  $N_0$  is the number of fry released (Table 9). Numbers at subsequent time periods were similarly calculated, using the appropriate mortality rate and number of days.

We then used the estimates of mortality for the hatchery stocks to estimate mortality and numbers of wild fish in our simulations. We assumed that daily mortality for wild fish during the littoral phase was the average of the daily rates for the three hatchery stocks. We again assumed that differences in survival among stocks were entirely due to the differences in mortality during the littoral phase. Thus, the proportion of wild juveniles at the end of the littoral period should be the same as the proportion of wild adults in the total run of chum salmon. The average proportions of wild and hatchery fish in the southeastern Alaska catch from 1997 to 2001 were 0.22 and 0.78, respectively (ADFG, 2003). To estimate the proportion of wild fish in the total run, we needed to adjust the proportion in the catch by the exploitation rates of the hatchery and wild fish:

$$PR_W = \frac{(PC_W/E_W)}{(PC_W/E_W + PC_H/E_H)},$$

where  $PR$  is the proportion in the total run,  $PC$  is the proportion in the catch,  $E$  is the exploitation rate for the catch,  $W$  is wild stock, and  $H$  is hatchery stocks. Exploitation rates of HF, MC, and GC have been reported as 0.94, 0.91, and 0.84, respectively; weighted for release numbers and survival rates, we derived an  $E_H$  of 0.92. Because no estimate of exploitation rate for chum salmon in southeastern Alaska is available, we assumed an  $E_H$  of 0.5, similar to exploitation rates estimated for pink salmon fisheries in southeastern Alaska (Steve Heintz, ADFG, personal communication). Based on these numbers, we calculated  $PR_W=0.34$  and conversely,  $PR_H=0.66$ .

The number of wild fry alive at the end of the littoral period ( $N_{1W}$ ) can now be estimated by calculating the simulated number of hatchery fry alive at the end of the period and applying the proportion of wild and hatchery fish:

$$N_{1W} = PR_W \left( \left( \sum_{a=1}^3 N_{1a} \right) / PR_H \right).$$

The starting number of wild fry for the simulations on May 1 is then calculated as:

$$N_{0W} = N_{1W} / e^{(-r_{1W} \cdot t_{1W})}.$$

The starting numbers depend on the initial littoral mortality, and are considerably higher under the assumption of high littoral mortality (Table 9).

#### *Estimation of chum salmon numbers and zooplankton consumption in Icy Strait*

We used trawl catches and area swept to directly estimate numbers of salmon in Icy Strait for area-specific point estimates of daily consumption that could be compared with estimates of zooplankton standing crop. No estimates or assumptions for mortality rates were needed for these estimates. Average catch of fish per unit effort (CPUE, where  $E$ =one trawl haul) was calculated for juvenile chum salmon during diurnal periods (0700–2100) at all stations for each sampling period (Table 10). Catchability of the trawl was assumed to be 100%. The number of salmon per  $\text{km}^2$  in Icy Strait ( $N_{ISi}$ ) at each time period  $i$  was calculated as:

$$N_{ISi} = CPUE_i / 0.036.$$

We sampled one station (ISC) throughout a 24-h period during each month to compare juvenile salmon abundance with other planktivorous fish to gain insight into their relative trophic impacts on the zooplankton standing crop. For this diel fish sampling, we made five hauls during the diurnal period (1000–1900) and three hauls during a crepuscular/nocturnal period (2200–0700). Ambient light intensities ( $\text{W}/\text{m}^2$ ) were recorded during the start of each trawl with a LiCor Model 189 radiometer. Average diurnal and crepuscular/nocturnal abundance of salmon and other fishes were estimated using the area-swept approach.

We estimated the monthly percentage of the available standing crop of zooplankton consumed by hatchery and unmarked salmon in the neritic marine habitat of Icy Strait in four time periods. The time periods comprised 1-day snap shots at the ends of June, July, August, and September. In each period, and for each stock group, the percent of zooplankton consumed was estimated by using the numbers of fish (num-

Table 10. Average catch per trawl haul (CPUE) and density of juvenile chum salmon used to estimate their prey consumption in Icy Strait, southeastern Alaska from June to September 2001

Sample dates	Median calendar date	Number of hauls	Juvenile chum salmon		
			Total catch	CPUE	Density of fish/km <sup>2</sup>
28 June–01 July	180	8	236	29.50 (3.50)	819.44 (97.22)
29 July–01 August	211	8	353	44.13 (11.53)	1,225.83 (320.28)
27–30 August	240	8	66	8.25 (3.02)	229.17 (83.89)
27–28 September	271	8	15	1.88 (0.64)	52.22 (17.78)

Monthly average CPUE was based on sampling stations ISA, ISB, ISC, and ISD twice each during diurnal periods (0700–2100). Mean densities of fish per km<sup>2</sup> were based on a trawl area swept of 36,000 m<sup>2</sup> and an assumed catchability of 1. Standard errors of the means are shown in parenthesis.

bers/km<sup>2</sup>) converted to biomass (g/km<sup>2</sup>), combining biomass estimates with model-generated consumption estimates (g prey/g predator d<sup>-1</sup>), and then comparing consumption to estimates of zooplankton standing crop available from two water column depths (upper 20 m and integrated). All modeling was done with the 1-m surface temperature simulation and previously identified parameters.

## Results

### Scenario 1: Consumption by chum salmon stocks in inside waters of the northern region

#### Estimation of stock numbers, mortality, and biomass

Our estimates of initial cohort size of wild juvenile chum salmon emigrating to marine waters were 328 and 438 million fish based on low and high early littoral marine mortality assumptions (Table 9), whereas the initial cohort sizes for the three hatchery stocks were the actual reported releases (Table 1). Under both littoral marine mortality assumptions, all stock groups declined dramatically during the 01 May to 09 June early littoral phase (calendar days 120–160) compared to the later 10 June to 30 September neritic phase (calendar days 161–273) (Figure 2a, b). Numbers of wild juvenile chum salmon declined more rapidly than hatchery stocks during their littoral marine phase due to their longer residence during this phase. Despite much larger initial numbers of all stock groups at the beginning of the simulation,

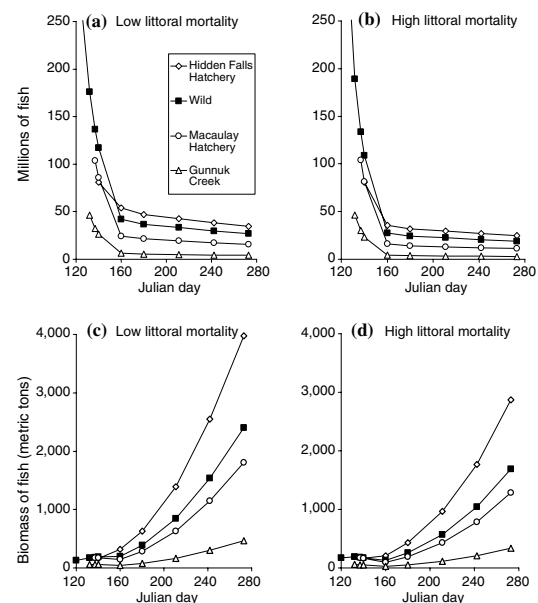


Figure 2. Numbers (a, b) and biomass (c, d) of wild and hatchery stock groups of juvenile chum salmon based on bioenergetics model runs of low (a, c) and high (b, d) littoral mortality scenarios in the northern region of southeastern Alaska in 2001. Littoral residence was modeled from 01 May to 08 June (Julian days 120–159) and neritic residence was modeled from 09 June to 30 September (Julian days 160–273). Sizes and times of marine residence for each stock group are in Table 8 and mortality rates for each scenario are in Table 9.

their biomass was relatively low during the littoral phase compared to the neritic phase. Differences in stock numbers that entered the neritic phase (day 160) under low and high littoral mortality assumptions resulted in substantially higher biomass when initial mortality was low compared to when it was high (Figure 2c, d).

### Zooplankton consumption

In our simulations, zooplankton consumption by juvenile chum salmon was substantially lower for wild stocks, which declined to lower numbers, than for combined hatchery stocks in the northern region of southeastern Alaska. Under the two neritic temperature regimes and littoral mortality estimates, total zooplankton consumption from May until September was 6000–8000 t for wild fish and 22,000–32,000 t for hatchery fish (Figure 3). Simulating warmer temperatures in the neritic habitat resulted in small increases in zooplankton consumption by each chum salmon stock group: 100–200 t more for wild fish and 500–800 t more for hatchery fish. Within each stock group, the proportion of maximum consumption ( $p$ -value) changed little between model runs for 1-m and integrated 20-m neritic temperatures, even though they differed by as much as 2.5 °C in late June (Table 3).

The effect of different cohort sizes on total prey consumption was dramatic. Simulations applying lower littoral mortality rates resulted in large increases in zooplankton consumption by each chum salmon stock group: 2200–2300 t more for wild fish and 9000–9200 t more for hatchery fish (Figure 3). Zooplankton consumption by both stock groups increased temporally (Figure 4), but consumption by the combined hatchery stocks was greater than consumption by the wild stocks in each period. Hatchery stocks consumed 57% of all zooplankton eaten in the initial littoral period and

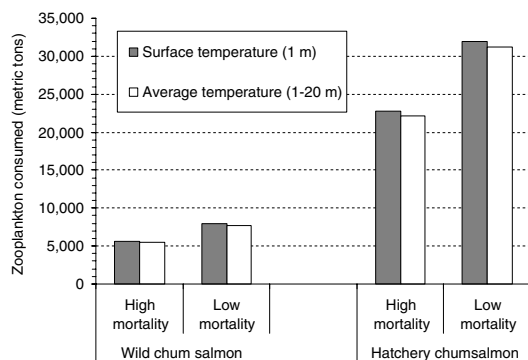


Figure 3. Total zooplankton consumption estimated for wild and hatchery stocks of chum salmon based on bioenergetics model runs of two simulated early littoral mortality rates and two neritic thermal conditions in the northern region of southeastern Alaska, May, June, July, August, and September, 2001.

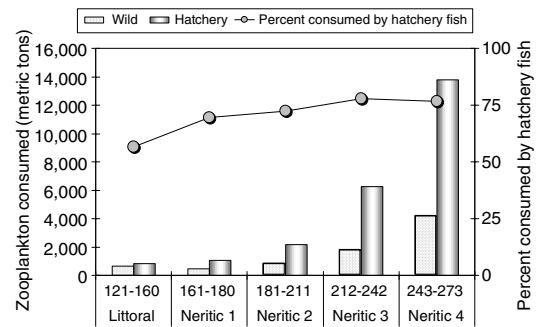


Figure 4. Estimated total consumption of zooplankton by wild and hatchery stocks of chum salmon in the northern region of southeastern Alaska in 2001. Consumption was estimated using a bioenergetics model with a low mortality scenario for all stock groups and an assumed surface (1-m) thermal experience (high temperature).

77% of all zooplankton eaten in the final neritic period.

Stock-specific consumption was examined in each period using the warmer, 1-m surface temperatures and low littoral mortality simulation. The  $p$ -values for each stock group followed a similar pattern, increasing from the first to the second period, generally declining in the third period, and reaching a maximum from the fourth to the fifth period (Figure 5a). Of the four stock groups, wild fish consumed the most zooplankton in the littoral period and the Hidden Falls stock consumed the most in each neritic period (Figure 5b).

### Scenario 2: Consumption by chum salmon stocks in the Icy Strait locality

**Predation impact of chum salmon on available prey**  
Monthly patterns in the numbers of juvenile chum salmon and the standing crop of zooplankton present were evident. Juvenile salmon densities were highest from June to July (800–1200 fish/km<sup>2</sup>), then declined dramatically from July to August, and remained at less than 200 fish/km<sup>2</sup> from August to September (Figure 6a, Table 10). Zooplankton also declined seasonally in both the upper 20-m and the integrated water columns (from 21 to 1 g/m<sup>2</sup> and from 192 to 60 g/m<sup>2</sup>), but was already declining by the time chum salmon numbers reached a peak in July (Figure 6a, Table 4). The standing crop of zooplankton (g/m<sup>2</sup>) was substantially (11–67 times) lower each month



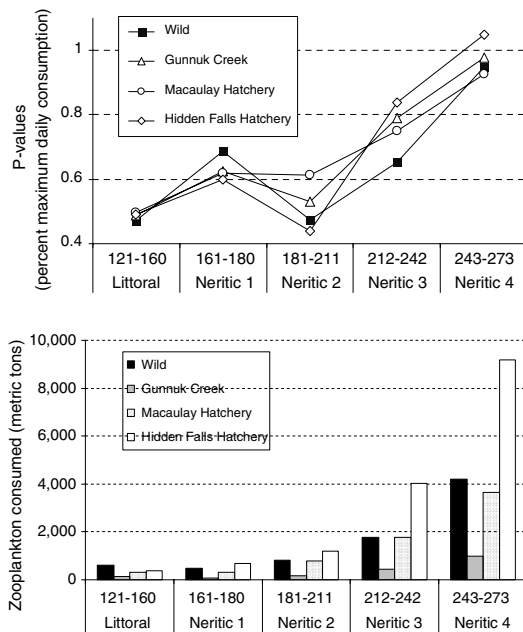


Figure 5. Stock-specific estimates for zooplankton consumed by wild and hatchery stocks of juvenile chum salmon in the northern region of southeastern Alaska. Panel (a) shows the proportion of maximum consumption ( $p$ ) for all stock groups and periods, and panel (b) shows the estimated zooplankton consumption of all stock groups and periods. Of the total amount of zooplankton estimated to be consumed by wild and hatchery chum salmon stocks, the percent of zooplankton consumed by all three hatchery stock groups is shown by the line graph over all periods.

in the upper 20-m compared to the integrated water column.

We estimated that only a small percentage of the standing crop of zooplankton was consumed by juvenile chum salmon. The percentages of the available total zooplankton standing crop consumed by all four salmon stock groups were less than 0.04% of the upper 20-m BONGO estimate and less than 0.005% of the integrated BONGO estimate (Figure 6b). Zooplankton consumption by juvenile salmon in Icy Strait differed monthly by stock group (Figure 7, Table 11). Initially in June, MC chum salmon consumed the most zooplankton, and then from July to September, unmarked stocks consumed the most zooplankton. Total daily consumption of zooplankton by all stock groups of juvenile chum salmon was estimated to be between 330 and 1764 g/km<sup>2</sup> d<sup>-1</sup> from June to September in the neritic habitat of Icy Strait.

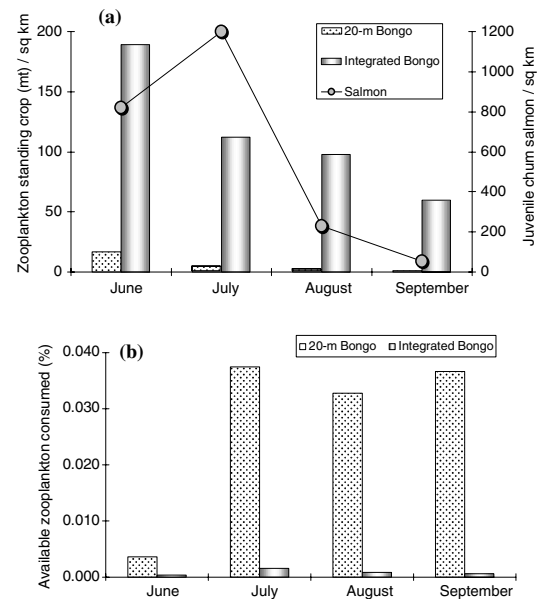


Figure 6. Estimates of zooplankton standing crop and consumption by juvenile chum salmon in the neritic habitat of Icy Strait, Alaska, June, July, August, and September, 2001. Panel (a) shows two estimates of zooplankton standing crop at two different sampling depths that is overlaid with juvenile chum salmon density estimates. Panel (b) shows the percentage of available zooplankton that is consumed by unmarked and hatchery stocks of chum salmon of the two estimates of zooplankton standing crop. Detailed stock-specific consumption rates are shown in Table 11.

#### Diel abundance of planktivorous fishes

Diel differences were apparent in the abundance and composition of planktivorous fish sampled between day and crepuscular/night periods in the neritic habitat of Icy Strait. The highest average ambient light levels in both periods were in June (200–500 W/m<sup>2</sup>) and the lowest were from July to September (0–150 W/m<sup>2</sup>) (Figure 8a, b). Catches of planktivores were highest during the crepuscular/night period in late summer and were predominantly composed of non-salmonid fishes (Figure 8a, b). Conversely, juvenile salmon dominated the catches during day sampling from June to September, and few other planktivores were encountered. The monthly CPUE for juvenile salmon averaged 50 during the day period, and juvenile chum salmon comprised 40% of the salmon catch (Figure 8a). However, during the crepuscular/night period from July to September, age 1+ walleye pollock (*Theragra chalcogramma*) and eulachon (*Thaleichthys pacificus*) dominated the catches (Figure 8b). The monthly CPUE for

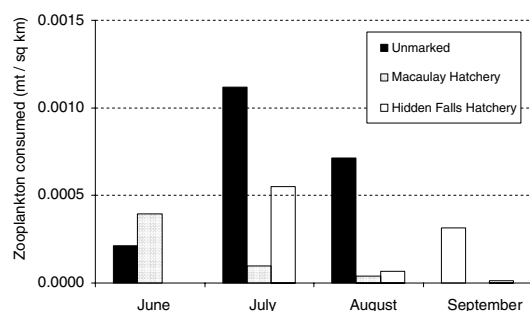


Figure 7. Zooplankton consumption by unmarked and hatchery stocks of juvenile chum salmon in the neritic habitat of Icy Strait, Alaska, June, July, August and September, 2001.

juvenile salmon also averaged 50 in the crepuscular/night period from June to September; but chum salmon comprised only 19% of the salmon catch. The differences in fish abundance and species composition between diel periods were remarkable; monthly CPUE for age 1+ walleye pollock and eulachon combined ranged from 1096 to 9037 and 102 to 1227, compared to 50 for juvenile salmon.

## Discussion

Zooplankton consumption was most influenced by the rate of early marine mortality of wild and hatchery stocks of juvenile chum salmon. Fukuwaka and Suzuki (2002) reported that initial marine mortality of chum salmon is variable, and can be as high as 99% during their first 32 days at sea off of coastal Japan. In our first scenario, wild

and hatchery stocks of juvenile chum salmon initially consumed similar amounts of zooplankton in their respective littoral phases. However, due to their earlier arrival and therefore longer residence in the littoral habitat, wild stocks sustained a higher early marine mortality than hatchery stocks, leading to lower estimates of wild stock numbers in the subsequent neritic phase; this decline resulted in the wild stocks consuming about half the amount of zooplankton as hatchery stocks in the neritic phase. In contrast, in our second scenario, where we examined only marked hatchery stocks and unmarked stocks in the neritic habitat of Icy Strait from June to September, consumption of zooplankton by unmarked stocks was higher than that of marked hatchery stocks from July onward. The higher consumption of zooplankton by unmarked stocks at this time may be explained by a rapid exodus of hatchery marked stocks from the neritic habitat, a rapid influx of mixed unmarked southerly stocks, or an unusually high survival of wild stocks in 2001. Without 100% marking of all hatchery chum stocks in southeastern Alaska, as is currently being practiced in other regions of Alaska (e.g., Prince William Sound, southcentral Alaska; McNair, 2002), it will be difficult to precisely discern hatchery and wild stock interactions in southeastern Alaska.

The different temperature regimes we used in the model had little effect on consumption of zooplankton by juvenile chum salmon. Our temperatures ranged from 8 to 14 °C between May and September, with about 2 °C variation between the two thermal regimes modeled for the neritic

Table 11. Stock-specific estimates of zooplankton consumption by juvenile chum salmon in the neritic habitat of Icy Strait in June, July, August, and September, 2001

Neritic period	Stock-specific consumption (g prey/g predator d <sup>-1</sup> )			Total weight of juvenile chum salmon stock groups (g/km <sup>2</sup> )			Total consumption of zooplankton by juvenile stock groups (g/km <sup>2</sup> d <sup>-1</sup> )			
	UM	MC	HF	UM	MC	HF	UM	MC	HF	Total
Late June	0.075	0.091	0.065	2843	4322	0	211	393	0	604
Late July	0.084	0.087	0.105	13240	1112	5253	1116	97	551	1764
Late Aug.	0.096	0.084	0.096	7391	503	678	713	42	65	820
Late Sept.	0.070	0.063	0.070	4514	0	190	317	0	13	330
Total	—	—	—	—	—	—	2357	532	629	3518

Stock-specific consumption rates are from model runs. Total weight of juvenile chum salmon stock groups is based on stock compositions (Table 5), date-specific weights (Table 9), and salmon density estimates (Table 10). Total consumption of zooplankton by juvenile stock groups is based on the stock-specific consumption of the total weight of the stock groups. The abbreviations for chum salmon stocks are: unmarked (UM), Macaulay hatchery (MC), and Hidden Falls hatchery (HF).

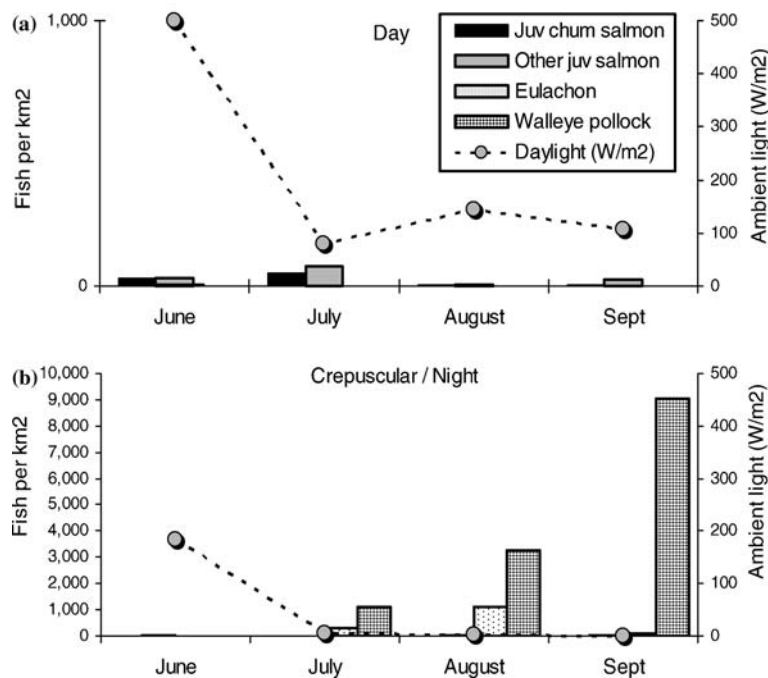


Figure 8. Ambient light and densities of primary fish species caught during day (0700–1600) and night/crepuscular periods (2200–0400) at station ISC on the Icy Strait transect in June, July, August, and September, 2001. Fish catches were averaged from each month and each diel period, and are based each month on  $\geq 5$  hauls for day sample and 3 hauls for the night/crepuscular sample. Ambient light intensities ( $\text{W}/\text{m}^2$ ) are indicated by a dotted line for each period.

habitat. By comparison, juvenile chum salmon migrating offshore from the coast of Japan are mainly found in areas with SST from 9 to 13 °C (Irie, 1985 and 1990 as cited in Mayama and Ishida, 2003). Optimal growth occurs at temperatures of 6–14 °C off the coast of Russia (Karpenko, 2002). Boldt and Haldorson (2002) also used a bioenergetics model with juvenile pink salmon to estimate the effect of temperature on consumption. Using monthly temperatures of 6, 8, 10, and 12 °C to represent a 92-day residence period from May to August, and varying temperature by 2 °C, they found that consumption increased by 10% for higher temperatures and decreased by 8% for lower temperatures. The consumption differences we observed with temperature for juvenile chum salmon were not this great. Our zooplankton consumption estimate for juvenile chum salmon in the two thermal regimes (average June–September temperatures of 11.5 versus 9.8 °C) was about 2% higher for the warmer temperature regime for all combined stocks over a longer 153-day residence.

The fact that consumption rates and amounts were insensitive to temperature in our model runs

may have been a result of our use of adult parameters for juvenile fish. Using adult fish parameters to model larval or young-of-the-year fish and assuming allometric mass relationships can result in significant biases. We were forced to use physiological parameters derived from adult pink and sockeye salmon, and to assume that they did in fact represent those of juvenile chum salmon, because no other values were available (Hanson et al., 1997). Intra-specific changes in physiological parameters between different life history phases may be greater than the differences between closely related conspecifics. For example, intrinsic growth rates for juvenile salmon are typically higher than those for adults at similar temperature regimes (Heard, 1991; Salo, 1991). Similarly, consumption and growth varied more with temperature for juvenile striped bass than for adults (Hartman and Brandt, 1995). Adult parameters generally work well for fish greater than 10 g, and give mixed results for fish between 1 and 10 g; parameter modifications are necessary for fish less than 1 g (Post, 1990; Madon and Culver, 1993; Johnson, 1995; Hanson et al., 1997).

The sizes of juvenile chum salmon we used in the model were 0.4–2 g in May, 3–10 g in June, 16–23 g in July, 34–55 g in August, and 89–122 g in September. Therefore, the physiological parameters in the first two sampling periods of the model likely need refinement to better estimate the effect of water temperature on prey consumption by juvenile salmon.

Our estimate of the percentage of available prey consumed by juvenile salmon in the neritic habitat of Icy Strait was less than 0.05% of the available standing stock. This low consumption estimate is corroborated by several other studies. Karpenko (2002) reported that juvenile chum salmon consumed between 0.1 and 1.1% of the total stock of zooplankton in the upper 10 m of Karaginskii Bay, Kamchatka from June to August over a 5-year period. Boldt and Haldorson (2002) reported that juvenile pink salmon near Prince William Sound, Alaska could consume 15–19% of preferred prey taxa such as large calanoid copepods and amphipods if the available standing crop was fixed over a 10-day period; however, on a daily basis, consumption of no taxon exceeded 2% of the standing stock. Other studies indicated that juvenile chum salmon migrate to offshore waters in response to a decrease in food abundance (Irie, 1990), foraging success (Healey, 1982), or the lack of preferred prey items (Simenstad and Salo, 1982). However, juvenile salmon may impact the available standing crop of zooplankton by consuming certain prey groups at high levels relative to their estimated availability, thus adversely impacting their own ability to feed successfully (Brodeur et al., 1992).

Our low estimates of total zooplankton consumption by juvenile chum salmon in the neritic habitat of Icy Strait are not surprising considering the seasonal patterns in the relative abundance of the prey and the other planktivores. Zooplankton standing crop declined dramatically from May to September in both the upper 20 m and the integrated water column. Average chum salmon densities increased to a peak in July before declining in late summer, while at the same time, densities of planktivorous walleye pollock and eulachon increased dramatically during the crepuscular/night period. We found that compared to juvenile salmon, diel migrating age 1+ walleye pollock numerically dominated the catch by one to two orders of magnitude. Furthermore, we did not

consider other potential planktivores that are abundant in Icy Strait. For example, Purcell and Sturdevant (2001) documented high dietary overlap between planktivorous jellyfish and ctenophores and juvenile walleye pollock, Pacific herring (*Clupea pallasii*), Pacific sandlance (*Ammodytes hexapterus*), and pink salmon in Prince William Sound, Alaska during July and August. Our results suggest that compared to juvenile chum salmon, the other, more abundant planktivores play a major role in seasonal consumption of zooplankton.

Besides the co-occurrence of numerous planktivores, other evidence suggests that juvenile chum salmon were not food limited in the neritic habitat of Icy Strait. The stomach fullness of juvenile chum salmon examined in our study averaged between 67 and 87% over the diel sampling in each month from May until September (Sturdevant et al., 2002), further suggesting that zooplankton standing crop was sufficient. Landingham et al. (1998) also reported that no empty stomachs of chum salmon were observed in pursed seined juvenile chum salmon from the inside waters of southeastern Alaska in July and August.

Our assumptions about prey consumption of zooplankton by juvenile chum salmon could have large implications for the interpretation of the analyses. For this paper, we did not examine zooplankton composition in detail or compute prey selectivity. We assumed that the zooplankton samples represent prey fields actually consumed by the salmon. We determined that five major taxa composed 95% of the prey biomass consumed by juvenile chum salmon (Table 6). However, preliminary results indicate that on average, these taxa represent no more than half of the average total volume of the zooplankton samples from the four stations in Icy Strait in June, July, August, and September, 2001 (data on file, Auke Bay Laboratory). Furthermore, greater percentages of these five prey taxa were found in the zooplankton samples from the integrated water column (49%) compared to those from the upper 20-m water column (26%), indicating substantial differences in prey composition of the two strata. Nonetheless, if we use the reduced estimate of zooplankton standing crop, the maximum consumption at any one period or depth stratum is still less than 0.2% of adjusted prey field. Net selectivity, prey diel migration, prey selection by juvenile chum salmon,

and predator avoidance behaviors of the zooplankton could explain the observed differences between zooplankton present in net and stomach samples. Finally, both the integrated and the upper 20-m water column samples were taken during diurnal periods across Icy Strait, while a companion study using diel zooplankton samples collected in the 20-m water column at one station (ISC) indicate that peak abundances of some prey taxa occurs at night (Sturdevant et al., in press). Detailed diet and zooplankton analyses are currently underway in our laboratory.

Other potential limitations in our approach include assumptions about mortality, timing, and size of juvenile chum salmon. We used simplistic and unverified assumptions about natural mortality during different phases of chum salmon life history. We assumed that the emigration of all wild chum salmon fry was synchronous and limited to a single day (May 1), when in reality, they emigrate from freshwater habitats over a protracted period from March to June, with peak timing varying among stocks and locations. The initial appearance of marked stocks in Icy Strait was clearly related to the proximity of their release site to the study area. Conversely, abundances of certain stocks in Icy Strait declined over time, indicating that the main body of fish had probably migrated seaward to the Gulf of Alaska. However, we assumed that monthly samples in Icy Strait were representative of the marked stock groups even though limited recoveries were available in later months. Thus, we may have underestimated the average size of fish in the stock groups in later periods, thereby reducing stock-specific growth rates and consumption estimates.

We also lacked stock-specific, seasonal WBEC values for both predator and prey. Our WBEC values for juvenile chum salmon were generally similar to those from other studies, but we did not have sufficient samples of individual marked stocks to test for seasonal or geographic differences. Our WBEC values for juvenile chum salmon ranged from 3.8 to 4.2 kJ/g wet wt, with the highest values in May and September. These values are nearly identical to those reported from Prince William Sound, Alaska (3.2–4.4 kJ/g wet wt), where they differed between marine habitats (Paul and Willette, 1997). Boldt and Haldorson (2002) performed a sensitivity analysis with a bioenergetics model using a similar range of

WBEC values for juvenile pink salmon (3.9 and 4.1 kJ/g wet wt) and found only a 4% difference in consumption from May to July. We detected differences in the average WBEC values for mixed stocks across months from May to September, but did not detect differences in the average WBEC values between marked hatchery and unmarked (wild) chum salmon stocks in May. For prey energy densities, we used values from related species that were collected in different geographic areas, and we often did not have complete information on seasonal variation (Groot et al., 1995). Further studies are needed to validate local prey and predator seasonal energy densities.

Our calculations of the percent of available zooplankton consumed by juvenile salmon could have been biased by our assumptions about trawl catchability and our subsequent estimates of salmon densities. We assumed that our trawl catchability was 100%, and that no juvenile salmon either escaped the trawl or were herded into the trawl. Shuntov et al. (1993) reported a salmon catch coefficient of 0.3 for waters in the western North Pacific, with a surface trawl that was fished for 60 min at 4.5–5.0 knots. If we apply the Shuntov et al. (1993) catch coefficient to our trawling operations (20 min at 2.5 knots), then our salmon catches would need to be multiplied by a factor of 3.3. Moreover, large peak catches of juvenile salmon would also increase localized prey consumption. The largest historical catch of juvenile chum salmon in Icy Strait that we have observed using our standard rope trawl was 1231 fish (data on file, Auke Bay Laboratory). This catch exceeds the largest average catch in 2001 (44.1 in July) by a factor of 27.9. If we then multiply the catch coefficient factor (3.3) by this aggregation factor (27.9), the resulting consumption increases by approximately 92.1 times. However, even a 100-fold increase in consumption of the zooplankton standing crop by juvenile chum salmon would only result in a consumption estimate of less than 0.1% of what is available.

Understanding the timing of individual juvenile chum salmon stock groups as they pulse through the littoral and neritic habitats within the Icy Strait migration corridor is important in order to properly estimate their relative consumption of zooplankton resources. This study and others (Courtney et al., 2000; Orsi et al., 2000a, b) have shown that stock timing in Icy Strait is related to

the distance from release of the individual marked release groups.

Unmarked stocks recovered in Icy Strait come from no closer than 200 km away (Table 1). In late May, juvenile chum salmon present in the littoral habitat were all unmarked and were most representative of local stocks of wild chum salmon because of this isolation from hatcheries. In addition, samples of unmarked chum salmon that we collected along the beaches of Icy Strait in late May were smaller (0.7 g) in size than the fish from the nearest hatchery releasing unmarked chum salmon (Gunnuk Creek, 1.3 g on 13 May). Given the distance and the difference in size, the unmarked juvenile chum salmon sampled in Icy Strait were very unlikely to have migrated in from Gunnuk Creek in 8 days. In the neritic habitat, we also maintain that the unmarked fish captured in Icy Strait by trawl offshore in the neritic habitat during June and July represent wild stocks. In late June, the MC stock from 85 km away was most abundant (55%); in late July, the HF stock from 135 km away was most abundant (25%); and in late August, the composition of these marked stocks had diminished to less than 6% each (Table 5). Therefore, there was a distinct pulsing of these marked hatchery stocks through the Icy Strait migration corridor in June and July. The unmarked component that dominated the later catches was likely represented by at least some stocks from the central and southern region. Evidence for this comes from recoveries of a small marked stock from Port Camden near Gunnuk Creek (from 200 km away), which was documented in August (Courtney et al., 2000). Therefore, the late timing (August) of the stocks closest to Icy Strait is good evidence that a high proportion of the unmarked stocks in June and July was comprised of unmarked wild chum salmon rather than unmarked hatchery fish. The mixing of these stocks also occurs at a time when the consumptive demand by juvenile chum salmon on the zooplankton standing crop is greatest. Thus, because of the timing of individual stock groups, wild and hatchery stock trophic interactions are likely to be greatest in June and July, when they most overlap in distribution.

Our estimation of foraging demand by juvenile chum salmon in the northern region of southeastern Alaska is comparable to a coastal marine study directed at pink salmon. Cooney and

Brodeur (1998) estimated the coastal foraging demand of hatchery and wild pink salmon fry on zooplankton in Prince William Sound in 1995. The authors estimated that 669 million pink salmon fry (181 million wild and 488 million hatchery) consumed 24,100 or 62,700 t of zooplankton after 120 or 150 days out; this estimate assumed a 4% growth rate (percent body weight per day), and a gross growth efficiency of 0.45. By comparison, we estimated for conditions in the year 2001 in the northern region in southeastern Alaska, that 559–669 million chum salmon fry (328–438 million wild and 231 million hatchery) consumed 28,000–40,000 t of zooplankton after 133–153 days out; our estimate was bracketed by high and low littoral mortality scenarios and two different temperature ranges that four stock groups were exposed to. These two estimates of zooplankton consumption by ecologically similar, planktivorous salmonids are remarkably close, despite the differences in modeling approaches and regions studied.

An important aspect of our research using the bioenergetics approach has been to attempt to quantify and understand the biophysical parameters associated with consumption of the available zooplankton by hatchery and wild juvenile chum salmon in southeastern Alaska. Our study presents a spatial and temporal collection of biophysical input data, specific to juvenile chum salmon stocks, as they migrate seaward through the Icy Strait corridor. Understanding mechanisms limiting salmon production and carrying capacity is predicated on the identification and measurement of the appropriate biophysical input parameters. One recommendation made after an extensive review of studies conducted by U.S. researchers on the early ocean life history of Pacific salmon, was to place a greater research emphasis on local interactions between hatchery and wild juvenile salmon and their prey resources (Brodeur et al., 2003). Our research attempts to fill this knowledge gap. Refinement of this data will serve to assess the biophysical conditions that impact the survival of juvenile salmon.

### Summary/conclusion

Interactions between hatchery and wild stocks of juvenile chum salmon do occur temporally in the

neritic habitat of Icy Strait, Alaska, particularly during June and July; however, prey resources are large relative to the consumption demands of these stock groups. We estimated that hatchery and wild stocks of juvenile chum salmon consumed only a small fraction of the available prey resource in the habitat. Under the modeling assumptions, this result infers that current levels of hatchery production in southeastern Alaska do not represent a significant impact on the prey resource available in neritic marine habitats represented by the Icy Strait migration corridor. Identifying physiological parameter values specific to juvenile chum salmon is critical, because the standard adult salmon parameter values available may have influenced our consumption rate estimates, particularly for juveniles less than 10 g. Improved estimates of the early marine abundance and mortality of juvenile chum salmon are also needed.

Further bioenergetics modeling of prey consumed by abundant planktivores that co-occur with juvenile salmon is needed to illustrate predation pressure on the available prey resource. Predation by other planktivorous fishes, such as walleye pollock, eulachon, herring, capelin, and pink salmon, likely has greater impact on the seasonal zooplankton standing crop than juvenile chum salmon do. Validation of the abundance and distribution patterns of these planktivores, in addition to their degree of prey selection from the total zooplankton prey resource, is needed to determine their actual impact on the standing crop of zooplankton also utilized by juvenile salmon. In spite of these caveats, a bioenergetics approach enabled us to identify data gaps, biological interactions, and the scale of consumptive demand that could have direct bearing on the study of the carrying capacity of the nearshore ecosystem for juvenile salmon.

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