Early marine distribution and trophic interactions of juvenile salmon in Puget Sound

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A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

University of Washington

2003

Program Authorized to Offer Degree: School of Aquatic and Fishery Sciences

University of Washington
Graduate School

This is to certify that I have examined this copy of a master’s thesis by

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Abstract

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Some species of Pacific salmon (*Oncorhynchus* spp.) in Puget Sound have been experiencing widespread declines. Of particular concern are the wild fall-run chinook salmon (*Oncorhynchus tshawytscha*), which are believed to have the longest residence in and dependence on the estuarine environment. There is mounting evidence that growth during the early marine residence of most ocean-type species of anadromous Pacific salmon determines overall marine survival trends. I studied juvenile salmon at delta, nearshore, and neritic sites in a northern (NPS) and a southern (SPS) Puget Sound sampling region from April through September 2001 and 2002 to evaluate spatial and temporal differences in distribution, size structure, and diet among species (chum, pink, coho, and chinook) of salmon and between hatchery and unmarked (coho and chinook) salmon. With this basic life history information, I used the Wisconsin bioenergetics model to compare spatially and seasonally relevant quantitative estimates of consumption demand and growth performance between species of juvenile salmon, and between hatchery and unmarked chinook salmon emigrating through nearshore environments in Puget Sound. I found that foraging conditions for juvenile salmon were dynamic, varying spatially, annually, and seasonally. Ultimately, spatial and temporal differences in environmental conditions and the forage base may significantly influence the potential for growth and survival of juvenile salmon entering different areas of Puget Sound.

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Acknowledgements

I would like to thank my committee, Dave Beauchamp, Ray Buckley, and Si Simenstad for all their help over the past three years, from inspiring me to come to UW, to help with project planning and design, to long yet exciting hours in the field, and to many helpful discussions on improving (or trying to) my science and writing skills. Thanks to many hard workers of the Beauchamp lab - including Nathanael Overman, Chris Sergeant, Michael Humling, Steve Damm, Angie Lind, Jim Matilla, Kenton Finkbeiner, Mistie Hammer, and Josh Robins - for their tireless efforts during long and tiring hours in the field and in the lab. I am also very grateful for the additional field help from Dave Molenaar, Kip Killeprew, Dave Tipton, Trevor King, and Larry LeClair, as well as many others. Many thanks to Ayesha Gray, Mike Mazur, Jen McIntyre, and Jamal Moss for showing me those grad student ropes, and for their friendship, insight, and support throughout my experience here. Thanks to Alison Cross and Sarah McCarthy for help with the art of fish scales and all sorts of other useful information.

I owe a special thanks to my family, who always encourage and support me in my endeavors and inspire me to strive for noble achievements. And more thanks to Adam, for helping to keep me well fed and in excellent spirits, and for forcing me to think intelligently and to try to communicate with an audience greater than the fisheries community. And of course, thanks always to Deb Orgera, Bonnie Ponwith, Narelle Hall, and Sylvia Earle for helping to guide me onto such an exciting and fulfilling path, encouraging adventure, exploration, and striving to save what we love.

This research was made possible by funding from the Hatchery Scientific Review Group (HSRG), the UW Mason Keeler fellowship, the Washington Department of Fish and Wildlife (WDFW), and the Washington Cooperative Fish and Wildlife Research Unit (WACFWRU).

INTRODUCTION

Need/Rationale

Many Pacific salmon stocks in Puget Sound are experiencing widespread declines. All Puget Sound chinook salmon (*O. tshawytscha*) and Hood Canal summer-run chum salmon (*O. keta*) are listed as threatened, while Puget Sound coho salmon (*O. kisutch*) are candidates for listing under the Endangered Species Act (ESA). These species employ different (and often multiple) life history strategies, however all use Puget Sound for feeding and migration on their journey to the Pacific Ocean. While there is valuable background information on juvenile salmon in Puget Sound and Hood Canal from the 1970's and 1980's, little is known about the ecology of juvenile salmon in current times during their residence in Puget Sound. Puget Sound may serve as an important rearing environment during a potentially critical transition from freshwater to the open ocean for these juvenile salmon.

The highest mortality during the period between seaward migration and adult return of Pacific salmon is believed to occur in the estuarine and early marine stages (Parker 1962; Royal 1962; Furnell and Brett 1986). Estimates for this early "coastal" mortality rate ranged between 55 and 75% for juvenile pink salmon (*O. gorbuscha*) in British Columbia (Parker 1968). A modeling study on factors affecting declines in Snake River spring/summer chinook salmon concluded that, while much-advocated mitigation to dam-induced mortality, including dam breaching, may reduce mortality on chinook salmon, reductions in estuarine/early ocean mortality must be reduced by 5-10% to stabilize these salmon stocks (Kareiva et al. 2000). There is mounting evidence that estuarine/early marine residence is a "critical period" (Hjort 1914) for most species of anadromous Pacific salmon and that growth during this period determines overall marine survival trends (Holtby et al. 1990; Hargreaves 1997; Murphy et al. 1998; Tovey 1999).

Most explanations for early marine mortality have focused on either food limitation or predation. Beamish and Mahnken (1998) incorporated both of these explanations into a cohesive and more explicit "critical size – critical period" hypothesis. In their hypothesis, regulation of salmon abundance through ocean mortality occurs in two stages. The first stage occurs soon after juvenile salmon enter the estuarine or nearshore marine environment. Mortality in this phase is hypothesized to be mainly due to predation. Size at this stage is critical because it partially determines the amount of predation risk. According to size-spectrum theory, larger, fast-growing individuals spend less time vulnerable to the many gape-limited predators than their smaller and slower-growing conspecifics (Sogard 1997). The densities of the predators and juvenile salmon also affect predation risk. The second big peak in mortality comes in the late fall and winter of their first year in the ocean and is a function of the condition of the juvenile. It is the growth preceding this stage, mainly during the summer, which is critical in ensuring the juvenile reaches a size and condition that will reduce its chances of being "culled" during its critical first winter. The final size of salmon populations are mainly set after this first winter, and shifting ocean-climate conditions will cause the stock level to fluctuate around a mean carrying capacity (Beamish and Mahnken 1998).

Smolt size at ocean entry is considered important for the survival of some salmon stocks (Parker 1971; Healey 1982; Ward et al. 1989; Henderson and Cass 1991). Dietary overlaps among juvenile salmon, and between hatchery and wild salmon, may result in inter- and intra-specific competition that would negatively affect growth rates and overall smolt size (Fisher and Pearcy 1996; Sturdevant 1999). In addition, seasonal shifts in prey resources and water temperature may affect the potential growth rates of juvenile salmon. Poor quality feeding areas, which may vary over short and longer time frames, may result in increased susceptibility to predation due to poorer condition and smaller sizes of fish (Brodeur et al. 1992; Perry et al. 1996). The quality of feeding areas can also affect migration rates and residence times, since salmon are believed to leave areas of poor food quality faster than when food sources are abundant (Healey 1982; Simenstad and Salo 1982; Orsi et al. 2001). The carrying capacity of localized areas may be exceeded when episodically high densities of salmon are produced by coincident releases of large numbers of hatchery salmon during peak wild salmon emigrations, leading to competition for a limited food supply if diets are similar.

Background

Estuarine and coastal marine environments play an important role in the life history of salmon, although the relative importance differs among species due to differences in residence times and utilization of these environments (Simenstad et al. 1982; Aitken 1998). Salinity gradients in estuaries provide a physiological transition zone for migrating juveniles as they undergo smoltification (Simenstad et al. 1982; Thorpe 1994). Physical characteristics, including structure provided by shallow water habitat and emergent aquatic vegetation or woody debris, and high turbidity regions, may facilitate predator avoidance (Simenstad et al. 1982; McMahon and Holtby 1992; Gregory and Levings 1996, 1998). The higher productivity of prey communities in estuarine and marine waters (relative to freshwater) provides favorable foraging conditions and valuable rearing and nursery habitat for juvenile salmon (Simenstad et al. 1982; Thorpe 1994; Aitken 1998). Rapid growth rates of up to 5-10% body weight/day (which is among the highest for all life history stages) have been recorded in coastal and estuarine waters (Table 1).

Estuarine and nearshore marine environments may be particularly important to chinook salmon, which reside much longer in estuarine environments than the other species of Pacific salmon (Stober et al. 1973; Shepard 1981; Simenstad et al. 1982). The diverse life history strategies of chinook salmon result in migrations of juveniles into estuaries throughout much of the year (Reimers 1973; Iwamoto and Salo 1977). Fall-run chinook salmon subyearlings and spring-run yearlings enter Puget Sound as early as March, and populations peak in nearshore areas in the summer months, although some may persist through the fall. Juvenile chinook salmon are known to spend 6-16+ weeks in Puget Sound and Hood Canal with individuals remaining for 1-7 weeks (Simenstad et al. 1982). There are also resident chinook salmon that remain in Puget Sound until maturity (Simenstad et al. 1982). Rapid growth rates, 0.37-0.87mm/day, have been recorded for juvenile chinook salmon in Puget Sound (Salo 1969). The relatively high usage of (and potential dependence on) Puget Sound estuaries by ESA-listed fall-run chinook salmon suggests that juvenile outmigration through Puget Sound may be a critical period in their life history.

Salmon, while often described as opportunistic feeders (Healey 1982), do show some diet preferences in estuaries by species, size, season and habitat (Table 2**;** Kaczynski et al. 1973; Conley 1977; Harris and Hart 1977; Fresh et al. 1978; Simenstad et al. 1980; Fresh et al. 1981; Godin 1981; Healey 1982; Pearce et al. 1982; Parametrix 1985; S. Bollens, San Francisco State University, unpublished data; J. Cordell, University of Washington, unpublished data; J. Cordell and C. Simenstad University of Washington, unpublished data; C. Simenstad and J. Cordell, University of Washington, unpublished data). Chinook and coho salmon, which are larger in size during their seaward migration, tend to be increasingly piscivorous as they grow, whereas pink and chum salmon feed mainly on invertebrates (Kaczynski et al. 1973; Healey 1982; Simenstad et al. 1982). Epibenthic and planktonic crustaceans are dominant prey items in the diets of all salmon species. In general, as fish grow and move from shallow nearshore environments to offshore waters, diets shift from epibenthic and neustonic prey items to more planktonic and nektonic prey. Early in their estuarine residence, and at the smaller sizes, pink and chum salmon feed mainly on epibenthic harpacticoid copepods and other epibenthic crustaceans. Chinook salmon, which tend to have the most diverse usage and dependence on estuarine environments, have the most diverse diets, feeding largely on neustonic and drift insects. Coho salmon also have diverse diets but tend to focus more on larger planktonic crustaceans (euphausiids, amphipods, and crab larvae) and fish.

Diet information for juvenile salmonids in nearshore (Kaczynski et al. 1973; Conley 1977; Fresh et al. 1978; Fresh et al. 1981; Pearce et al. 1982; Parametrix 1985; S. Bollens, San Francisco State University, unpublished data; J. Cordell, University of Washington, unpublished data; J. Cordell and C. Simenstad University of Washington, unpublished data; C. Simenstad and J. Cordell, University of Washington, unpublished data) and neritic (Fresh et al. 1981; Beamish et al. 1998) Puget Sound waters is relatively limited and dates mainly to the 1970’s (Table 3). Major diet items for all species included euphausiids, crab larvae, insects, amphipods and copepods (epibenthic and planktonic), as well as larval and juvenile fishes for chinook and coho salmon. The greatest potential for dietary overlap appeared to exist between comparably sized chinook and coho salmon (Conley 1977; Parametrix 1985), and between chum and pink salmon

(Kaczynski et al. 1973; Conley 1977; Simenstad et al. 1980; Parametrix 1985) at nearshore sites, and between coho and chum salmon in neritic waters (Beamish et al. 1998). In addition, there may be substantial dietary overlap and potential for competition between and among hatchery and wild salmon, especially during large hatchery releases which tend to coincide with peak outmigration of wild salmon. In Puget Sound, hatchery production constitutes 70-75% of the salmon (mainly chinook and coho salmon) population in Puget Sound (HSRG 2002).

In the estuarine and marine environment, juvenile salmon face many potential predators including larger salmon and trout, Pacific cod (*Gadus macrocephalus)*, walleye pollock (*Theragra chalcogramma)*, spiny dogfish (*Squalus acanthias*; Table 4), birds and marine mammals (Emmett 1997). Few studies in estuaries have quantified juvenile salmonid mortality due to piscivores. In Puget Sound, there is concern that releases of yearling hatchery chinook salmon and juvenile coho salmon may result in intrageneric predation and cannibalism that may negatively impact natural populations (Buckley 1999). A few studies have reported low levels ($\leq$ 1 fish/stomach) of salmonid predation based on estimates from limited diet analysis (Mathews and Buckley 1976; Cardwell and Fresh 1979; Fresh et al. 1981; Simenstad et al. 1982), however most studies were not designed to investigate predation. In order to infer an overall potential predation impact, diet data must be collected at the appropriate spatial and temporal scales and used in conjunction with predator abundances (Beauchamp et al. 1995). Even low apparent rates of predation could produce significant impacts if the predator abundance is high.

It is essential to take a food web perspective in order to understand the complicated array of potential processes and interactions affecting aquatic communities (Paine 1980, 1988). Determining which processes regulate populations in a food web, and the strength of interactions between populations, gives us insight into the underlying mechanisms and conditions that may mediate them (Paine 1980; Brandt and Hartman 1993). Quantifying consumption rates of a predator on specific prey populations is one way to estimate interaction strengths. There are various methods for estimating consumption (Ney 1990). Direct measurements are the most labor and time-intensive, involving field (and laboratory) measurement of gut contents, fullness, and gastric evacuation rate. Results are subject to sampling bias, but this method produces realistic data for individual fish over discrete time intervals. Production-based approaches take a broad and simplified view of the food web, relating the biomass of a consumer population to the biomass of its prey base. This approach can be used with minimal labor and data to rapidly calculate consumption for populations on an annual basis, however individual and intra-annual consumption estimates are not possible and results are limited by the accuracy of the inputs.

Bioenergetically-based food web models, used in conjunction with directed field sampling, provide an effective method for quantifying trophic interactions in a temporal, spatial, and ontogenetic framework (Ney 1990; Hansen et al. 1993). The requisite field sampling is less labor-intensive than for direct measurement methods, and much of the physiology of feeding and metabolism is built in as model parameters. The widely used Wisconsin bioenergetics model (Hanson et al. 1997) uses an energy-balance approach in which total energy consumption (C), over a particular time frame, equals the sum of growth (G, positive or negative), metabolic costs (M), and waste losses (W). The Wisconsin model is very adaptable and operates on a daily time step, which allows for a fine-grained analysis of trophic interactions over short time scales. This sensitivity is particularly appropriate for dynamic conditions, like those experienced by emigrating juvenile salmon, where residence times are variable and short-term, and environmental factors (i.e., water temperature), diets, and sizes are rapidly changing. Bioenergetic models are, however, limited by the accuracy of their assumptions and input parameters, and expanding individual consumption estimates to a population level may magnify the individual error. The model is most useful for making relative comparisons of fish consumption rate estimates, more so than for making precise quantitative predictions or estimates of growth (Kitchell et al. 1977; Bartell et al. 1986; Ney 1993).

The Wisconsin bioenergetics model has been used successfully to identify carrying capacity of systems, seasonal bottlenecks in food supply, and impacts of predation primarily in freshwater systems (Kitchell et al. 1977; Stewart et al. 1981; Stewart and Ibarra 1991; Beauchamp et al. 1995; Rand et al. 1995; Cartwright et al. 1998; Baldwin et al. 2000). The model has also been used to estimate temporal consumption demand and growth in estuarine and marine waters (Brandt et al. 1992; Brodeur et al. 1992; Ciannelli et al. 1998; Davis et al. 1998). In coastal marine waters, the bioenergetics model has yielded consumption estimates within 5-10% of independently generated field estimates for juvenile chinook and coho salmon (Brodeur et al. 1992). Other applications of the model include estimating mortality due to predation and evaluating and comparing growth performance under differing conditions like water temperature, prey quality and availability, and consumer density.

In the following chapters, I examine the feeding conditions and growth performance of juvenile salmon in Puget Sound by using bioenergetics modeling to synthesize information on their early marine trophic dynamics obtained from two years of sampling and from supporting literature. During two seasons of field sampling in a northern and a southern Puget Sound area, I obtained information on timing, size structure and diet of juvenile salmon at nearshore and neritic locations. Focusing on ESA listed chinook salmon, I used the Wisconsin bioenergetics model to determine and compare spatially and seasonally relevant quantitative estimates of consumption demand and growth performance between hatchery and wild (unmarked) chinook salmon and between different salmon species. I also investigated how seasonal, annual, and regional shifts in diet, temperature, and structure and sizes of the salmon community affect consumption of key prey taxa and salmon growth performance. A better understanding of the temporal distribution, trophic interactions, and survival of Puget Sound salmon stocks is necessary to identify and potentially remedy factors contributing to their decline.

NULL HYPOTHESES

Overarching hypothesis: Early marine residence represents a critical period for growth and survival of juvenile salmon in Puget Sound.

***Primary question**: What is the role of nearshore and neritic Puget Sound habitat in the life history of juvenile salmon?*

1. There are no differences in the timing and relative abundance (as measured by catch rates) among sizes and species of salmon, between hatchery and unmarked juvenile salmon, rearing in or migrating through northern and southern Puget Sound sites.
2. There is no difference in catch timing, relative abundances, sizes, and temporal diet composition patterns of salmon between 2001 and 2002, between northern and southern Puget Sound sites and between nearshore and neritic sites.
3. There is no significant diet overlap among salmon species or between hatchery and unmarked salmon conspecifics.
4. There is no predation among juvenile salmon species or between hatchery and unmarked salmon in nearshore Puget Sound waters.

***Secondary question**: Do feeding conditions (thermal experience, prey composition and energetic quality) or growth performance of juvenile salmon change during their residence in Puget Sound?*

1. There are no differences in the estimated growth and modeled consumption demand among sizes and species of salmon, or between hatchery and unmarked juvenile salmon, rearing in or migrating through northern and southern Puget Sound sites.
2. There are no differences in the estimated growth and modeled consumption demand for salmon within the outmigration “season”, between sampling years, between northern and southern Puget Sound sites, and between nearshore and neritic sites.
3. There is no difference in growth efficiency for salmon within the outmigration “season,” between sampling years, between northern and southern Puget Sound sites, and between nearshore and neritic sites.

OBJECTIVES

1. Measure and compare temporal and spatial distributions of juvenile salmon by species, size, age, and by hatchery or wild (unmarked) origins for chinook and coho salmon, in delta, nearshore and neritic waters of northern and southern Puget Sound during April through September, 2001 and 2002.
2. Describe and compare the temporal diet composition of juvenile salmon by capture zone (delta, nearshore or neritic), species, size, age, and by hatchery or wild (unmarked) origin for chinook and coho salmon, in the northern and southern regions of Puget Sound.
3. Using the bioenergetics model, estimate spatially and seasonally relevant temporal consumption demand and compare growth performance metrics for pulses of outmigrating juvenile salmon.
4. Determine the potential role of predation by juvenile salmon on the mortality of other juvenile salmon during their overlapping residence in Puget Sound.

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Table 1. Estuarine/early marine growth rates for outmigrating juvenile salmon.

Salmon Species	**Growth Rate (mm/d or % wt/d)**	**Sample Area**	**Reference**
Chinook (*O. tshawytscha*)	0.37mm/d	(Duwamish estuary) Puget Sound, WA	Salo 1969
Chinook (*O. tshawytscha*)	0.81-0.87mm/d	Nanaimo estuary, B.C.	Sibert 1975
Chinook (*O. tshawytscha*)	5.5%	Nanaimo estuary, B.C.	Healey 1982
Chinook (*O. tshawytscha*)	3.5%	Nitinat estuary, B.C.	Healey 1982
Chum (*O. keta*)	5.7%	Nanaimo estuary, B.C.	Healey 1979
Chum (*O. keta*)	5.7-8.6%	Hood Canal, WA	Salo et al. 1980
Chum (*O. keta*)	2.3-4.1%	Gulf of Alaska ("straits")	Orsi et al. 2001
Pink *(O. gorbuscha)*	3.1-7.1%	Auke Bay, Gulf of Alaska	Mortensen et al. 2000
Pink *(O. gorbuscha)*	1.5-7.6%	British Columbia	LeBrasseur and Parker 1964; Healey 1980
Pink *(O. gorbuscha)*	3.5-5.2%	Prince William Sound, AK	Willette 1996
Coho (*O. kisutch*)	1.5%	Nanaimo estuary, B.C.	Healey 1982
Coho (*O. kisutch*)	1.9%	Strait of Georgia, B.C.	Healey 1982

Table 2. Prey items, and their associated habitat, for juvenile Pacific salmon in estuarine and nearshore marine waters.

Habitats are ranked in order of importance to dietary contribution.

HABITAT	PREY	CHINOOK	COHO	CHUM	PINK
Benthos/Epibenthos		3	3	1	2
	Cumacean				
	Fish/invertebrate eggs				
	Gammarid amphipod	*		*	
	Harpacticoid copepod			*	*
	Isopod				
	Mysid		*		
	Ostracod				
	Polychaete	*	*		
	Shrimp		*		
Plankton		4	1	2	1
	Barnacle larvae/slough				
	Calanoid copepod			*	*
	Cladoceran				
	Crab larvae	*	*	*	*
	Euphausiid	*	*		
	Gammarid amphipod				
	Hyperiid amphipod				
	Larvacean			*	*
Nekton	Fish (larval, juvenile)	2	2	4	4
	Herring	*			
	Sand lance	*	*		
	Salmon		*		
Neuston	"Insects" - terrestrial and aquatic	1	4	3	3
	Arachnidae				
	Coleoptera				
	Diptera	*		*	
	Homoptera				
	Hymenoptera	*		*	
	Lepidoptera				
	Trichoptera				

* Dominant prey types

Table 3. Studies detailing dietary information on juvenile salmon in nearshore and neritic Puget Sound and Hood Canal waters.

REFERENCE	AREA*	ZONE**	DATE	JUVENILE SALMON DIETS
Bax et al. 1978	Hood Canal	nearshore, neritic	Jan-Jul 1977	chum, coho, chinook, cutthroat
Beamish et al. 1998	CPS	neritic, offshore pelagic	Apr-Sep 1997	chinook, chum, coho
S. Bollens, San Francisco State University, CA, unpublished data	Hood Canal	nearshore, offshore	Apr-Oct 1985-1987	chinook, chum
Conley 1977	Everett Bay, NPS	nearshore, neritic	Apr-May 1975	chinook, chum, coho
J. Cordell, University of Washington (UW), Seattle, WA, unpublished data	Shilshole Bay, CPS	nearshore	Jun-Aug 1999	chinook
J. Cordell and C. Simenstad, UW, unpublished data	Commencement Bay, CPS	nearshore	Mar-Jun 1983-1985	chinook, chum, coho
Fresh et al. 1978	Nisqually Reach, SPS	nearshore, neritic	Mar-Aug 1977-1978	chinook, chum, coho, pink
Fresh et al. 1981	CPS, SPS	nearshore, neritic, offshore pelagic	Aug 1978-Sep 1979	chinook, chum, coho
K. Fresh, NOAA-Fisheries, Seattle, WA, unpublished data.	SPS	nearshore, neritic	Mar 1974-Feb 1975; Feb-Jul 1978	chinook, chum, coho; chinook
Kaczynski et al. 1973	Port Susan - NPS, Anderson Island - SPS, Hood Canal	nearshore	Apr-Jun 1970-1971	chum, pink
Parametrix 1985	Everett Bay, NPS	nearshore, neritic	Apr-May 1984	chinook, chum, coho, pink
Pearce et al. 1982	Nisqually Reach, SPS	nearshore	Apr-Sep 1979-1980	chinook, chum, coho
Simenstad et al. 1980	Hood Canal	nearshore, neritic	Jan - Jul 1977-1979	chum, coho, chinook, cutthroat
C. Simenstad and J. Cordell, UW, unpublished data	Duwamish Head, CPS	nearshore	June 1980	chinook

*central Puget Sound (CPS), northern Puget Sound (NPS), southern Puget Sound (SPS)

**nearshore = intertidal and shallow subtidal (beach seine); neritic = shallow surface waters (tow net); offshore pelagic = top 30-45m of surface waters over deep bottom (purse seine, trawl)

Table 4. Potential piscivorous juvenile salmon predators in the estuary/early marine environment.

Predator Species	**Salmon prey**	**Sample Area**	**Reference**
Juvenile coho salmon	pink and chum salmon	British Columbia, Gulf of Alaska, Puget Sound	Parker 1971, Kaczynski et al. 1973, Mortensen et al. 2000
Subadult coho salmon	chinook salmon	Puget Sound, WA	Fresh et al. 1981
Adult coho salmon	juvenile salmon	Gulf of Alaska	Wing 1985, Orsi et al. 2000
Subadult chinook salmon	chinook salmon	Pacific Ocean (near mouth of Columbia River)	Fresh et al. 1981
Coastal cutthroat trout	juvenile salmon	Puget Sound and Hood Canal, WA	Salo et al. 1980; Fresh et al. 1981; Jauquet 2002
Steelhead	chinook salmon	Pacific Ocean (near mouth of Columbia River)	Fresh et al. 1981
Dolly varden	pink, juvenile salmon	Gulf of Alaska, B.C. and AK	Lagler and Wright 1962, Mortensen et al. 2000
Sculpins	pink salmon	Gulf of Alaska	Mortensen et al. 2000
Pacific staghorn sculpin	juvenile salmon	Hood Canal, WA	Salo et al. 1980
Pacific cod	juvenile salmon	Hood Canal, WA	Salo et al. 1980
Spiny dogfish	chinook and coho salmon	Straits of Georgia, Gulf of Alaska	Beamish et al. 1992, Orsi et al. 2000
Walleye pollock	juvenile salmon	Prince William Sound, AK	Willette 1996

Chapter I: Timing and size structure of juvenile salmon in nearshore waters of Puget Sound

ABSTRACT

I studied juvenile salmon in delta, nearshore, and neritic waters of northern (NPS) and southern (SPS) Puget Sound from April through September 2001 and 2002 to evaluate regional and temporal differences in distribution and size structure among species (chum, pink, coho, and chinook) of salmon and between hatchery and wild (coho and chinook) salmon. Water was consistently warmer (8-18.8°C) and less saline (0.0-27.7 ppt) in NPS than at SPS sites (9.5-14.6°C, 13.0-30.4 ppt). Delta sites had lower salinities and more variable water temperatures than nearshore and neritic sites. The timing of peak nearshore use was similar at delta and nearshore sites within sampling regions but differed between northern and southern Puget Sound. The majority of juvenile salmon were caught in nearshore marine sites between April and June (pink and chum salmon generally peaking earlier than chinook and coho salmon), with most peak catches in May. A second peak for chinook salmon occurred during July in NPS. Peak catches for chum and chinook salmon were greater at SPS than NPS sites in both years, whereas coho and pink salmon catches were greater at NPS sites. The proportions of hatchery fish were much greater in SPS than NPS for coho (29% in SPS vs. 6% in NPS during 2002) and chinook salmon (98% in SPS vs. 44% in NPS during 2002). With the exception of chum salmon in NPS, total and peak catches of each species were greater in 2002 than 2001. Peak catches of all juvenile salmon species in neritic waters occurred in June in southern Puget Sound. Mean sizes of juvenile salmon were slightly but consistently smaller in northern Puget Sound than at southern sites and at delta versus nearshore and neritic sites. Overall, hatchery coho and chinook salmon were slightly larger than their unmarked counterparts. Extended species residence times (their seasonal duration in the catches) suggest that nearshore environments may be particularly important to chinook salmon in NPS, and to chum salmon in SPS. Differences in the magnitude and timing of hatchery inputs, salinity and water temperature may affect the

sizes, nearshore use, and potential for growth of juvenile salmon entering different areas of Puget Sound.

INTRODUCTION

As in many areas of the Pacific Northwest, some stocks of anadromous Pacific salmon in Puget Sound are experiencing widespread declines. Puget Sound chinook salmon (*O. tshawytscha*) and Hood Canal summer-run chum salmon (*O. keta*) are listed as threatened, while Puget Sound coho salmon (*O. kisutch*) are candidates for listing under the Endangered Species Act (ESA). These species employ different (and often multiple) life history strategies; however, all use Puget Sound as a migration corridor on their journey to the Pacific Ocean as smolts. There is mounting evidence that estuarine/early marine residence is a “critical period” (Hjort 1914) for most species of anadromous Pacific salmon and that growth during this period often affects overall marine survival trends (Neilson and Geen 1986; Holtby et al. 1990; Hargreaves 1997; Murphy et al. 1998; Tovey 1999). Puget Sound may serve as an important rearing environment during a potentially critical transition from freshwater to the open ocean for these juvenile salmon.

The relative importance of estuarine and coastal marine environments differs among species due to differences in residence times and utilization of these environments (Healey 1982a; Simenstad et al. 1982; Aitken 1998). Of the juvenile salmon that migrate to sea during their first year (age-0), pink (*O. gorbuscha*) and chum salmon usually arrive in estuarine waters earliest (February-April) and at the smallest size (pink salmon often the smallest), followed by chinook (April through July). Most stream-type coho and chinook salmon migrate to sea after rearing for one year in freshwater, and arrive in estuarine waters substantially bigger than subyearling migrants (April through June). Ocean-type chinook salmon are believed to be the most dependent (Healey 1982a) on estuarine environments, followed by chum and then coho salmon (Bostick 1955; Stober et al. 1973; Shepard 1981; Healey 1982a; Simenstad et al. 1982). Pink and sockeye salmon (*O. nerka*) migrate rapidly to the ocean, and are considered the least dependent on estuaries.

The high productivity of prey communities in estuaries and nearhshore marine waters provides favorable foraging conditions and valuable rearing and nursery habitat for juvenile salmon (Healey 1982a; Simenstad et al. 1982; Thorpe 1994; Aitken 1998). Rapid growth rates of up to 5-9% body weight/day (among the highest for all life history stages) have been recorded in coastal and estuarine waters (LeBrasseur and Parker 1964; Healey 1979; Healey 1982b; Mortensen et al. 2000). Juvenile salmon reside mainly in surface waters and nearshore environments are considered important to smaller fish for feeding and predator avoidance (Iwamoto and Salo 1977; Simenstad et al. 1982). Potentially significant predators include larger salmon and trout (Kaczinski et al. 1973; Fresh et al. 1981; Mortensen et al. 2000; Jauquet 2002), birds and marine mammals (Emmett 1997), with low incidences of predation also observed by Pacific cod (*Gadus macrocephalus*, Salo et al. 1980*)*, sculpins (Mortensen et al. 2000*)*, and spiny dogfish (*Squalus acanthias*, Beamish et al. 1992; Orsi et al. 2000). Transition to offshore surface waters is believed to be associated with increased size (potentially a size threshold) and/or a temporal component (LeBrasseur and Parker 1964; Wetheral 1970; Blackbourn 1976; Healey 1980; Salo et al. 1980; Dawley et al. 1986).

Seasonal differences in community structure, prey availability, and water temperature may affect the quality of nearshore environments for feeding and growth as well as exposure to predators. Timing and size of smolts at arrival to estuaries have been positively correlated to survival (Blackbourn 1976; Parker 1971; Healey 1982a; Ward et al. 1989; Henderson and Cass 1991), whereas high densities of juvenile salmon in estuaries have been linked to reduced growth (Reimers 1973) and survival (Blackbourn 1976). In Puget Sound, hatchery production accounts for approximately 70% of the harvested salmon (HSRG 2002; Washington Department of Fish and Wildlife, unpublished data). Although precise ratios of hatchery to wild juvenile salmon production are unknown, releases of large numbers of hatchery fish during the normal spring outmigration by depressed natural stocks may lead to reduced growth if densities are high enough to cause localized reductions in the food supply and exceed the carrying capacity of nearshore Puget Sound waters. There is also concern that hatchery releases of the larger yearling chinook salmon and coho salmon during peak migrations of smaller wild fall chinook, pink, and chum salmon may result in significant predation mortality (Buckley 1999).

Juvenile salmon have been captured in moderate to high abundances at nearshore and neritic habitats in Puget Sound and Hood Canal between March and July, whereas small numbers were caught throughout the year (Tyler 1963; Fresh 1979; Miyamoto et al. 1980; Salo et al. 1980; Fresh et al. 1981; Pearce et al. 1982). In central Puget Sound, chinook and chum salmon persisted in large numbers in relatively shallow (0-15m, some down to 30m) offshore waters between July and September 1997, while most coho salmon had left the Sound after mid-summer (Beamish et al. 1998). Rapid growth rates have been recorded for juvenile chinook salmon in Puget Sound (0.37-0.87mm/day; Salo 1969) and chum salmon in Hood Canal (5.7-8.6% body weight/day; Salo et al. 1980). The relatively high usage of Puget Sound estuaries by listed ocean-type chinook and chum salmon suggests that juvenile emigration through Puget Sound may be a critical period in their life history. While valuable information on juvenile salmon in Puget Sound and Hood Canal was collected in the 1970's and 1980's when there was not conclusive evidence that wild salmon populations were in decline (Simenstad et al. 1982), little is known about the recent ecology of juvenile salmon during their residence in Puget Sound. In this study, I provide basic ecological information about the timing, size structure, and residence time of juvenile salmon at nearshore and neritic environments in two regions of Puget Sound in 2001 and 2002.

METHODS

STUDY AREA

Puget Sound is a deep, elongated glacial fjord composed of underwater valleys, ridges and basins with an average depth of 135m. The maximum depth of 285m occurs just north of Seattle in the large main basin. Saltwater from the ocean is mixed with fresh water draining from the surrounding watershed. A shallow sill separates the main basin from the southern basin near the Tacoma Narrows. The southern basin receives <10% of the freshwater draining into Puget Sound, primarily from the Nisqually and Deschutes rivers plus smaller rivers and streams (Burns 1985). Northeast of the main basin, the

Whidbey basin includes the waters of Possession Sound, Port Susan, Saratoga Passage and Skagit Bay. The Whidbey basin is fed by the some of the Sound's largest rivers (the Skagit, Snohomish and Stillaguamish) and receives 60% of the freshwater entering Puget Sound (Burns 1985).

For this study, I focused on two sampling areas: a northern Puget Sound (NPS) region encompassing Possession Sound/Port Susan/Port Gardner in the Whidbey basin, and a southern Puget Sound (SPS) region, south of the Tacoma Narrows sill, encompassing Cormorant Passage/Wollochet Bay/south of the Narrows in the southern basin. These two sampling regions include freshwater exit points for both wild juvenile salmon and those from several major hatchery-based stock enhancement programs (Table 1.1).

Within each sampling region, I chose five to six comparable shallow sublittoral sites, suitable for beach seining, and three offshore "neritic" transects for tow netting (Figure 1.1). Of the beach seining sites, two per region were chosen at or near the mouth of a freshwater input source, and were considered "delta" sites. The other three (or four in SPS) sites were along beaches at increasing distances from a freshwater source, and were termed "nearshore" sites. This arrangement was designed to target likely salmon emigration routes. The shallow sublittoral sites in NPS radiated outward from the Snohomish River. Based on an earlier study in 1986-1987 (Beauchamp et al. 1987), these sites were selected from a pool of 20 beach seining sites, because they consistently reflected the temporal trends in catch rate for all salmon species in NPS. The shallow sublittoral sites in SPS radiated outward from the mouth of Chambers Creek. Sites were located in proximity to release sites for hatchery salmon (Tulalip Bay and Snohomish River, Chambers Creek and Nisqually River), major freshwater inflows (Snohomish and Nisqually Rivers), and along suspected emigration corridors (Table 1.2a). At each neritic site, three parallel tow netting transects were generally located 100-2000 m from shore over increasing depths and distances from shore, parallel to a subset of the beach seine sites (Table 1.2b).

FISH SAMPLING

Field sampling was designed to characterize migration timing, size structure, and diet of juvenile salmon in both NPS and SPS, although I was unable to sample in February-March, which are potentially peak outmigration months for pink and chum salmon. I conducted biweekly beach seining (two sets per site) at each site in both regions from April through September 2001 and 2002 using a floating beach seine (37.0m length x 2.0m height, with mesh grading from 3 cm in the wings to 6 mm at the cod end) according to standard estuarine fish sampling protocol (Simenstad et al. 1991). In 2002, I sampled fish from neritic (offshore surface waters) sites monthly (three tows per site) during May-September in NPS and June-September in SPS) using a Kvichak two-boat surface trawl ("tow net," 3.1m height x 6.1m width x 15.0m length with mesh grading from 76.0 mm in the mouth to 6.4 mm at the cod end). Sampling gear (i.e., beach seine and surface trawl) were chosen based on successful past performance and to maximize consistency and potential comparison with similar past and current efforts in Puget Sound (Hodgson and Brakensiek 2003; C. Rice, NOAA-Fisheries, Mukilteo, WA, pers. comm.; C. Simenstad, University of Washington, pers. comm.). All sampling occurred over varying tidal stages, and during daylight hours, which may have contributed to increased gear avoidance (especially in the tow net sampling).

In an effort to investigate the scale of this potential bias in the distribution of juvenile salmon, I also conducted beach seining (one day per region) over a near-24 hour interval during the peak juvenile salmon migration period in May 2002. In NPS, duplicate beach seines were made between 3am and 11pm, mainly at the Possession site, although all other sites were sampled during daylight (N5, Table 1.2a). In SPS, the diel sampling was conducted at the Solo Point creek site (S2, Table 1.2a), with all other sites sampled during daylight.

Counts of all fish were recorded by species. Hatchery chinook and coho salmon were identified by adipose fin-clips or coded-wire-tag (cwt) detectors (in 2002 only). Unmarked chinook and coho salmon were assumed to be wild fish, however, the total (and regional) proportions of hatchery chinook and coho salmon that are mass-marked with adipose fin-clips (used by WDFW since 1996) are not accurately known, and marking success rates may differ by hatchery facility. Individual fork lengths (FL, to the nearest 1mm) and wet weights (Wt, to the nearest 0.1g) were recorded for each species (at least 30 fish per species, when available). I took representative sub-samples (5-10 fish from each size mode, but at least 10 of the larger potential piscivores >200mm when available, and all fish with cwt) of each salmon species and of both hatchery and unmarked chinook and coho salmon for gut content and scale analysis.

The catch per unit effort (CPUE; average catch per seine haul or tow at each site on each sampling date) and average size (FL) was calculated for each salmon species. Log (base 10) transformed catch (CPUE) data and fish lengths were analyzed initially with MANOVA (Zar 1999) to examine the effects of interannual (2001 versus 2002) and seasonal (April-September, sampling weeks 1-24) variability, region (NPS, SPS), zone (delta, nearshore, neritic-2002 only), and origin (marked hatchery versus unmarked chinook and coho salmon) on catch and size. Two-way and higher-order interaction terms were omitted if initial analysis confirmed they were not significant. These initial results were screened for only those effects and species that showed significant main effects or interaction terms, after Bonferroni correction for multiple comparisons, and subsequent analyses were conducted on each species using one-way ANOVA (Zar 1999).

PHYSICAL PARAMETERS

At each site, I recorded water temperature (degrees Celsius, °C) and salinity (parts per thousand, ppt) at a depth of 0.5 – 1.0m using the YSI Model 55 temperature sensor on every sampling date.

CWT READING

The coded-wire-tags were read by the Washington Department of Fish and Wildlife (L. Anderson, WDFW, unpublished data). Coded-wire-tag information, including release date, location and size, was used to help determine growth and residence time for specific release groups of hatchery fish.

RESIDENCE TIME FROM CWT SALMON

Recoveries of coded-wire-tagged (cwt) chinook and coho salmon provided estimates of individual residence times in nearshore habitats within northern and southern Puget Sound sampling regions. Residence times were calculated as the number of days between the first release day at the hatchery (April 9th-June 29th 2001, April 2nd-June 15th 2002) and the date of capture. Hatcheries employed a mix of forced (release on one day only) and volitional (fish have the option of lingering at the hatchery over a longer time interval, in this case 1-29 days) releases; therefore these residence time calculations represented maximum estimates of residence in Puget Sound (assumes that fish head immediately to Puget Sound upon release).

RESULTS

WATER TEMPERATURE

Surface water temperatures increased over the sampling seasons with peak temperatures of 16-19^{o}C recorded between mid-July and mid-August. After mid-June, average water temperatures were consistently lower at sites in SPS than in NPS. Temperature ranges within each region were similar for both 2001 and 2002, with slightly warmer maximum temperatures in 2001 for NPS delta sites (18.8°C in 2001, 17.6°C in 2002). Water temperatures were more variable at NPS sites (8-18.8°C) than at SPS sites (9.5-14.6°C; Figure 1.2). At the delta sites in NPS, temperatures were generally lower than at nearshore sites through the spring, but exceeded peak nearshore temperatures during July and August. In SPS, temperatures were similar among sampling zones, although surface waters at delta sites were slightly warmer than at nearshore and neritic sites until mid-July. Water temperatures at neritic and nearshore sites in both regions were very similar.

SALINITY

Due to the substantially greater freshwater inputs, NPS sites exhibited lower salinities than all of the sites in SPS (Figure 2.2). In both regions, salinities at delta sites

(0.0-25.3 ppt in NPS, 13.0-29.5 ppt in SPS) were consistently lower than those at nearshore sites (13.6-27.7 ppt in NPS, 25.7-30.4 ppt in SPS), although the differences were less pronounced at SPS sites. Salinities at neritic and nearshore sites in both regions were nearly identical. Average salinities were similar between years, and generally increased throughout the sampling season with peak salinities (21.5-27.7 ppt in NPS, 29.3-30.4 ppt in SPS) in mid-August to late-September.

DIEL PATTERNS IN CATCH AND SIZE DISTRIBUTION

Average catch of all juvenile salmon species was highly variable among diel periods, without a consistent pattern linking period or tidal stage to catch rate (Figure 1.3). At NPS sites, coho salmon were the only species to show significantly higher catches during daylight (ANOVA, P=0.02). At SPS sites, pink salmon were only caught at one site during daylight, and catches of chum salmon were significantly higher during the day (P=0.01). Size patterns shifted with time of day. At NPS sites, chinook, coho, and chum salmon from night–time beach seine samples were significantly larger than from crepuscular and daylight samples (P<0.001), whereas pink salmon were largest at crepuscular periods (P<0.001). At sites in SPS, coho and chum salmon caught during the day were larger than those caught at night and crepuscular periods (P<0.01), while chinook salmon sizes did not significantly differ with time of day.

CATCH TIMING

Most juvenile salmon were caught in nearshore habitats between April and June, with peak catches generally in May (Figure 1.4). Spatial-temporal overlap among peak catches of different species was much stronger in SPS than NPS, although timing of the actual peaks could have differed at time scales shorter than the 2-week sampling intervals of this study. Peak catches for chum and chinook salmon were greater at SPS than NPS sites in both years, whereas coho and pink salmon catches were greater at NPS sites. Catches at the neritic sites were minimal in NPS, whereas the catches of all salmon species in SPS were relatively high in June (mainly at Hale Passage site #S9; Figure 1.5). The proportions of hatchery chinook (Figure 1.6) and coho (Figure 1.7) salmon in beach seine sets were much greater at sites in SPS than in NPS in both years with high temporal and spatial overlap between hatchery and unmarked fish. Hatchery chum salmon, which were not visibly distinguishable from wild chum salmon, represented approximately 17% of the average run size (sum of escapements and the all-citizen and tribal net harvests) of fall-run chum salmon in northern Puget Sound and 11% in SPS from 1995-2000, WDFW unpublished data). Total and peak catches of each species were greater in 2002 than 2001, except chum salmon in NPS, which had a slightly higher peak catch in 2001 (180 fish) than 2002 (138 fish).

Chinook Salmon (Hatchery and Unmarked)

Catches of juvenile chinook salmon were much higher in 2002 than in 2001. In NPS, juvenile chinook salmon exhibited a small pulse during May and a larger main pulse during July in both 2001 and 2002 (Figure 1.4). In July, peak catches at delta sites were higher and two weeks earlier than peak catches at nearshore sites. Chinook salmon persisted in catches at nearshore sites until early August in NPS, but were generally absent by September. Neritic catches of chinook salmon were very low in NPS, but measurable peaks occurred in early June and September (Figure 1.5). Many more chinook salmon were captured in SPS than in NPS (15-fold higher than the NPS catch in 2002). In both years, chinook salmon in SPS were caught at nearshore sites in concentrated peaks in May. Catches at neritic sites peaked in June (2002 only, Figure 1.5). Catch rates were higher and one week earlier at nearshore sites than at delta sites, and chinook salmon were nearly absent after mid-June. A higher proportion of chinook salmon in SPS (87% in 2001, 98% in 2002) than in NPS (28% in 2001, 44% in 2002) were marked hatchery fish. In both sampling regions, timing of hatchery and unmarked fish was nearly coincident (Figure 1.6).

Coho Salmon (Hatchery and Unmarked)

In NPS, juvenile coho salmon exhibited only one main peak during late May in both 2001 and 2002, and catch rates were much higher at delta than at nearshore sites (Figure 1.4). In SPS, most coho salmon were caught at nearshore sites in May (17th)

2001 and April (18th) 2002, whereas catches at delta sites were negligible. In 2002, there was also a smaller pulse at nearshore sites on May 15th, and peaks both at nearshore and neritic sites in early-mid June. The timing of hatchery coho salmon (6-21% and 29-40% of total catch, NPS-SPS) generally coincided with unmarked conspecifics in both sampling regions (Figure 1.7).

Chum Salmon

Chum salmon were caught at both delta and nearshore NPS sites in one pulse in early May 2001, whereas in 2002, pulses of chum salmon were caught at delta sites in April, up to a month before catches peaked nearshore on May 10th (Figure 1.4). Very few were caught after May 21st, with only two chum salmon caught at neritic sites in July (Figure 1.5). Over three times as many chum salmon were caught at sites in SPS than in NPS in both years. In SPS, catches of chum salmon declined earlier at delta sites (after May) than in nearshore areas (after June). In 2001, catches at delta sites peaked on May 17th, offset from earlier May and mid-June peaks nearshore. In 2002, the peak catch of chum salmon for delta and nearshore sites both occurred on May 15th, 2002, although there were also minor peaks nearshore in April and in mid-June at both nearshore and neritic (499 chum salmon) sites.

Pink Salmon

Most pink salmon in Puget Sound are odd-year spawners and even-year outmigrants. Although the Snohomish River also supports a very small even-year pink salmon run (HSRG 2002), I did not catch any juvenile pink salmon in 2001. In 2002, over six times as many pink salmon were captured at sites in NPS than in SPS, with peak catches during the week of April 21st in both regions (Figure 1.4). Pink salmon occupied nearshore sites only through mid-May in NPS, whereas pink salmon persisted through June at nearshore and neritic sites in SPS (Figure 1.5).

SIZE STRUCTURE

Average fish lengths for all species increased fairly steadily over the sampling period each year (Figure 1.8). Overall, species-specific fish sizes were smaller at delta sites than at nearshore sites (P<0.001) and at sites in NPS versus SPS (P<0.001). Sizes at neritic sites were generally the same or slightly larger than those caught concurrently at nearshore sites. Overall, hatchery chinook (Figure 1.9) and coho (Figure 1.10) salmon were larger than unmarked fish (P<0.001). There was no consistent difference in sizes between 2001 and 2002, although chinook and chum salmon were larger overall in 2001 than 2002 (P<0.001).

Chinook Salmon (Hatchery and Unmarked)

Overall, chinook salmon were larger during 2001 than 2002 (P<0.001), larger at sites in SPS than NPS (P<0.001), larger at nearshore and neritic sites than at delta sites (P<0.001), and hatchery fish were larger than unmarked conspecifics (P<0.001; Figure 1.8). Unmarked chinook salmon were larger at SPS than at NPS sites (P=0.001), at nearshore versus delta sites (P<0.001), and in 2001 than 2002 (P=0.038). Hatchery chinook salmon were also larger at nearshore than delta sites (P<0.001) and in 2001 than 2002 (P<0.001), although they did not significantly differ between regions (P=0.13). I caught very few distinctly larger chinook salmon, which I assumed to be age-1 based on size frequency histograms (>130mm before June, > 135mm in June, >150mm in July, >160mm in August, and > 185mm in September). There was a wider range in sizes of age-1 chinook salmon in NPS (137-231 mm FL) than in SPS (142-185 mm FL; Figure 1.9).

In NPS, chinook salmon were larger at nearshore than at delta sites (P=0.002), hatchery salmon were larger than unmarked conspecifics (P<0.001), and chinook salmon were slightly, though not significantly, larger in 2001 than 2002 (P=0.24). During the peak catches in May, there were very few marked hatchery fish in 2001, and those in 2002 were only larger than unmarked fish at nearshore sites (P<0.001). Chinook salmon during the July pulse were larger in 2001 than 2002 (P<0.001). Hatchery and unmarked chinook salmon were the same size in July 2001, whereas in 2002, unmarked fish at both delta (July 2nd) and nearshore (July 17th) sites were smaller than hatchery fish ($P<0.001$). Chinook salmon at neritic sites were of similar size to fish at nearshore sites.

During peak spring catches at sites in SPS, chinook salmon were smaller at delta than at nearshore sites in 2001, whereas the opposite was true in 2002 ($P<0.001$). Although there was no difference in 2001 ($P>0.05$), in 2002 hatchery chinook salmon were larger than unmarked chinook salmon at nearshore sites, and smaller than unmarked counterparts at delta sites. Sizes of fish at neritic sites (85-104mm FL) were similar to those caught at nearshore sites ($P>0.05$).

Coho Salmon (Hatchery and Unmarked)

Unmarked coho salmon were larger at sites in SPS than in NPS ($P=0.001$), and were larger in 2002 than 2001 ($P<0.001$). Sizes of hatchery salmon were similar between regions, although they were slightly larger in 2002 than 2001 ($P=0.054$). Some unmarked coho salmon were substantially smaller (34-79mm FL) than the average size of age-1 salmon; therefore, I assumed these were wild (assuming hatcheries released only age-1 coho salmon) age-0 ocean-type coho salmon (Figure 1.10).

At NPS sites, the size of age-1 coho salmon during the pulses in mid to late May were similar both years (106-108mm in 2001 and 105mm FL in 2002; Figure 1.8). Hatchery coho salmon were significantly larger than unmarked coho salmon ($P<0.001$; Figure 1.10). In 2001, coho salmon were smaller (84 ± 2 mm FL) during the pulse at nearshore sites in SPS on May 17th than at sites in NPS, and unmarked fish (86 ± 2 mm FL) were bigger than hatchery conspecifics (76 ± 6mm). In 2002, hatchery and unmarked coho salmon were the same size during peaks on April 18th and May 15th. During the last small peak on June 4th, hatchery coho salmon were significantly larger than unmarked coho salmon ($P<0.001$) at nearshore sites, while both were larger than those caught at delta sites ($P=0.05$). Coho salmon caught at neritic sites were similar in size (110-130 mm FL; $P>0.05$) to fish caught at nearshore sites on nearby dates (Figure 1.8).

Chum Salmon

Overall, chum salmon were larger in 2001 than 2002 ($P<0.001$), larger at SPS sites than at NPS sites ($P<0.001$), and increased in average size progressively from delta to nearshore ($P<0.001$) to neritic sites ($P<0.001$; Figure 1.8). At sites in NPS, however, chum salmon were larger in 2002 (mean FL = 54 mm) than 2001 (45 mm; $P<0.001$) during peak catches in May (54mm versus 45mm average FL). Although chum salmon were the same size at delta and nearshore sites in April, those caught at delta sites were significantly smaller than those caught at nearshore ($P<0.001$) and at neritic sites ($P<0.001$) throughout the rest of the season. At sites in SPS, chum salmon during peak catches in May were larger in 2001 (56-74mm FL) than 2002 (41-53mm FL; $P<0.001$). During peaks in May and June during both years, chum salmon were larger at nearshore than at delta sites ($P<0.001$). Sizes (FL) ranged from 34-92 mm at delta sites, and 31-143 mm at nearshore sites between April and June. Chum salmon caught at neritic and nearshore sites in SPS were in the same size range.

Pink Salmon

In 2002, pink salmon during peak catches were significantly smaller at delta than nearshore sites in NPS ($P<0.001$; Figure 1.8). Pink salmon were largest at nearshore sites in late-May (83 ± 25 mm FL) and at neritic sites in mid-June (83 ± 5 mm, average of two fish). Pink salmon caught at sites in SPS were significantly larger than those in NPS ($P<0.001$). In SPS, pink salmon from mid-April to early June were slightly, but not significantly, smaller at delta than at nearshore sites ($P>0.05$). Pink salmon caught at neritic and nearshore sites were very similar in size.

LENGTH-WEIGHT REGRESSIONS

Fork length to wet weight (FL-Wt) regressions were calculated from the available data for each of the salmon species as follows:

Chinook salmon Wt (g) = $0.000006 * \mathrm{FL(mm)}^{3.1068}$ $r^2 = 0.9526$; n = 532; 51-203 mm FL
Coho salmon Wt (g) = $0.000006 * \mathrm{FL(mm)}^{3.0926}$ $r^2 = 0.9162$; n = 242; 77-196 mm FL

Chum salmon Wt (g) = 0.000003 * FL(mm) $^{3.2506}$ $r^2 = 0.9786$; n = 425; 31-145 mm FL

Pink salmon Wt (g) = 0.000002 * FL(mm) $^{3.3689}$ $r^2 = 0.9804$; n = 185; 31-97 mm FL

RESIDENCE TIME FROM CWT SALMON

Chinook Salmon

I recaptured age-0 chinook salmon (from fall, spring and summer-runs) that had been released during May and June in 2001 (32 fish) and 2002 (142 fish). Residence times of known-origin hatchery chinook salmon ranged 1-130 days. The majority of cwt chinook salmon recovered from NPS sites were released by hatcheries on the Snohomish River (Wallace River hatchery) and Tulalip Bay (Bernie Kai-Kai Gobin hatchery), while Nisqually River hatchery (Clear Creek hatchery) releases dominated cwt recoveries from SPS sites. At NPS sites, most of the recaptured fish had been released June 29th 2001 and May 14th or June 15th 2002. At sites in SPS, most of the fish recaptured in 2001 and 2002 came from releases between May 7-8th. Most (83%) of the fish originating from the Snohomish River were caught three weeks later (20 ± 1 days; Figure 1.11) at NPS sites. Eight fish (8%) were caught six weeks later (42 ± 7 days) at SPS sites. Fish released into central Puget Sound (CPS) were re-captured only at SPS sites after an average of 28 (± 4) days. Nisqually River fish were caught at SPS sites 15 (± 1) days after being released from hatcheries.

Coho Salmon

Residence times for age-1 coho salmon ranged 7-38 days. I recaptured age-1 coho salmon that had been released between early April and mid-May in 2001 (four fish) and 2002 (20 fish). Coho salmon released by hatcheries in the Snohomish River basin (Wallace River) and Tulalip Bay (Bernie Kai-Kai Gobin) comprised all of the cwt recoveries at sites in NPS, while releases from Nisqually River hatcheries (Kalama and Clear Creek) dominated recoveries from SPS sites. In 2002, most Snohomish River coho salmon were recaptured at NPS sites during the pulse on May 21st, 18 ± 3 days after being released on May 3rd (Figure 1.12). Only two fish released from central Puget

Sound (CPS) were recaptured. One was caught at the mouth of the Snohomish River (site N2, Table 1.2a) 407 days post-release (on May 21, 2002), and the other was caught at a site in SPS after 23 days. In 2002, most Nisqually River coho salmon, released April 2nd, were caught at SPS sites 16 (± 2) days later during the pulse on April 18th.

DISCUSSION

Within each region, the intra-annual timing patterns of juvenile salmon at delta and nearshore Puget Sound sites were generally similar in 2001 and 2002, and consistent with previous findings at similar locations (Tyler 1963; Pearce et al. 1982; Beauchamp et al. 1987). It is probable that there were also early spring (February-early April) pulses before sampling began during both years. In other sampling efforts in 2002, a pulse of age-1 chinook salmon was caught in early April in the Nisqually River (Hodgson and Brakensiek 2003) and age-0 salmon were caught as early as February in Skagit Bay (2002, C. Rice, NOAA-Fisheries, Mukilteo, WA, unpublished data).

Differences in timing of peak catches were most apparent between sampling regions. Timing of downstream and estuarine migration has been linked to river flow rates and hatchery releases in the Columbia river (Dawley et al. 1986). Timing of peak catches at NPS sites was likely influenced more by river flow than at SPS sites, due to the substantially greater fresh water inflow to the northern basin. Hatchery releases were primarily responsible for the timing of peak catches at sites in SPS, where hatchery production accounted for at least 98% of the chinook salmon and likely most of the pink and coho (only 10-20% of hatchery coho salmon were marked) salmon. At NPS sites, where unmarked populations made up a greater proportion of the catch, hatchery releases also appeared to influence peak timing, demonstrated by coincident timing of hatchery and unmarked chinook and coho salmon. Variations in hatchery practices, the proportional contribution of natural populations to the total, physical characteristics (water temperature), river inflow, and hydro-period likely drove differences between the NPS and SPS sampling regions.

Catch rates indicated that pink and coho salmon were more abundant at sites in NPS, whereas chum and chinook salmon were more abundant at sites in SPS. With the exception of chum salmon in NPS, total and peak catches of juvenile salmon were greater in 2002 than 2001, which reflected higher spawning escapements and hatchery releases (WDFW, unpublished data). In Puget Sound, juvenile chum salmon are more abundant overall during odd years than even years, which may be due to negative competitive interactions with pink salmon (Gallagher 1980; WDFW unpublished data at http://www.wa.gov/WDFW/fish/chum/chum-5c.htm).

The extremely low catches of salmon at neritic sites in NPS suggested either that juvenile salmon leave the region after using nearshore environments, or that this technique was ineffective for sampling salmon in offshore waters. Substantial numbers of juvenile salmon were captured at SPS sites using the identical technique, and other researchers (Fresh et al. 1981; C. Rice, NOAA-Fisheries, Mukilteo, WA, pers. comm.) have fished successfully with the same technique. One possibility is that salmon more successfully avoided the net due to a slower towing speed than in previous studies (resulting from working with smaller boats). Another possibility is that salmon were in deeper waters. Beamish et al. (1998), using a large rope trawl, caught salmon largely in the top 15m of the water column, whereas I sampled only the top 3m. Salmon may have more actively avoided the shallowest surface waters at sites in NPS than at SPS sites due to higher water temperatures, or perceived vulnerability to predators (birds, fish, and marine mammals).

In estuarine and marine waters, researchers have found that salmon move from shallow nearshore to offshore surface waters after either achieving some size threshold (at least 50-60mm for chum salmon; Simenstad 1982) or after a certain residence time (LeBrasseur and Parker 1964; Wetherall 1970; Blackbourn 1976; Healey 1980; Dawley et al. 1986). The only substantial catch of salmon at neritic sites in SPS occurred in June, but the lack of sampling at neritic sites in May precluded an evaluation of whether offshore movement coincided with or followed peak nearshore catches. Most of the chinook and coho salmon caught at neritic sites were the same average size as fish caught nearshore during the same time frame. While I was unable to determine a conclusive size threshold or timing cue for offshore movement due to limited sampling and small catches, the few pink and chum salmon caught at neritic sites in NPS were larger than those caught at nearshore sites, and the minimum size of salmon at neritic sites was larger than at nearshore sites. In July 1997, the average size of juvenile salmon (chum, coho, and chinook) caught in rope trawls in CPS (0-15m; Beamish et al. 1998) were larger than the sizes of each species I caught during July 2001 and 2002 at nearshore and neritic (2002 only) sites, which suggests that most of the salmon occupying offshore pelagic waters are a larger size than those in nearshore waters.

There is also evidence that some salmon in Puget Sound move into neritic waters early in the spring at a very small size. In 1962, Tyler found chinook in varying abundances in all inshore and offshore areas of Everett Bay, a part of the Snohomish River estuary. He found that a portion of the outmigrating juveniles moved offshore upon entry in early spring from the Snohomish River into Everett Bay. He proposed that strong currents prevailing during the ebb tide made it impossible for the juveniles to contact the shoreline in this area and hypothesized that a portion of these juveniles may never locate shoreline habitat (Tyler 1963). Similarly, very small chinook and chum fry enter offshore waters of Skagit Bay as early as February, apparently swept out by high river flows and strong tides (2002, C. Rice, NOAA-Fisheries, Mukilteo, WA, pers. comm.). Increased spatial and temporal (beginning earlier in the year and with increased frequency) distribution of sampling with alternate gear (e.g., a rope trawl) is needed to determine accurate information on the use of offshore waters by juvenile salmon.

Juvenile chinook salmon are known to spend 6-16+ weeks in Puget Sound and Hood Canal estuaries with individuals remaining for 1-7 weeks (Simenstad et al. 1982). There are also resident chinook salmon that remain in Puget Sound until maturity (Simenstad et al. 1982). I found that juvenile chinook salmon occur in nearshore Puget Sound waters for at least six months of the year (April through September), although peak occurrence spanned three months (May through July). Recovery of cwt hatchery chinook salmon revealed individual residence times of up to 18 weeks, while average time spent in a single sampling region was 1-3 weeks. Residence times for wild salmon may be up to twice as long as hatchery chinook salmon (Levings 1986). I found some evidence from cwt recoveries that chinook salmon also migrate from northern and central regions to southern Puget Sound (Figure 1.11). This may reflect a tendency to move to waters of increasing salinity, or it may suggest migration patterns for chinook salmon that become resident in Puget Sound. I found similar in-region residence times for coho salmon. Variability in residence times may be due to a combination of water temperature, food supply, population abundances, size, and timing related behaviors (Miller et al. 1967; Reimers 1973; Salo 1969; Simenstad et al. 1982; Orsi et al. 2001).

Hatcheries in Puget Sound released juvenile salmon at a slightly larger size than wild salmon occupying the same environments (this study; Hodgson and Brakensiek 2003). The dominance of hatchery production in the catch at SPS sites may, in part, explain the slightly larger sizes of fish at SPS sites compared to NPS sites where hatchery production made up less than half of the salmon catch. Juvenile salmon also appeared to use nearshore environments in high relative abundances during relatively short time intervals, especially at sites in SPS. Hatchery fish have increasingly been attributed to negative impacts on wild salmon stocks (Flagg et al. 2000). One possibility is the reduction of genetic variability in such traits as spawning and outmigration timing (life history strategies), which may have negative repercussions on the ability of salmon to respond to shifting climate, food, and environmental conditions. The co-occurrence of large numbers of hatchery salmon with small numbers of wild salmon may cause localized food limitation that mediates potential competition for limited food supplies and potential risk of predation when larger and/or older hatchery fish are released at the same time as smaller wild or hatchery fish.

Juvenile salmon occupy nearshore Puget Sound waters primarily during the spring and early summer. Juvenile chinook salmon persist in small numbers nearshore, and in larger numbers offshore (with chum and coho salmon), at least through the fall. Nearshore environments appear to be used most extensively, based on species residence times, by chinook salmon at sites in NPS, and chum salmon at SPS sites, areas where subsantial populations of both hatchery and wild populations exist. Spatial differences in hatchery inputs (magnitude and timing), salinity and water temperature may affect the local ecology of early marine residence for juvenile salmon. Differences in size, nearshore residence, and particularly the potential for predation and growth (interaction of food supply and physiological conditions) may lead to differential survival for juvenile salmon entering different areas of Puget Sound. This study examined relatively small, localized areas of Puget Sound and results cannot be extrapolated to make broad regional generalizations. Future efforts are needed to synthesize ongoing studies and expand the spatial coverage of areas used by juvenile salmon in Puget Sound, which, ultimately, will aid in determining which factors are important for high early marine survival of juvenile salmon in Puget Sound.

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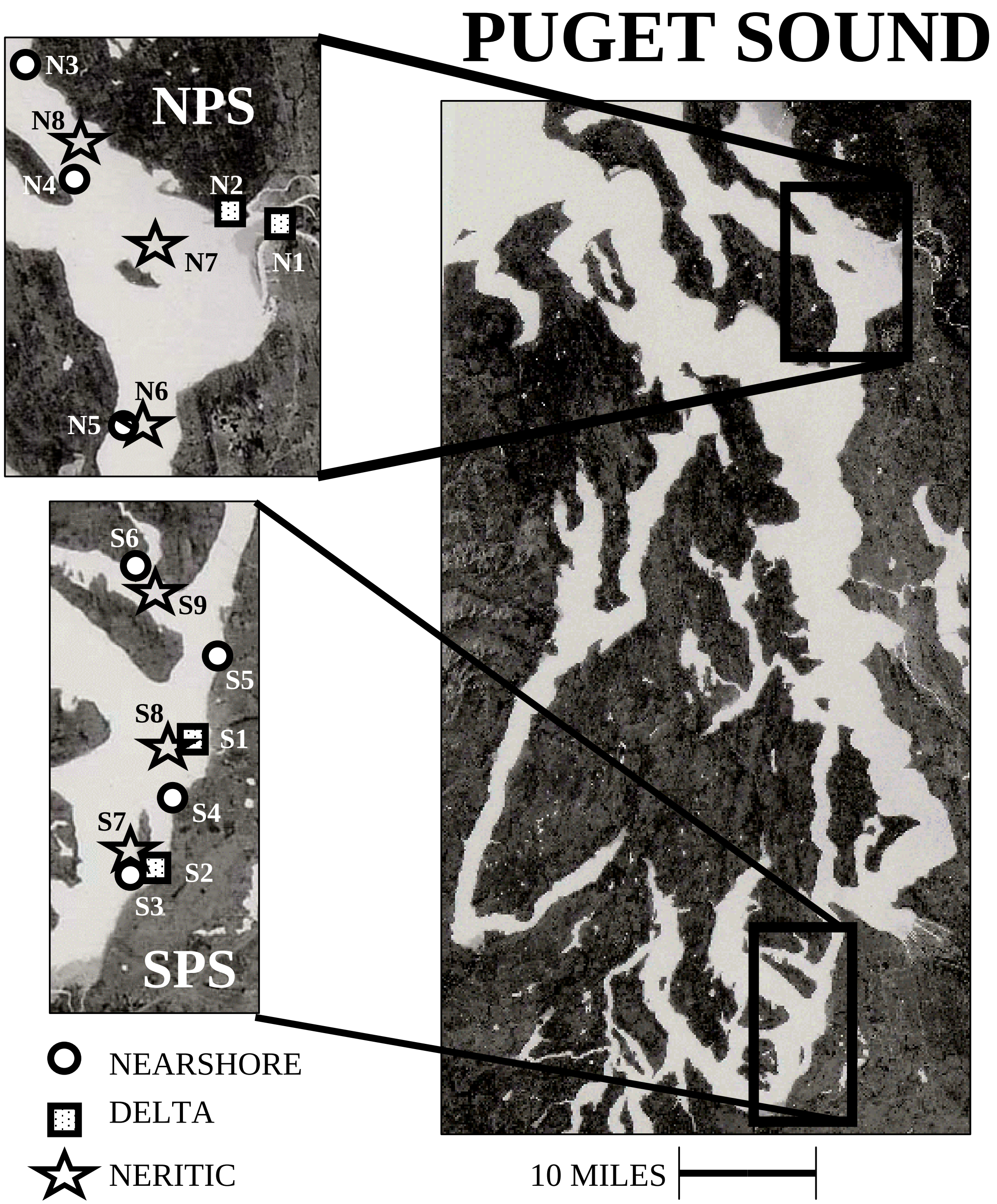

Figure 1.1. Puget Sound study regions and sampling locations. Circles and squares indicate nearshore and delta beach seine locations. Stars indicate neritic tow net locations. See Table 1.2a and 1.2b for information on sites.

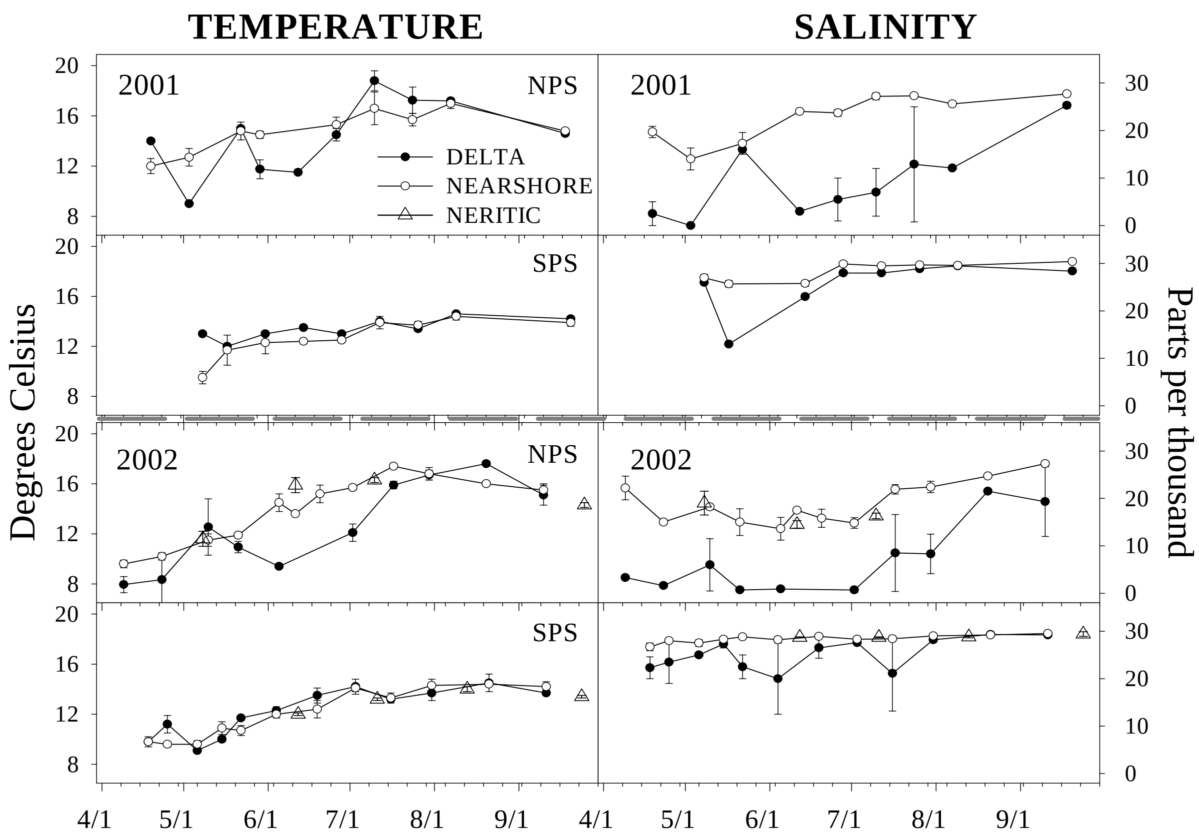

Figure 1.2. Average water temperature (degrees Celsius ± s.e.; left panels) and salinity (parts per thousand ± s.e., right panels), taken at 0.5-1.5m depths at delta, nearshore and neritic sites in northern Puget Sound (NPS) and southern Puget Sound (SPS).

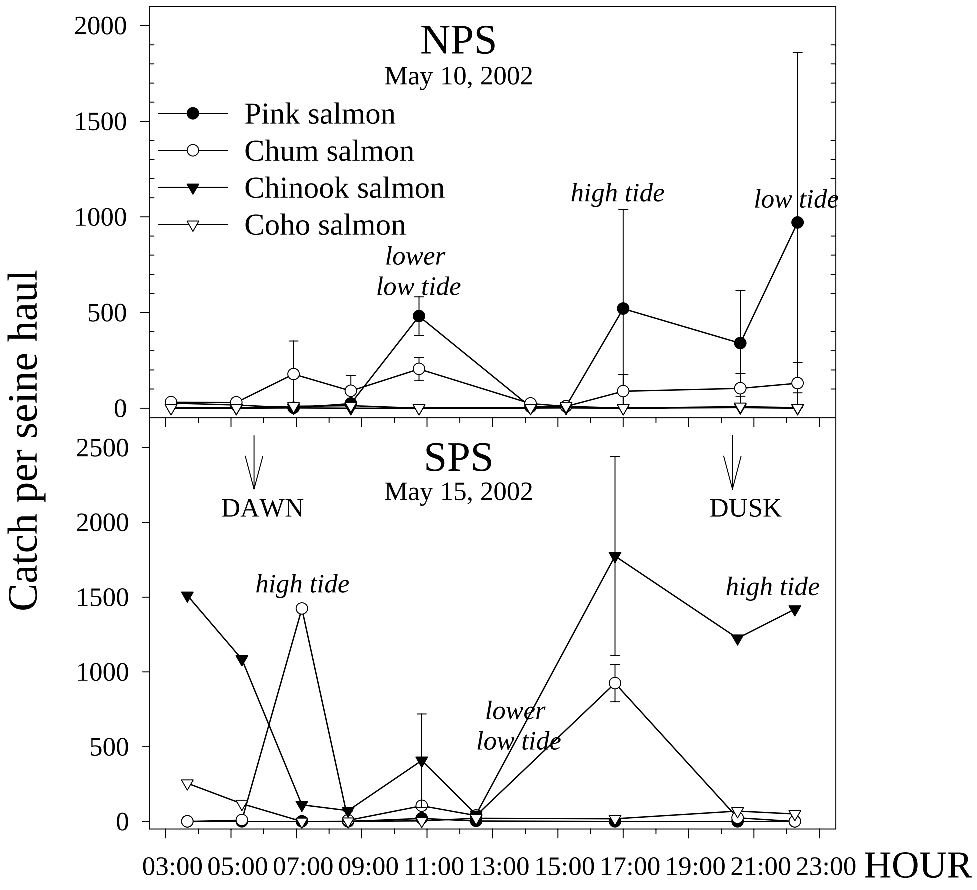

Figure 1.3. Catch (± s.d.) per beach seine haul of juvenile salmon at NPS and SPS sites over a near-24 hour sampling period that encompassed two dark, two crepuscular, and multiple day-time sampling events per region.

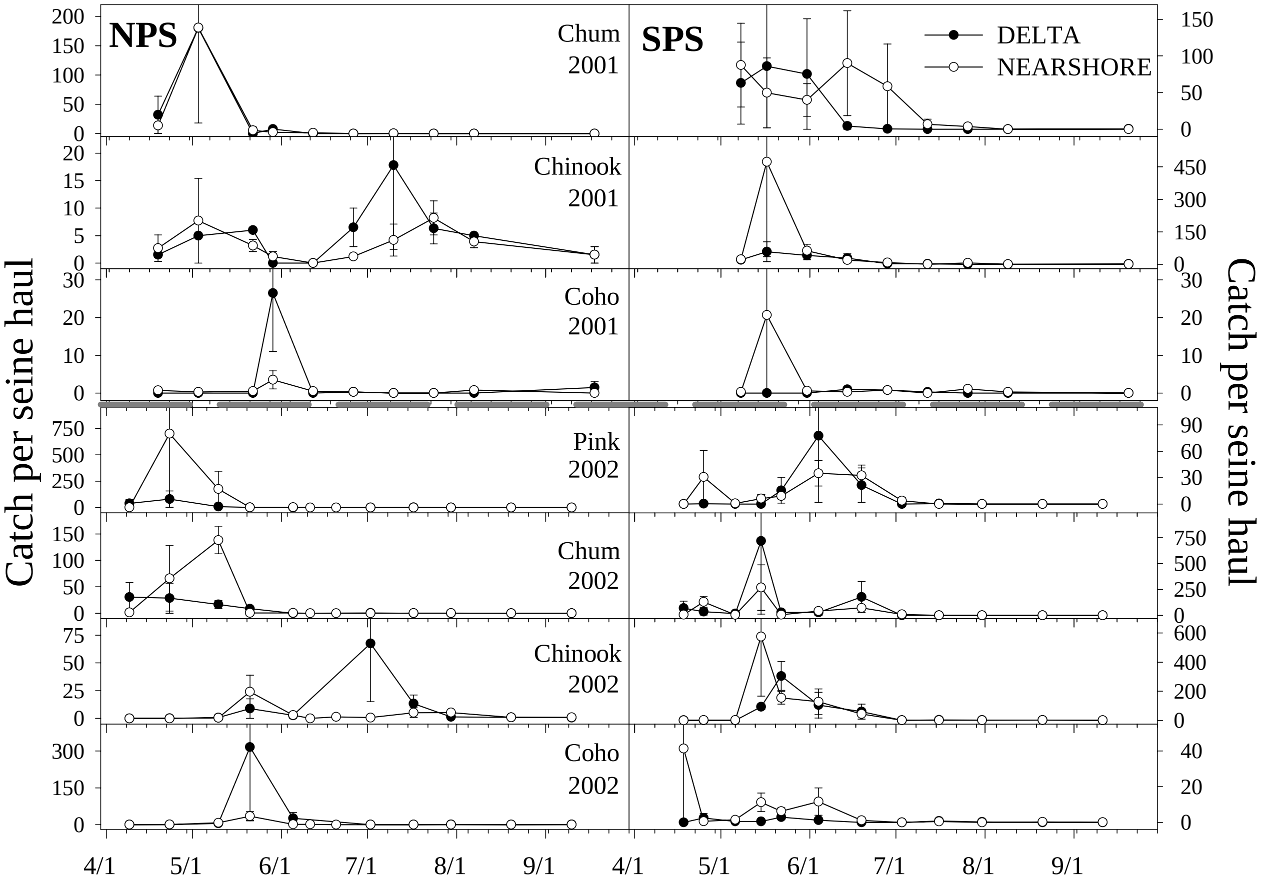

Figure 1.4. Average catch (± s.e.) of juvenile salmon in beach seine hauls at delta and nearshore marine sites in NPS (leftpanels) and SPS (right panels). Note that the scale changes by species, year and sampling region.

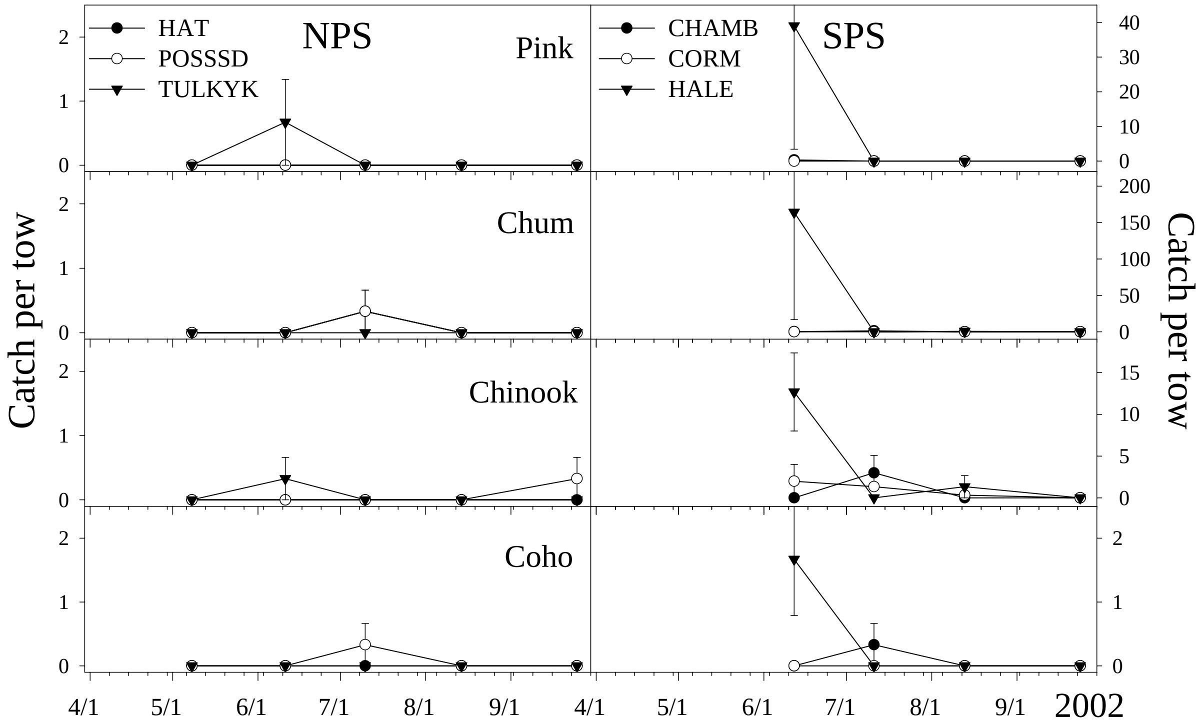

Figure 1.5. Average catch (± s.e.) of juvenile salmon in tow net hauls at neritic sites (Table 1.2b) in NPS (left panels) and SPS (right panels). Note that the scale changes by species for SPS.

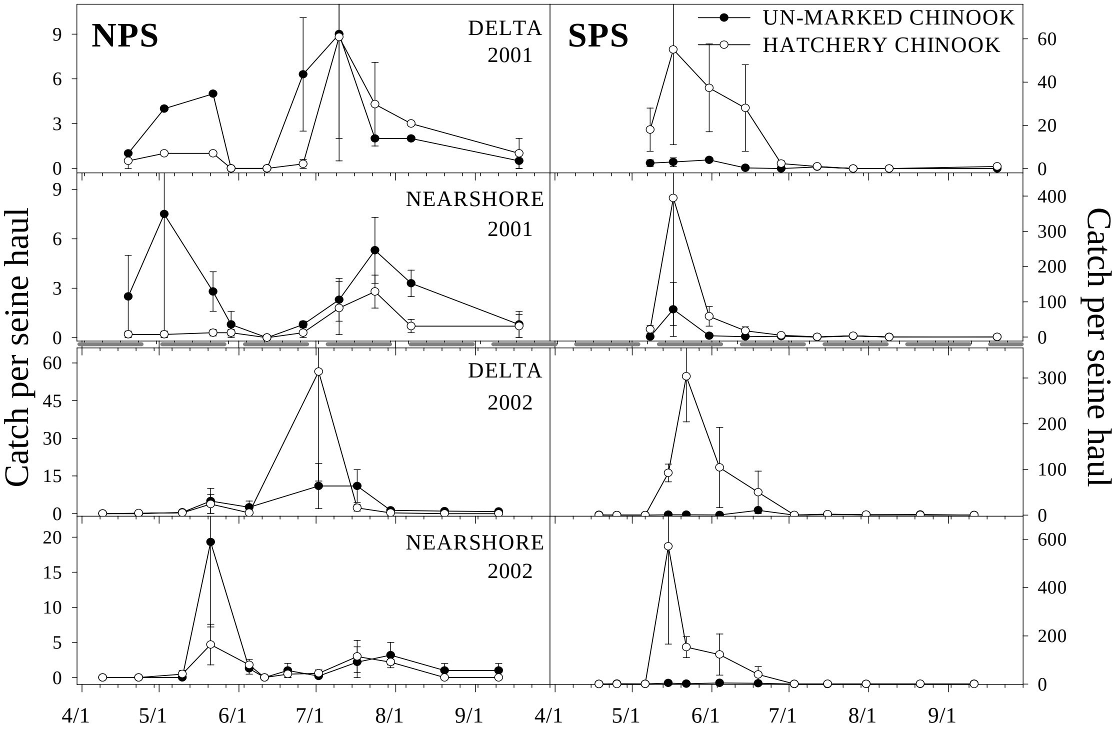

Figure 1.6. Average catch (± s.e.) of juvenile hatchery (adipose-clipped 2001 and/or cwt 2002) and unmarked chinook salmon in beach seine hauls at delta and nearshore marine sites in NPS (left panels) and SPS (right panels). Note that the scale changes by year, sampling region and zone.

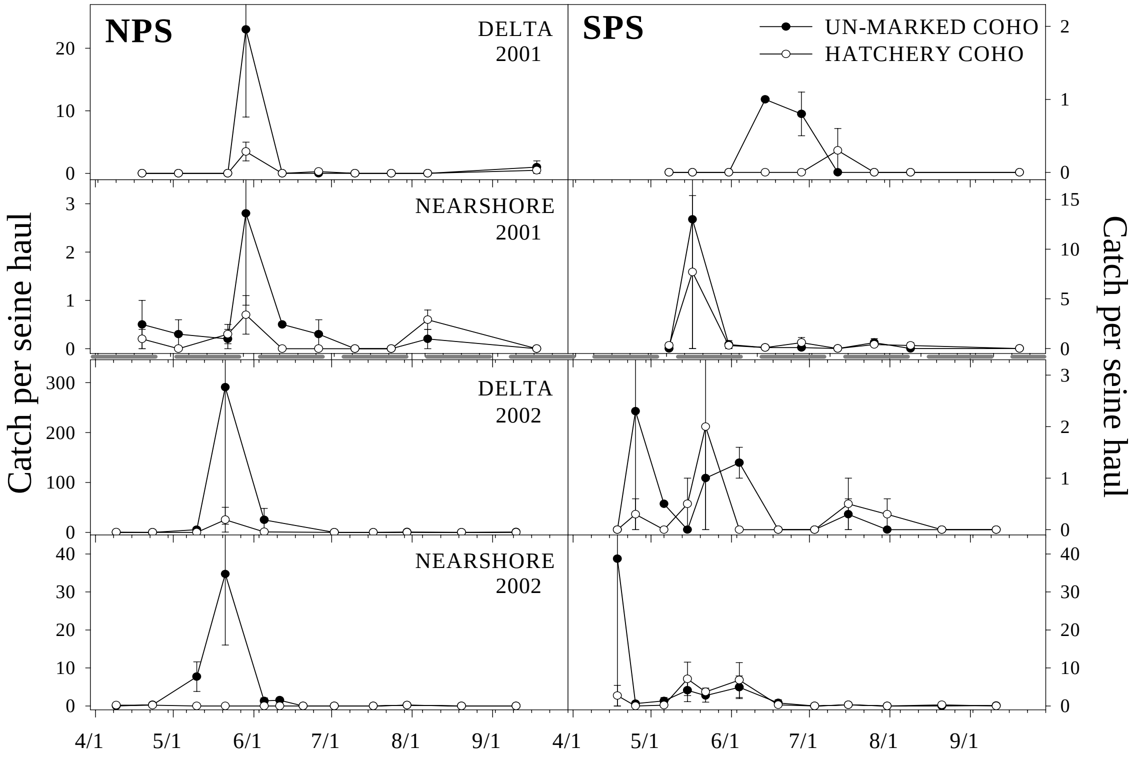

Figure 1.7. Average catch (± s.e.) of juvenile hatchery (adipose-clipped 2001 and/or cwt 2002) and unmarked coho salmon in beach seine hauls at delta and nearshore marine sites in NPS (left panels) and SPS (right panels). Note that the scale changes by year, sampling region and zone.

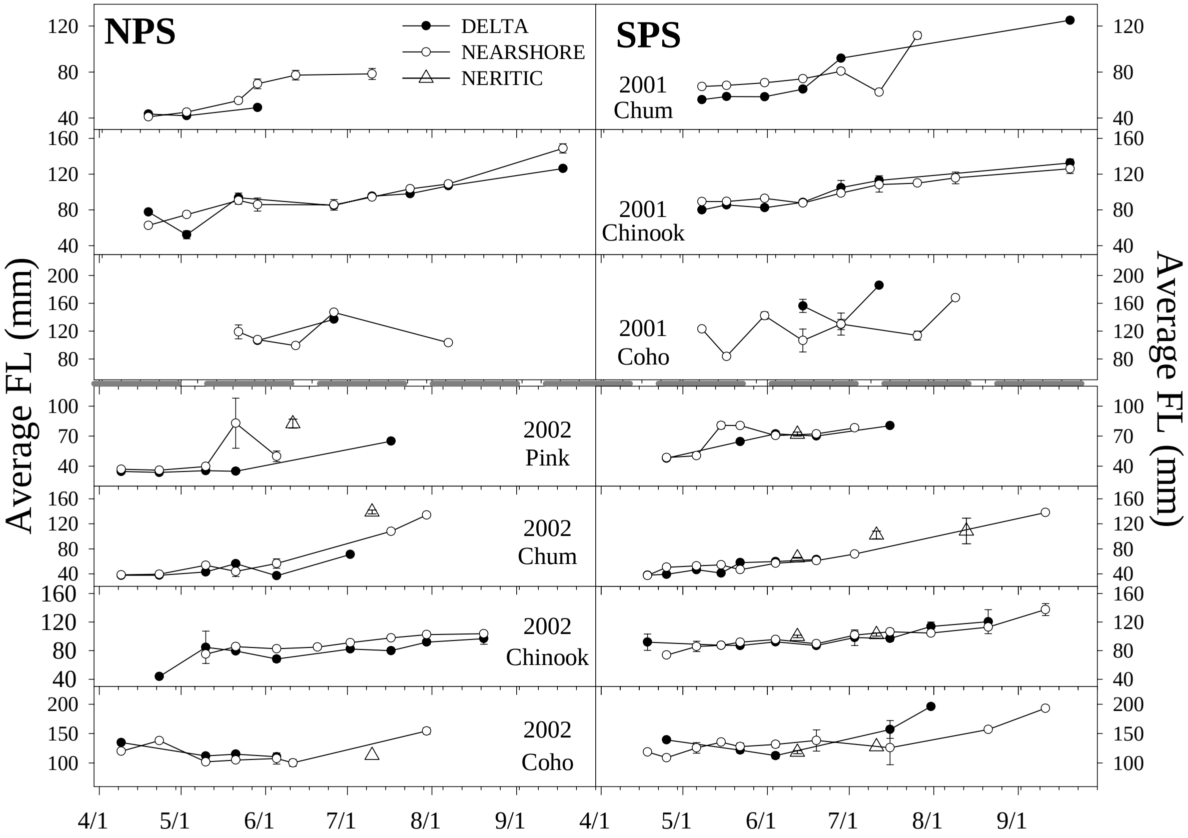

Figure 1.8. Average fork length (± s.e.) of age-0 juvenile salmon (except age-1 coho salmon) in beach seine hauls at delta and nearshore sites, and in tow net sets at neritic sites (2002 only) in NPS (left panels) and SPS (right panels). The scale changes by species.

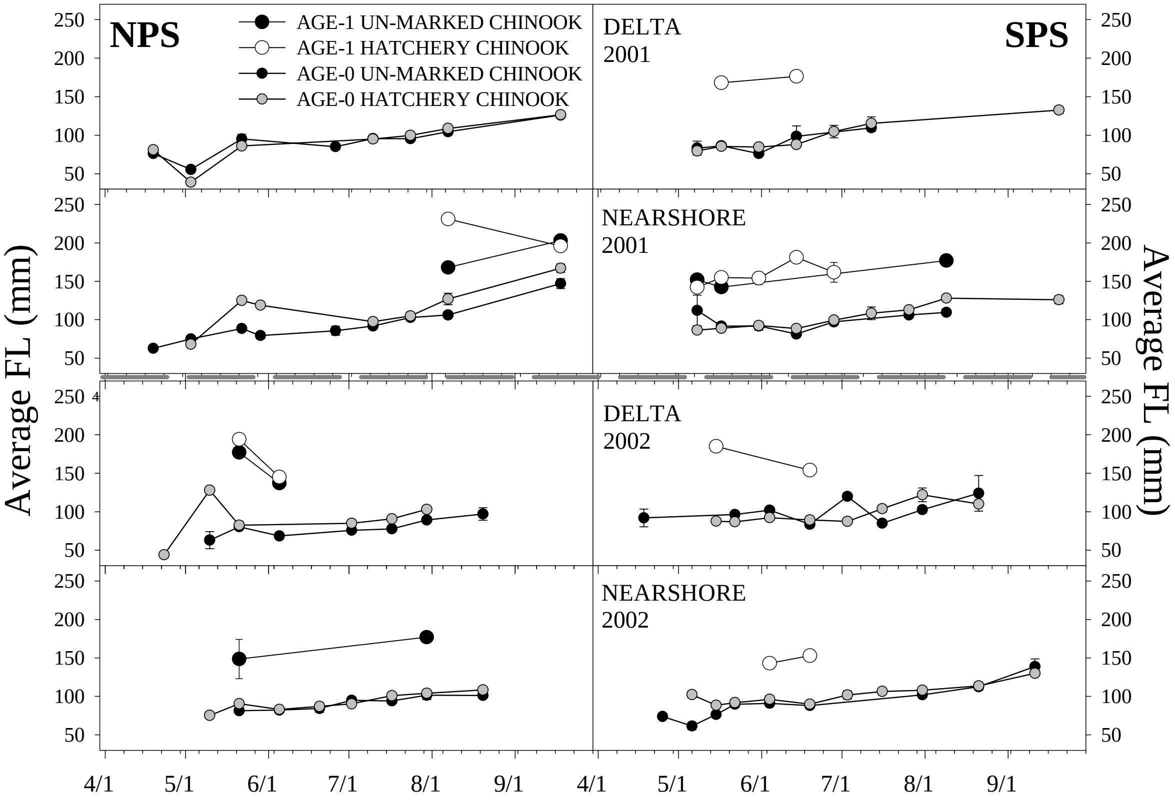

Figure 1.9. Average fork length (± s.e.) of age-1 (>130mm-185mm, date-dependent) and age-0 hatchery (adipose-clipped 2001 and/or cwt 2002) and unmarked chinook salmon in beach seine hauls at delta and nearshore sites in NPS (left panels) and SPS (right panels).

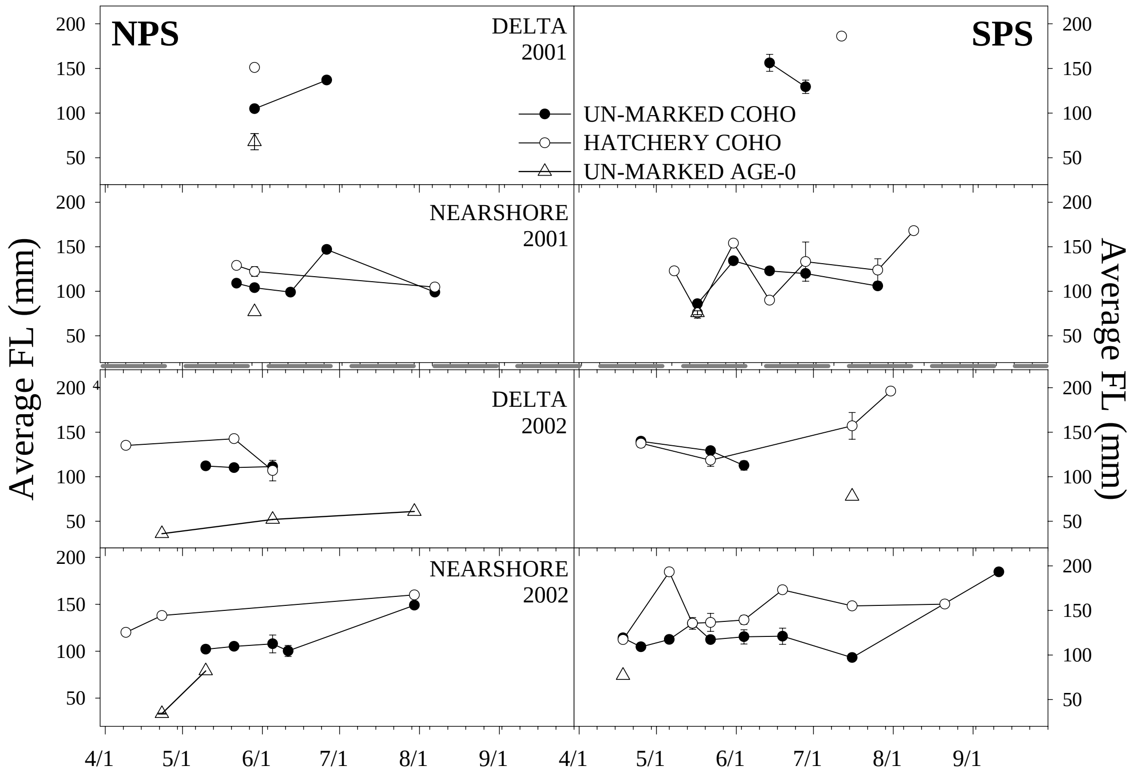

Figure 1.10. Average fork length (± s.e.) of age-1 hatchery (adipose-clipped 2001 and/or cwt 2002) and age-1 and age-0 unmarked coho salmon (less than 80mm FL) in beach seine hauls at delta and nearshore sites in NPS (left panels) and SPS (right panels).

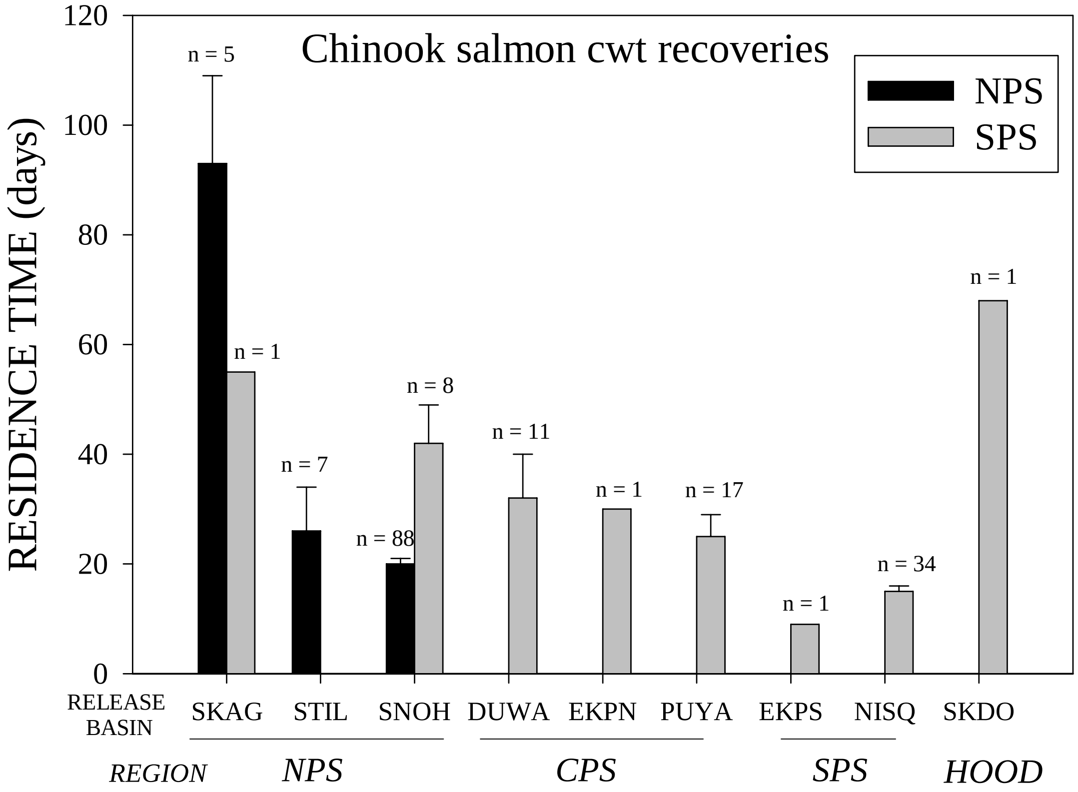

Figure 1.11. Average (± s.e.) residence time (calculated as time elapsed between 1st release date from hatchery and capture date) of age-0 cwt hatchery chinook salmon released from different basins* and captured at NPS (black bars) and SPS (gray bars) sampling sites. Sample sizes are listed above each bar.

*Release basins are Skagit River (SKAG), Stillaguamish River (STIL), Snohomish River (SNOH), Duwamish River (DUWA), East Kitsap North of the Narrows (EKPN), Puyallup River (PUYA), East Kitsap South of the Narrows (EDPS), Nisqually River (NISQ), Skokomish/Dosewallips Rivers (SKDO).

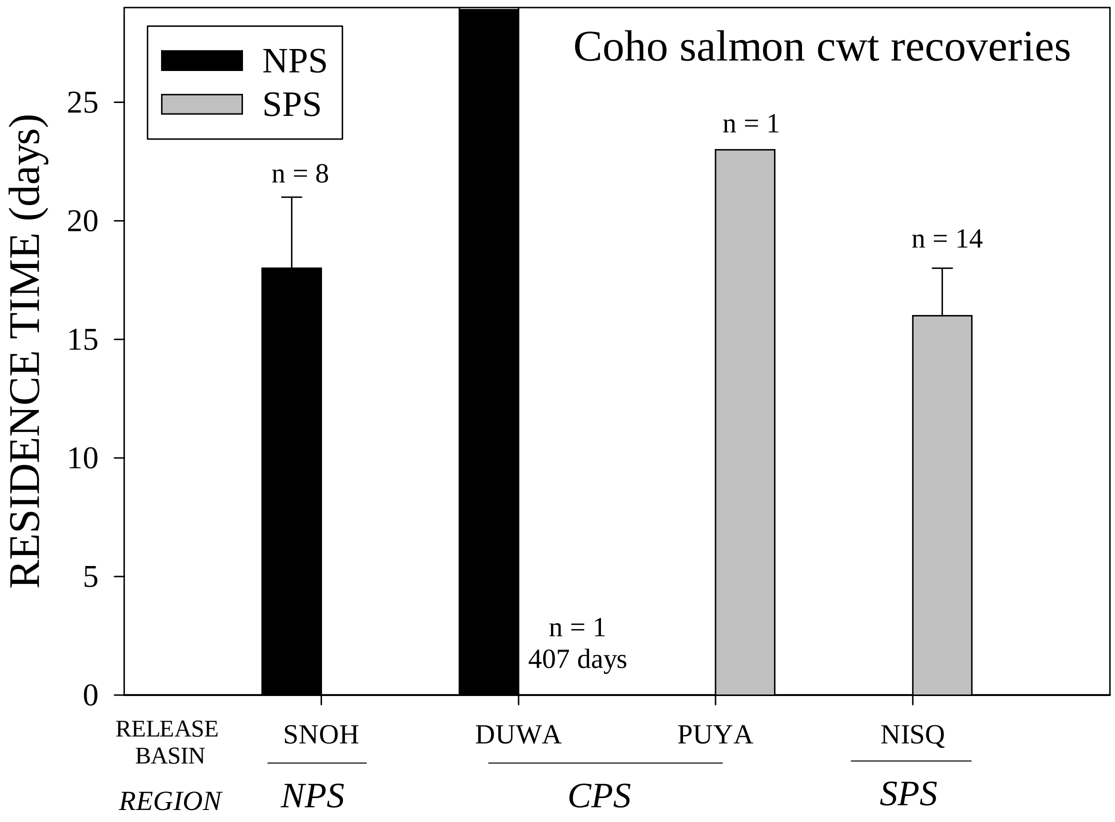

Figure 1.12. Average (± s.e.) residence time (calculated as time elapsed between 1^{st} release date from hatchery and capture date) of cwt hatchery coho salmon released at age-1 from different basins* and captured at NPS (black bars) and SPS (gray bars) sampling sites. Sample sizes are listed above each bar.

*Release basins are Snohomish River (SNOH), Duwamish River (DUWA), Puyallup River (PUYA), and Nisqually River (NISQ).

Table 1.1. Hatchery salmon released annually into Puget Sound estuaries in NPS and SPS sampling regions. When available, average sizes and months when fish are released are shown in parentheses.

(From: Hatchery Scientific Review Group's 2002 *Hatchery Reform Recommendations.*)

http://www.lltk.org/pdf/HSRG_Recommendations_Feb_02.pdf

REGION	**RELEASE ESTUARY**	**# HATCHERIES**	**PINK**	**CHUM**	**COHO AGE-1**	**CHINOOK AGE-0**	**CHINOOK AGE-1**
NPS	Stillaguamish	4		650,000*	45,000	220,000	
	Snohomish	1			170,000	1,000,000	250,000
	Tulalip Bay	1		7,500,000	1,000,000	1,700,000	40,000
	Possession Point				50,000		
	TOTAL	6		8,150,000	1,265,000	2,720,000	290,000
SPS	Nisqually River	3			980,000	5,100,000 (9.1g, May)	300,000 (75.7g, April)
	Peale Passage (net pens)	1			1,800,000 (45.4g, June)		
	Budd Inlet	1				3,800,000	250,000
	Carr Inlet	2	90,000 (≤1.0g)**	1,000,000 (1.0g)	1,400,000	1,800,000	
	Case Inlet	1				1,800,000 (3.0)	1,000,000**
	Chambers Creek Bay	1		50,000		850,000 (9.1g)	100,000
	TOTAL	11	90,000 (≤1.0g)**	1,050,000	4,180,000	13,350,000	1,650,000

*reduced to 225,000 in 2002 **released in even years only; to be discontinued in 2003

Table 1.2a. Location and description of beach seine sites.*

Region	**Zone**	**Site**	**Site #**	**GPS coordinates**	**Location**	**Slope**	**Substrate**	**Other**
NPS	Delta	Weyerhauser (WEY)	N1	N 48^{o}01.317' W 122^{o}12.310'	Mouth of Snohomish River	gentle	silt/sand/clay/ mud	woody debris and log storage
NPS	Delta	Priest Point (PRST)	N2	N 48^{o}01.834' W 122^{o}14.225'	N shore of Snohomish River delta	gentle	gravel	concrete bulkhead
NPS	Nearshore	Kayak Point (KYK)	N3	N 48^{o}08.087' W 122^{o}22.102'	Kayak Point regional park	gentle	sand/gravel	influenced by Stillaguamish River
NPS	Nearshore	SE Camano (CAM)	N4	N 48^{o}03.847' W 122^{o}21.624'	SE edge of Camano Island	moderate	gravel	undeveloped, steep vegetated bluff
NPS	Nearshore	Possession (POSS)	N5	N 47^{o}57.570' W 122^{o}20.953'	S of Clinton ferry terminal	steep	gravel	macroalgae, sparse seagrass
SPS	Delta	Chambers Creek (CHAMBCK)	S1	N 47^{o}11.434' W 122^{o}35.029'	N of Creek mouth	gentle	sand	dewaters at extreme low tides
SPS	Delta	Solo Point Creek (SOLOCK)	S2	N 47^{o}08.312' W 122^{o}37.945'	Mouth of small creek, overflow pipe	gentle	sand/gravel	macroalgae
SPS	Nearshore	Solo Point (SOLO)	S3	N 47^{o}08.284' W 122^{o}37.958'	S of Solo Point boat launch	gentle	gravel/cobble	
SPS	Nearshore	Gordon Point (GORD)	S4	N 47^{o}10.149' W 122^{o}36.772'	Public beach at Steilacoom	steep	cobble	
SPS	Nearshore	Sunset Beach (SUN)	S5	N 47^{o}13.625' W 122^{o}33.880'	Along railroad line S of Day Island	moderate	cobble/gravel	thick macroalgal beds
SPS	Nearshore	Wollochet Bay (WOLL)	S6	N 47^{o}16.238' W 122^{o}36.640'	Southern end of bay mouth/Hale Passage	moderate	sand/gravel	concrete bulkhead

*Also see Figure 1.1.

Table 1.2b. Location and bottom depth of sites sampled in 2002 by surface tow net (3.1m height x 6.1m width x 15.0m length with mesh grading from 76.0 mm in the mouth to 6.4 mm at the cod end).

Region	**Zone**	**Site**	**Site #**	**GPS coordinates**	**Location**	**Bottom depths (m)**
NPS	Neritic	Possession Sound (POSS SD)	N6	N 47°57.599' W 122°20.859'	S of Clinton ferry terminal	11-69
NPS	Neritic	Hat Island (HAT)	N7	N 48°00.595' W 122°18.078'	E shore of Hat Island	10-85
NPS	Neritic	Port Susan (TULKYK)	N8	N 48°04.784' W 122°19.430'	N of Tulalip Bay, S of Kayak Point	5-50
SPS	Neritic	Cormorant Passage (CORM)	S7	N 47°08.315' W 122°38.119'	SE Ketron Island	5-44
SPS	Neritic	Chambers Creek (CHAMB)	S8	N 47°11.181' W 122°35.372'	off Creek mouth/railroad bridge	9-37
SPS	Neritic	Hale Passage (HALE)	S9	N 47°16.201' W 122°36.707'	outside of Wollochet Bay	9-49

Chapter II: Dietary habits of juvenile salmon in Puget Sound

ABSTRACT

Between April and September 2001-2002, I assessed dietary habits of juvenile salmon at delta, nearshore, and neritic sites in northern (NPS) and southern (SPS) Puget Sound sampling areas to examine spatial and temporal differences or overlaps in diet and the potential for predation among chum, pink, coho, and chinook salmon, and between hatchery and unmarked coho and chinook salmon. Prey composition differed markedly between NPS and SPS, likely a result of the influence of substantially higher freshwater inputs to NPS on the structuring of prey resources. Insects (mainly terrestrial, with some aquatic forms) dominated juvenile salmon (especially chinook) diets at NPS sites, while euphausiids, larvaceans, and other planktonic crustaceans were prevalent at SPS sites. Epibenthic and planktonic copepods and larvaceans were the primary prey for pink and chum salmon. Epibenthic and planktonic crustaceans, including gammarid amphipods, crab larvae, euphausiids, and shrimp (primarily hippolyttid and pandalid), were major prey for coho salmon, whereas insects and fish prey were episodically important. Chinook fed mainly on insects at NPS sites, and on crab larvae, euphausiids and hyperiid amphipods at SPS sites. Fish constituted only 5-10% of the diet for chinook and coho salmon <200mm FL, but piscivory increased with size. Diet composition covaried with increasing body size through time. In general, juvenile salmon shifted from predominantly epibenthic feeding in April-May and at delta sites, to more planktonic and neustonic feeding during June-July and at nearshore marine and neritic sites. For chinook and coho salmon, diet composition was similar between hatchery and unmarked counterparts. Diel feeding chronologies indicated that juvenile salmon fed most actively during daylight, but diet composition changed between light and dark periods. Chum and pink salmon ate predominantly planktonic prey during daylight, but shifted to epibenthic prey during and after dusk. Larger chinook and coho salmon became more piscivorous at crepuscular and post-dusk hours, feeding mainly on Pacific sand lance and juvenile salmon (pink and chum) in April-June. The potential for dietary overlap was greatest between juvenile pink and chum salmon, between chinook and coho salmon of similar

size, and between hatchery and unmarked chinook salmon. Large juvenile and subadult chinook and coho salmon have the potential to be significant individual predators on smaller juvenile salmon (pink and chum salmon mainly, but also chinook salmon) during peak outmigration pulses (May, this study, Chapter 1).

INTRODUCTION

Estuarine and coastal marine environments provide important foraging and rearing habitat for juvenile anadromous Pacific salmon (*Oncorhynchus* spp.; Simenstad et al. 1982; Thorpe 1994; Aitken 1998). While juvenile salmon in coastal and estuarine waters experience some of the most rapid growth rates of all life history stages (LeBrasseur and Parker 1964; Healey 1979; Healey 1982b; Mortensen et al. 2000), they are also subject to the highest mortality rate during the period between seaward migration and adult return (Parker 1962; Royal 1962; Furnell and Brett 1986). There is evidence that growth during this period determines overall marine survival trends (Holtby et al. 1990; Hargreaves 1997; Murphy et al. 1998; Tovey 1999). In Puget Sound, chinook (*O. tshawytscha*) and Hood Canal summer-run chum salmon (*O. keta*) are listed as threatened under the Endangered Species Act (ESA), while coho salmon (*O. kisutch*) are candidates for listing. Very little is currently known about the basic ecology of juvenile salmon in Puget Sound. Changes in foraging conditions and food web dynamics may be contributing to declines in Puget Sound salmon stocks.

The relative importance of estuarine and coastal marine environments differs among species due to differences in residence times and utilization of these environments (Healey 1982a; Simenstad et al. 1982; Aitken 1998). Of the juvenile salmon that migrate to sea during their first year (age-0), pink (*O. gorbuscha*) and chum salmon usually arrive in estuarine waters earliest (February-April) and at the smallest size (pink salmon often the smallest), followed by chinook salmon (April-July). Most stream-type coho and chinook salmon migrate to sea after rearing for one year in freshwater, and arrive in estuarine waters substantially bigger than subyearling migrants (April-June). Ocean-type chinook salmon are believed to be the most dependent (Healey 1982a) on estuarine environments, followed by chum and then coho salmon (Bostick 1955; Stober et al. 1973;

Shepard 1981; Healey 1982a; Simenstad et al. 1982). Pink (and sockeye, *O. nerka*) salmon migrate rapidly to the ocean, and are considered the least dependent on estuaries.

Juvenile salmon enter the nearshore marine environment at a size vulnerable to many potential predators (including fish, birds, and marine mammals), which are hypothesized to be responsible for much of the mortality in this phase (Parker 1971; Beamish and Mahnken 1998). Size at this stage is critical because it partially determines the amount of predation risk. According to size-spectrum theory, larger, fast-growing individuals spend less time vulnerable to the many gape-limited predators than their smaller and slower-growing conspecifics (Sogard 1997). Densities of predators and juvenile salmon also affect predation risk. In the estuarine and marine environment, juvenile salmon face many potential predators including larger salmon and trout (Kaczynski et al. 1973; Fresh et al. 1981; Mortensen et al. 2000; Jauquet 2002); although few studies in estuaries have quantified juvenile salmon mortality due to predation. Juvenile coho and chinook salmon have been observed feeding on other salmon up to 40-50% of their length (Brodeur 1990; Pearsons and Fritts 1999). In Puget Sound, there is concern that releases of yearling hatchery chinook salmon and juvenile coho salmon during peak migrations of natural populations and smaller pink and chum salmon may result in significant predation mortality (Buckley 1999).

When the food supply is limited, dietary overlaps among species and between hatchery and wild salmon may result in intra- and inter-specific competition that would negatively affect growth rates and overall smolt size (Fisher and Pearcy 1996; Sturdevant 1999). Perry et al. (1996) relate spatial differences in zooplankton biomass and stable isotopic signatures in juvenile salmon to feeding and growth conditions off of Vancouver Island. They concluded that poorer feeding areas, which may vary over different time scales, may result in increased susceptibility to predation due to poorer condition and smaller sizes of fish. The quality of feeding areas might also affect migration rates and residence times, because salmon are believed to leave areas of poor food quality faster than when food sources are abundant (Healey 1982a; Simenstad et al. 1982; Orsi et al. 2001). The potential for competition may be increased by coincident releases of large numbers of hatchery salmon during peak wild salmon emigrations. In addition, seasonal shifts in prey resources and water temperature may affect the potential growth rates of juvenile salmon.

Fish diets reflect the local forage base and availability of prey as well as specific preferences. In this chapter, I examined whether diets of Puget Sound juvenile salmon varied in a spatial (northern sites vs. southern Puget Sound sites) and temporal (April through September) framework, and between a pink salmon (2002) and non-pink salmon (2001) juvenile outmigration year. Sites in both sampling regions were located adjacent to significant sources of hatchery and wild salmon, but differed in temperature and salinity, as well as timing and relative abundance of juvenile hatchery and unmarked salmon (Chapter 1). Within each region, I examined whether diets shifted as salmon moved from delta entry points to nearshore beaches to offshore surface (neritic) waters. A better understanding of their trophic interactions may help to identify factors contributing to the declines in Puget Sound salmon stocks.

METHODS

STUDY AREA

Puget Sound is an estuary - a semi-enclosed body of water where saltwater from the ocean is mixed with fresh water draining from the surrounding watershed. Puget Sound is a deep, elongated glacial fjord composed of underwater valleys, ridges and basins with an average depth of 135m. The maximum depth of 285m occurs just north of Seattle in the large main basin. A shallow sill separates the main basin from the southern basin near the Tacoma Narrows. The southern basin receives <10% of the freshwater draining into Puget Sound, primarily from the Nisqually and Deschutes rivers plus smaller rivers and streams (Burns 1985). Northeast of the main basin, the Whidbey basin includes the waters of Possession Sound, Port Susan, Saratoga Passage and Skagit Bay. The Whidbey basin is fed by the some of the Sound’s largest rivers (the Skagit, Snohomish and Stillaguamish) and receives 60% of the freshwater entering Puget Sound (Burns 1985).

For this study, I focused on sites in two areas: a northern Puget Sound (NPS) region encompassing Possession Sound/Port Susan/Port Gardner in the Whidbey basin, and a southern Puget Sound (SPS) region encompassing Cormorant Passage/Wollochet Bay/south of the Narrows in the southern basin. These two sampling regions include freshwater exit points for both wild juvenile salmon and those from several major hatchery-based stock enhancement programs. Within each sampling region, I chose five to six comparable shallow sublittoral sites, suitable for beach seining, and three offshore "neritic" transects for tow netting (Figure 1). Of the beach seining sites, two per region were chosen at or near the mouth of a freshwater input source, and were designated "delta" sites. The other three (or four in SPS) sites were located along exposed beaches at increasing distances from a freshwater source, and were termed "nearshore" sites.

This arrangement was designed to target likely salmon emigration routes. The shallow sublittoral NPS sites radiated outward from the Snohomish River. The NPS sites were a spatially-representative subset of 25 sites sampled weekly during April-July in 1986-1987 in a previous study (Beauchamp et al. 1987), and were chosen because they consistently reflected the overall trends in migration timing of all species of juvenile salmon through the outer estuarine and nearshore marine areas in this basin. The shallow sublittoral SPS sites radiated outward from the mouth of Chambers Creek. Sites were located in proximity to release sites for hatchery salmon (Tulalip Bay and Snohomish River, Chambers Creek and Nisqually River), major freshwater inflows (Snohomish and Nisqually Rivers), and along suspected emigration corridors. Tow netting transects were conducted over increasing depths and distances from shore, parallel to a subset of the beach seine sites (as described in Chapter 1).

FISH SAMPLING

Field sampling was designed to characterize migration timing, size structure, and diet of juvenile salmon in both NPS and SPS, although I was unable to sample in February-March, which are potentially peak outmigration months for pink and chum salmon. I conducted biweekly beach seining (two sets per site) at each site in both regions from April through September 2001 and 2002 using a floating beach seine (37.0m length x 2.0m height, with mesh grading from 3 cm in the wings to 6 mm at the cod end) according to standard estuarine fish sampling protocol (Simenstad et al. 1991). In 2002, I sampled fish from neritic (offshore surface waters; three tows per site) sites monthly during May-September in NPS and June-September in SPS) using a Kvichak two-boat surface trawl ("tow net," 3.1m height x 6.1m width x 15.0m length with mesh grading from 76.0 mm in the mouth to 6.4 mm at the cod end). Sampling gear (i.e., beach seine and tow net) were chosen based on successful past performance and to maximize consistency and potential comparison with past and current efforts in Puget Sound (Hodgson and Brakensiek 2003; C. Rice, NOAA-Fisheries, Mukilteo, WA, pers. comm.; C. Simenstad, University of Washington, pers. comm.). All sampling occurred during daylight hours, which may have contributed to increased gear avoidance (especially in the tow net sampling) and a potential bias in the salmon diet composition. In an effort to examine potential diel differences in their feeding patterns, I also sampled juvenile salmon diets (one day per region; see Chapter 1) over a near-24 hour interval during the peak juvenile salmon migration period in May 2002.

Counts of all fish were recorded by species. Hatchery chinook and coho salmon were identified by adipose fin-clips or coded-wire-tag (cwt) detectors (in 2002 only). Unmarked chinook and coho salmon were assumed to be wild fish, however, the total (and regional) proportions of hatchery chinook and coho salmon that are mass-marked with adipose fin-clips (used by WDFW since 1996) are not accurately known, and marking success rates may differ by hatchery facility. Individual fork lengths (FL, to the nearest 1mm) and wet weights (Wt, to the nearest 0.1g) were recorded for sub-samples (at least 30 fish per species, when available). I took representative sub-samples (5-10 fish from each size mode, but at least 10 of the larger potential piscivores >200mm when available, and all fish with cwt) of gut contents and scales from each salmon species and for both hatchery and unmarked chinook and coho salmon. Fish that were sacrificed were euthanized in an overdose of MS-222, then frozen with dry ice or preserved in 10% buffered formalin until further processing in the lab. For ESA listed (i.e., unmarked) chinook salmon, I obtained gut contents from anaesthetized (with MS-222) fish using non-lethal gastric lavage.

DIET COMPOSITION

Gut contents were analyzed from a subset of juvenile salmon. Using a dissecting microscope, invertebrate prey were separated into broad taxonomic categories, and fish prey to species where possible. Blotted wet weights of all prey categories, and for individual fish prey, were recorded to the nearest 0.0001g using an electronic scale. Prey were grouped by the habitats generally associated with them, and were defined as follows: Epibenthic/benthic prey items included cumaceans, fish/intertebrate eggs, gammarid amphipods (*Eogammarus* spp., *Corophium* spp. and others), harpacticoid copepods, isopods (*Gnorimosphaeroma* spp., and others), mysids (*Neomysis* spp.), ostracods, polychaetes, and shrimp (mainly pandalids and hippolyttids). Planktonic prey included barnacle “larvae” (cyprids and slough), calanoid copepods, cladocerans, decapod crab larvae (zoea and megalopa), euphausiids, marine gammarid amphipods, hyperiid amphipods, and larvaceans. “Insects” were associated with neuston or drift and included both terrestrial and aquatic insects (including Coleoptera, Diptera – especially chironomid pupae and adults, Homoptera, Hymenoptera, Lepidoptera, Trichoptera, Plecoptera) as well as spiders and water mites (Arachnida). Nektonic fish prey included mainly larval and juvenile fish species.

The proportional wet weight contribution of each prey category was calculated individually for all non-empty stomachs. Fish were binned by size when multiple ages of fish were present. For chinook salmon, age-0 fish were considered to be <130mm FL; age-1 fish were 130-200mm FL. Chinook salmon >200mm FL were considered age-1+. Age-1 coho salmon were <200mm FL; coho salmon > 200mm FL were considered age-1+. Square-root transformed diet proportions were analyzed initially with MANOVA (Zar 1999) to examine the effects of interannual (2001 versus 2002) and seasonal (April-September, sampling weeks 1-24) variability, region (NPS, SPS), zone (delta, nearshore, neritic-2002 only), and origin (marked hatchery versus unmarked chinook and coho, 2002 only) on diet composition. Two-way and higher-order interaction terms were omitted if initial analysis confirmed they were not significant. These initial results were screened for only those effects and prey categories that showed significant main effects or interaction terms after Bonferroni correction for multiple comparisons, and subsequent analyses were conducted on each prey category individually using one-way ANOVA (Zar 1999). For different species or hatchery-unmarked groups that exhibited potential overlap among major prey groups during periods of peak catches, I used one-way ANOVA (Zar 1999) to test for differences in dominant prey categories.

Fish prey were also measured (FL) and compared to predator length (FL) to assess for size limits (gape limitation) or size-selectivity. Predators were grouped in size bins to examine shifts in piscivory versus size. For chinook salmon, bins were <80mm, 80-100mm, 101-120mm, 121-200mm, and >200mm FL. For coho salmon, bins were <120mm, 121-200mm, and >200mm FL. To examine diel feeding chronologies and diet composition, I calculated the ratio of the wet weight of the gut contents to the whole body weight (less the weight of the gut contents) to get a measure of feeding intensity (Brodeur 1990).

RESULTS

DIET

Although many common prey items appeared in diets of different salmon species, each species displayed distinct diet composition patterns. Diet composition varied considerably among species ($P < 0.001$) and between sampling regions ($P = 0.001$) and zones ($P=0.015$) through time ($P < 0.001$), but were similar between years ($P > 0.05$). Diet composition covaried with increasing body size through time. Juvenile salmon shifted from predominantly epibenthic feeding in April-May and at delta sites, to more planktonic and neustonic feeding during June-July and at nearshore marine and neritic sites. Neritic diets of pink and chum salmon (almost solely larvaceans) were more different from nearshore diets than for chinook and coho salmon. In general, prey resources were more similar between zones in each sampling region than between NPS and SPS. Insects (mainly terrestrial, with some aquatic forms) were dominant prey items in the diets of juvenile salmon at NPS sites, while euphausiids, larvaceans, and planktonic crustaceans were more dominant in diets at SPS sites.

Chinook Salmon

Age-0 chinook salmon diets varied by sampling region ($P<0.001$), zone ($P=0.012$), and sampling week ($P<0.001$; Table 2.1a). Based on prey biomass, insects were an important part of chinook salmon diets in all months in Puget Sound. Insects (mainly dipterans, chironomid pupae and adults and hymenopterans, but also lepidopterans, arachnids, aphids, coleopterans, and trichopterans) were much more dominant in NPS than in SPS diets ($P<0.001$), and in delta and neritic diets than in those at nearshore sites ($P<0.001$). Within SPS sites, insects were more prevalent prey items in 2002 than in 2001. Crab larvae (May- June primarily, but also July-August), euphausiids, and planktonic hyperiid amphipods (July-September) were dominant prey in diets at SPS sites ($P<0.001$). Chinook salmon fed more on epibenthic gammarid amphipods ($P<0.001$) at delta sites and plankton at nearshore sites, especially in SPS. Neritic diets were composed primarily of crab larvae and insects and were similar to, but less diverse than nearshore diets. Age-0 chinook salmon were more piscivorous in 2002 than in 2001 ($P=0.014$), and fed mainly on Pacific sand lance (*Ammodytes hexapterus*). In 2002, fish prey composed small proportions of juvenile chinook salmon diets at SPS sites during April-June, whereas at NPS sites, fish prey became increasingly important in July-September. Other fish prey included pink salmon and three-spine stickleback (*Gasterosteus aculeatus*). Though hatchery fish ate more crab larvae than unmarked fish at sites in SPS ($P<0.001$), and were less piscivorous than unmarked fish at NPS sites ($P<0.001$), overall diets of hatchery and unmarked chinook salmon were very similar (Table A.2.1).

Larger, age-1 (131-200mm FL) and age-1+ (>200mm FL) chinook salmon diets differed by region ($P=0.039$; Table 2.1b). In 2001, these older fish were more piscivorous at sites in NPS than in SPS ($P=0.001$), at nearshore sites versus delta sites ($P=0.037$), and piscivory increased with size (>200mm chinook salmon were more piscivorous than 131-200mm fish, $P=0.04$). Fish prey included pink, chum and chinook salmon, surf smelt (*Hypomesus pretiosus),* shiner perch (*Cymatogaster aggregata)*, sculpins (*Leptocottus armatus, Artedius spp.),* and bay pipefish (*Syngnathus leptorhynchus*). None of the larger chinook salmon caught in 2002 had eaten fish. Other important prey were gammarid amphipods, more prevalent in diets at delta than nearshore sites (P<0.001), and in 2002 than 2001 (P=0.014), insects, euphausiids, and crab larvae, more dominant in diets at SPS sites than at NPS sites (P=0.05),.

Coho Salmon

Age-1 coho salmon diets varied by sampling region (P<0.001), zone (P<0.001), and sampling week (P<0.001; Table 2.2). At NPS sites, gammarid amphipods were a major prey item for coho salmon during April-June, particularly at delta sites (versus nearshore and neritic sites, P<0.001). Fish prey were dominant, particularly in April and May. Insects were a minor but consistent proportion of the diet in NPS in both years, and greater than at SPS sites (P<0.001). Crab larvae, a dominant prey item, particularly in June (except in July, not June, 2002 for NPS sites), were more dominant in 2002 than 2001 (P=0.005) and in SPS versus NPS (P=0.034). Crab larvae also became increasingly important in the diet as fish made the transition from delta to nearshore to neritic sites (P<0.001). At SPS sites, coho salmon consumed a wide variety of epibenthic and planktonic prey, some insects (more at delta than nearshore sites) and a small proportion of fish in May.

Coho salmon were more piscivorous in NPS (mainly nearshore sites) than at SPS sites (P<0.001). In April and May, the main fish prey for coho salmon were juvenile pink and chum salmon. Other prey fish prey included Pacific sand lance, Pacific herring (*Clupea pallasii)*, and juvenile flounders (*Pleuronectes spp*., *Platichthys stellatus)*. Hatchery and unmarked coho salmon exhibited similar diets, although insects (P=0.07) and polychaetes (P=0.001) were slightly more important to unmarked than to hatchery coho salmon at NPS sites (Table A.2.2). A few age-1+ coho salmon were caught in April and May during both years (5 in 2001, 2 in 2002). These larger (235-390mm FL) fish ate mainly planktonic crustaceans (crab larvae and gammarid amphipods in NPS, euphausiids in SPS) and fish (Pacific sand lance and Pacific herring; Table 2.2).

Chum Salmon

Chum salmon diets varied by sampling region (P<0.001) and sampling week (P<0.001). Copepods, both calanoid (more common in SPS diets than NPS, P<0.001) and harpacticoid, dominated diets of chum salmon at nearshore Puget Sound sampling sites (Table 2.3). Insects (mainly hymenopterans, dipterans - principally chironomid pupae and adults - but also aphids and arachnids) were more dominant in NPS diets (P<0.001), whereas larvaceans, the dominant prey in all neritic diets, were more common in diets at nearshore sites in SPS than in NPS (P=0.012). In NPS, epibenthic gammarid amphipods were more dominant prey items at delta than at nearshore sites (P=0.028) where planktonic organisms, like crab larvae (P=0.077) and larvaceans (P=0.01), were more important components of the diet. Chum salmon ate only slightly more harpacticoid copepods (not significant) at delta than at nearshore sites in SPS. Polychaetes, hyperiids, cladocerans, cumaceans, and isopods occasionally appeared as major prey items, but were generally absent.

Pink Salmon (*2002 only*)

Pink salmon diets varied by sampling region (P<0.001), zone (P<0.001), and sampling week (P<0.001). Both epibenthic harpacticoid and planktonic calanoid copepods dominated pink salmon diets, although in differing proportions, between April and July, 2002 (Table 2.4). Overall, there was a transition from epibenthic feeding (harpacticoid copepods and ostracods) to more planktonic and neustonic feeding between April and July, and between delta and nearshore sites (P<0.001), which coincided with increasing fish size. Pink salmon ate more insects (mainly dipterans, chironomid pupae and adults, and hymenopterans; P<0.001) and ostracods (P<0.001) at NPS sites and more euphausiids (P<0.001) and harpacticoids (P=0.03) at SPS sites. Larvaceans were slightly (not significant) more prevalent in the diets of fish caught at sites in SPS than in NPS, but significantly more dominant in all diets of fish caught at neritic sites (P<0.001) than in other zones. Fish egg sacs (species unknown), although not a gravimetrically significant prey item, were relatively common in pink salmon stomachs. Other prey, like cladocerans and polychaetes, occasionally appeared as dominant prey items, but were otherwise absent.

DIEL FEEDING CHRONOLOGY

Juvenile salmon fed most actively during daylight (Figure 2.2), especially at sites in SPS. Diet composition varied with the time of day. Larger chinook (Figure 2.3) and coho salmon (Figure 2.4) were more piscivorous at crepuscular and post-dusk hours, feeding mainly on juvenile pink and chum salmon. Chum (Figure 2.5) and pink (Figure 2.6) salmon ate epibenthic prey mainly during and after dusk, while planktonic prey (copepods, larvaceans, and cladocerans) dominated the diets during daylight.

PISCIVORE-PREY SIZE RELATIONSHIPS

Chinook and coho salmon were more piscivorous at larger lengths ($P<0.001$; Figure 2.7). Whereas only 5% of the diet (by weight) of chinook salmon <120mm FL consisted of fish, fish were 10% of the diet for chinook salmon 121-200mm, and 37% for chinook salmon larger than 200mm FL (Table 2.1b). Fish prey constituted 5-10% of the diets of coho salmon <200mm FL, but 54% for larger coho salmon, on average. Coho salmon <200mm FL fed more heavily on juvenile salmon than larger fish, primarily during April and May. Both chinook and coho salmon were more piscivorous at sites in NPS than at SPS sites ($P=0.04$).

Lengths of fish prey eaten by chinook salmon ranged from 4-51% of their FL (Figure 2.8; Pacific sand lance, 4-46% FL; bay pipefish, 32-51%FL), while coho salmon consumed fish 7-44% of their FL (Figure 2.9). Chinook salmon fed mainly on Pacific sand lance while coho salmon ate predominately juvenile salmon. Salmon were rarely eaten by chinook salmon <200mm FL, but made up 8% of the diet of chinook salmon >200mm FL. One subadult chinook salmon, 353mm FL, consumed a juvenile chinook salmon approximately 30% of its length, in June 2001, while chinook salmon, 114-195mm FL, ate pink and chum salmon 15-33% of their FL in 2002.

DIET OVERLAP

During April-June, 2002, chum (Table 2.3) and pink salmon (Table 2.4) had very similar diets, with no significant differences in wet weight proportions of major prey items includinmg calanoid and harpacticoid copepods and larvaceans (P>0.25). Differences in minor prey items included the higher consumption of crab larvae (P<0.02) and gammarid amphipods (P<0.03) by chum salmon than pink salmon, which consumed slightly more cumaceans (P<0.05). Proportions of major prey items (euphausiids, crab larvae, insects, gammarid amphipods, shrimp, and polychaetes) in diets of similarly-sized (<100mm or 100-130mm FL) chinook and coho salmon during April-June 2002 were not significantly different (P>0.05) at sites in each sampling region. However, there were few significant dietary overlaps among the different size classes of chinook and coho salmon, at NPS sites in particular. While diets of hatchery and unmarked chinook were very similar overall during May-August, 2002, there were significant differences in a few prey items. Hatchery chinook salmon ate more crab larvae than unmarked fish at sites in SPS (P<0.001), and were less piscivorous than unmarked fish at NPS sites (P<0.001). In this analysis, diet similarities were based on general taxonomic prey categories and may have obscured differences in dietary preferences at a more specific level. Therefore these results represent potential overlaps.

DISCUSSION

The diet composition of juvenile salmon varied spatially, temporally and among species, supporting the conclusion that they are generally opportunistic feeders with species-specific foraging habits (Healey 1982a). The most striking dietary differences occurred between the northern and southern Puget Sound sampling sites. The dominance of largely terrestrial insects in diets at NPS sites differed markedly from the largely planktonic crustacean-dominated diets at SPS sites, and piscivory was more common for chinook and coho salmon as well. Kaczynski et al. (1973) reported a similar regional difference for chum and pink salmon in the early 1970's: diets were more diverse at Port Susan (NPS), including insects, mysids and copepods, whereas diets at Anderson Island

(SPS) consisted almost entirely of copepods. Consistent with present findings, Fresh et al. (1981) found that larvaceans were more important and fish larvae less important in diets of fish from SPS than for salmon further north in central Puget Sound (CPS), while insects were less important overall (both SPS than CPS). The greater proportion of neustonic drift insects in NPS was likely a result of substantially greater freshwater flow into that region. Higher precipitation (United States Geological Survey, USGS, unpublished data) during winter and spring 2002 likely contributed to the greater proportion of insects in SPS chinook diets in 2002 than during the near-drought of winter 2001. Lower surface salinities in NPS than SPS (Chapter 1) may be linked to differences in neustonic prey communities. Other sources of insects that may differ between the sampling areas are fallout (Simenstad et al. 1982) and transport by wind (Cheng and Birch 1978) from vegetation in wetlands and uplands.

The overall transition from predominantly epibenthic feeding in April-May and at delta sites, to more planktonic and neustonic feeding during June-July and at nearshore and neritic sites, is consistent with similar studies and is seen most distinctly with chum salmon (Kaczynski et al. 1973; Fresh 1979; Fresh et al. 1981; Pearce et al. 1982; Simenstad et al. 1982). In other studies, the nearshore to offshore, epibenthic to planktonic diet transition is often associated with an observed size threshold. In this study, it was difficult to separate temporal effects from size effects or habitat-type, because size and habitat zones by juvenile salmon generally covaried with time. Neritic diets of pink and chum salmon (almost solely planktonic larvaceans) were the most distinct from nearshore diets, whereas nearshore and neritic diets were similar for chinook and coho salmon. Consistent with the studies mentioned above, this suggests that pink and chum salmon have distinct nearshore and offshore stages, both for feeding and residence. Chinook and coho salmon, on the other hand, appeared to use a wider variety of prey resources and potentially move more opportunistically between habitats. I was unable to find clear size thresholds either for offshore movement (Chapter 1) or for diet shifts, although piscivory was only observed in chinook salmon at least 70mm FL.

In laboratory conditions, coho and chinook salmon were able to consume salmon prey up to 40-47% of their FL (Pearsons and Fritts 1999). Chinook and coho salmon off the coast of Washington and Oregon consumed salmon up to 50% of their length, although the average prey fish was 20% of the predator’s length (Brodeur 1990). The majority of intrageneric salmon predation in Puget Sound occurred during the spring (April-June). Juvenile chinook salmon at NPS and SPS sites preyed on salmon 15-33% of their length, although they most commonly ate more streamlined Pacific sand lance up to 46% of their FL and were able to consume bay pipefish up to 51% of their FL. Chinook salmon as small as 95mm FL preyed on pink salmon, but most chinook salmon that preyed on salmon were larger than 150mm. This is likely due to gape-limitation since most pink (34-60mm FL) and chum (38-56mm FL) salmon present in Puget Sound during peak age-0 chinook salmon abundances were 36-61% of their FL (56-95mm FL; Chapter 1). Age-1 coho salmon (105-145mm FL), at least 10-50mm larger than chinook salmon during peak emigrations, were more piscivorous on salmon, eating salmon prey 7-44% their FL.

Little is known about the similarity of diets between hatchery and wild salmon in estuarine and marine environments. Myers (1980) found that diets of hatchery and wild chinook and coho salmon were very similar overall, although dietary differences were apparent soon after hatchery fish were released and declined over time. Initially, hatchery fish ate objects like styrofoam, paint chips and plastic that was presumably similar in size and shape to hatchery food pellets. Hatchery coho salmon were also less piscivorous than wild coho salmon while in the river channels near the mouth of the estuary (Myers 1978). This was taken as evidence that hatchery fish required a period of learning in order to forage successfully in the wild. In a recent study (C. Simenstad, University of Washington, unpublished data), distinct diet differences were found between hatchery and wild chinook salmon by the Hiram M. Chittenden locks in Shilshole Bay, Puget Sound, which may also be evidence of a period of learning. The locks, however, present a unique environment where freshwater and salt water meet abruptly, and findings here may not be directly applicable to other nearshore Puget Sound areas. The high similarity between diets of hatchery and wild chinook and coho salmon in the present study may mean that hatchery fish have already learned to forage successfully in the wild by the time they were caught at NPS and SPS sites. It may also mean that many of the unmarked fish were also hatchery-produced or experienced very similar behaviors (e.g., genetic homogeneity).

In this study, I assumed that stomach contents of juvenile salmon collected broadly during daylight hours were representative of typical dietary patterns. While based on limited data, I did observe that juvenile salmon are mainly daylight feeders, at least in May 2002. This is consistent with observations for pink salmon in estuaries of Alaska and British Columbia (Gosho 1976; Godin 1981), although Gosho (1976) also found evidence of increased feeding at night and shifts in diet patterns between day and night. In Hood Canal, Feller (1974) found that diets of chum and pink salmon shifted from planktonic prey during the day to epibenthic prey during darkness, which is consistent with our findings in Puget Sound. Tidal level may have also affected diet composition, although feeding is known to occur at high and low tides (Healey 1979), and there did not appear to be distinct diet shifts with tidal stage during the diel samples. In this study, the most significant dietary shift in non-daytime hours was the increase in predation by chinook and coho salmon during crepuscular and dark hours.

It is widely known that fish piscivory tends to be highest during crepuscular hours (Howick and O'Brien 1983; Beauchamp 1990; Beauchamp et al. 1992), a common trend when predators and prey rely on visual contrast (Breck 1993). In May, the most significant predation on pink and chum salmon occurred during dusk by chinook salmon approximately 160-265mm FL and during crepuscular hours by coho approximately 110-135mm FL (up to greater than 300mm FL). Chinook and coho salmon, at this size in May, are likely age-1 juveniles or older subadults that had been resident in Puget Sound for at least several months. During peak outmigrations in 2001-2002, most juvenile coho salmon, and some juvenile chinook salmon were at least 40-70% longer and therefore potentially could have consumed juvenile pink, chum, and some chinook salmon. Parker (1971) suggested that juvenile coho salmon predation was responsible for most of the early marine mortality of pink salmon in a British Columbia inlet and that coho salmon preyed preferentially on the smaller individuals. In order to get a better idea of the extent of juvenile salmon predation by chinook and coho salmon (and other piscivores), I would recommend more intensive sampling during and around crepuscular periods between April and June (or known peak outmigration times).

The greatest potential for dietary overlap existed for chum and pink salmon, and between hatchery and unmarked chinook salmon, particularly in April and May. There was some potential for dietary overlap between chinook and coho salmon of similar sizes, however since most coho salmon in this study were larger than the chinook salmon caught in the same sets, the likelihood of high dietary overlap, coincident in time and space, was low. All of these juvenile salmon species occurred in high relative abundances, with peak catches, often coincident (at SPS sites in particular), between April and June. In addition, substantial proportions of these pulses were hatchery fish (chinook and coho salmon), which were, on average, slightly larger than the naturally produced fish. There is potential for competition between these hatchery and wild fish as well, particularly for chinook salmon at SPS sites, where 98% of the chinook salmon caught in this study were from hatcheries. Depending on the composition and density of the prey resources, fish densities and dietary overlaps may be high enough to cause competition, likely in localized pockets. Fresh et al. (1981) found that the potential for competition existed between chinook and coho salmon juveniles (similarly-sized) in shallow sublittoral and nearshore pelagic waters, while chum salmon (juvenile pink salmon diets not available) were likely competing with baitfish (Pacific herring, Pacific sand lance and surf smelt) for similar food resources. However, most of this diet information was summarized using general taxonomic prey categories, and must be interpreted cautiously. Differences in dietary preferences at a more specific level may have reduced the potential for dietary overlap and competition.

In the late 1970’s, juvenile salmon diets in Puget Sound were similar to today, with the apparent exception of chinook. Chinook salmon were more piscivorous, eating primarily Pacific sand lance, Pacific herring, and crab larvae (Fresh et al. 1981). Insects and polychaetes were only moderately important, and prevalent later in the summer (August). This may reflect spatial (regional) differences in sampling locations, or a potential shift in prey resources. Fresh et al. (1981) found that the density of surface zooplankton (calanoid copepods and crab larvae) in CPS and SPS was highest in spring

(June peak), greater offshore than nearshore, and greater in CPS than SPS. This would suggest that prey resources in 1978-1979 were abundant during peak residence of juvenile salmon, however other key prey sources, such as prey fish, insects, and epibenthic crustaceans, were not sampled. The status of prey resources in Puget Sound today is unknown. In order to have a comprehensive understanding of foraging and food web dynamics (specifically the potential for predation and competition, in a limited carrying capacity situation), it is essential to examine both the prey resources and the larger food web.

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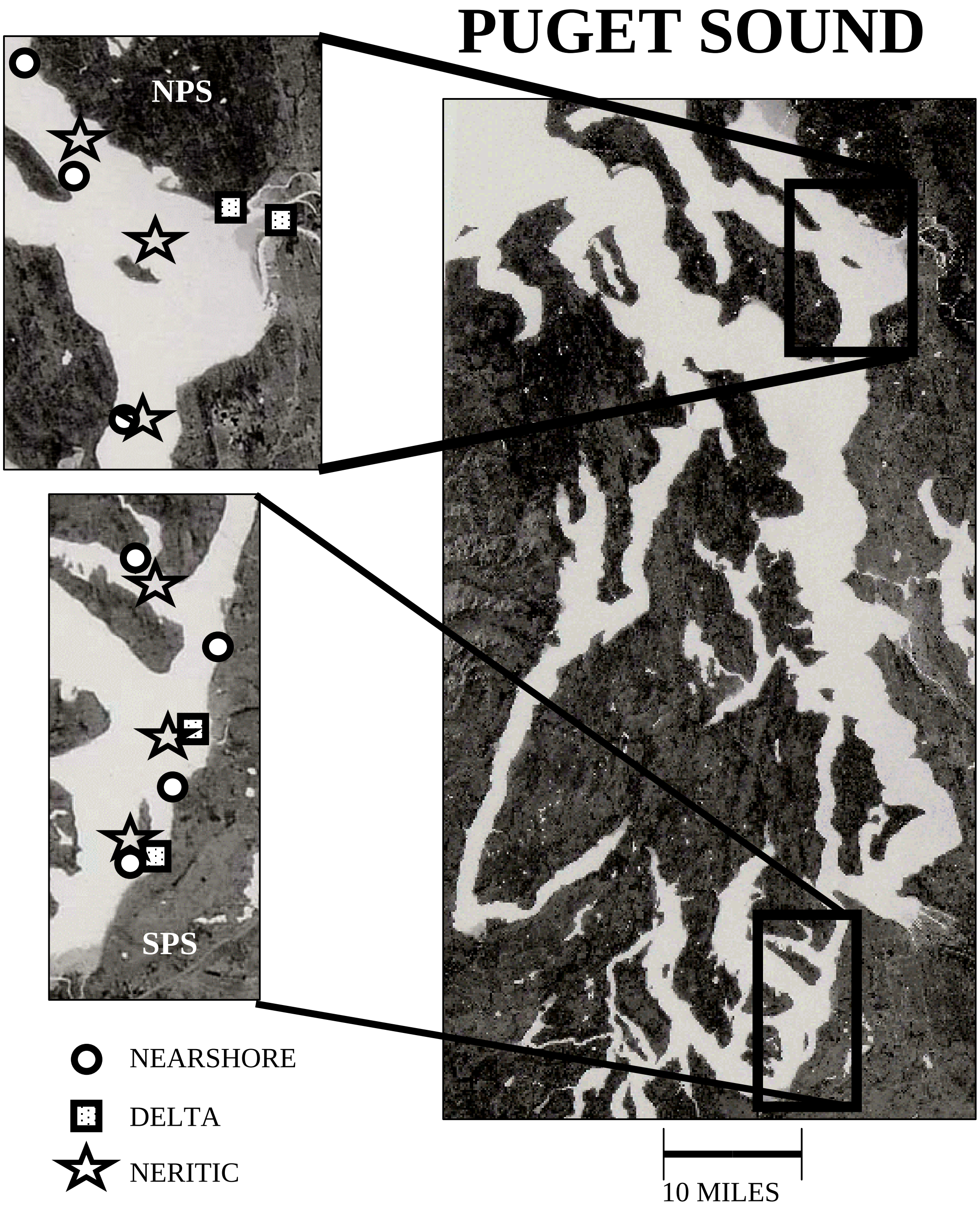

Figure 2.1. Puget Sound study regions and sampling locations. Circles and squares indicate nearshore and delta beach seine locations. Stars indicate neritic tow net locations.

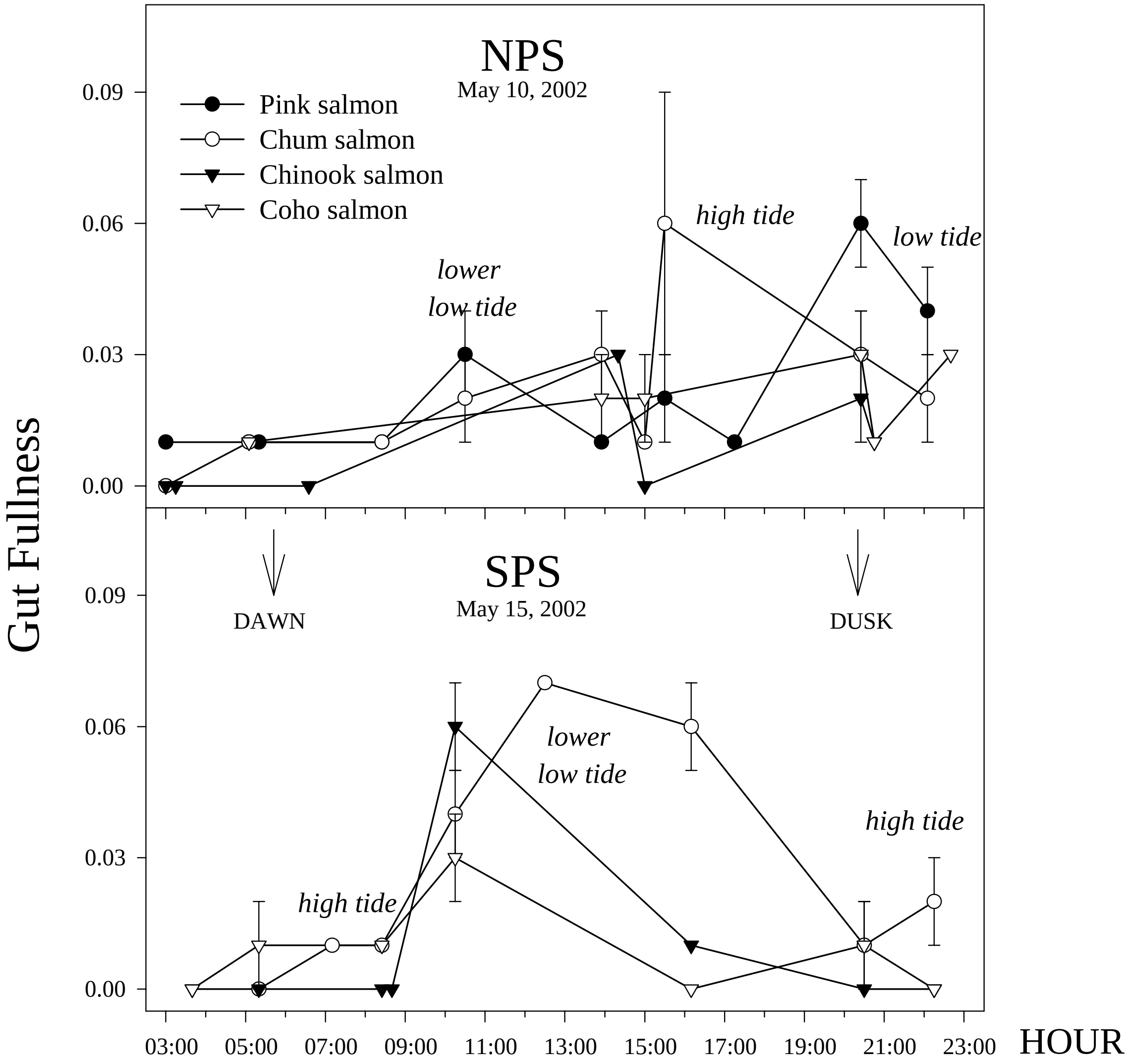

Figure 2.2. Gut fullness (ratio of gut contents wet weight to the whole body weight, less the weight of the gut contents) ± standard error, of juvenile salmon over diel sampling periods in NPS and SPS.

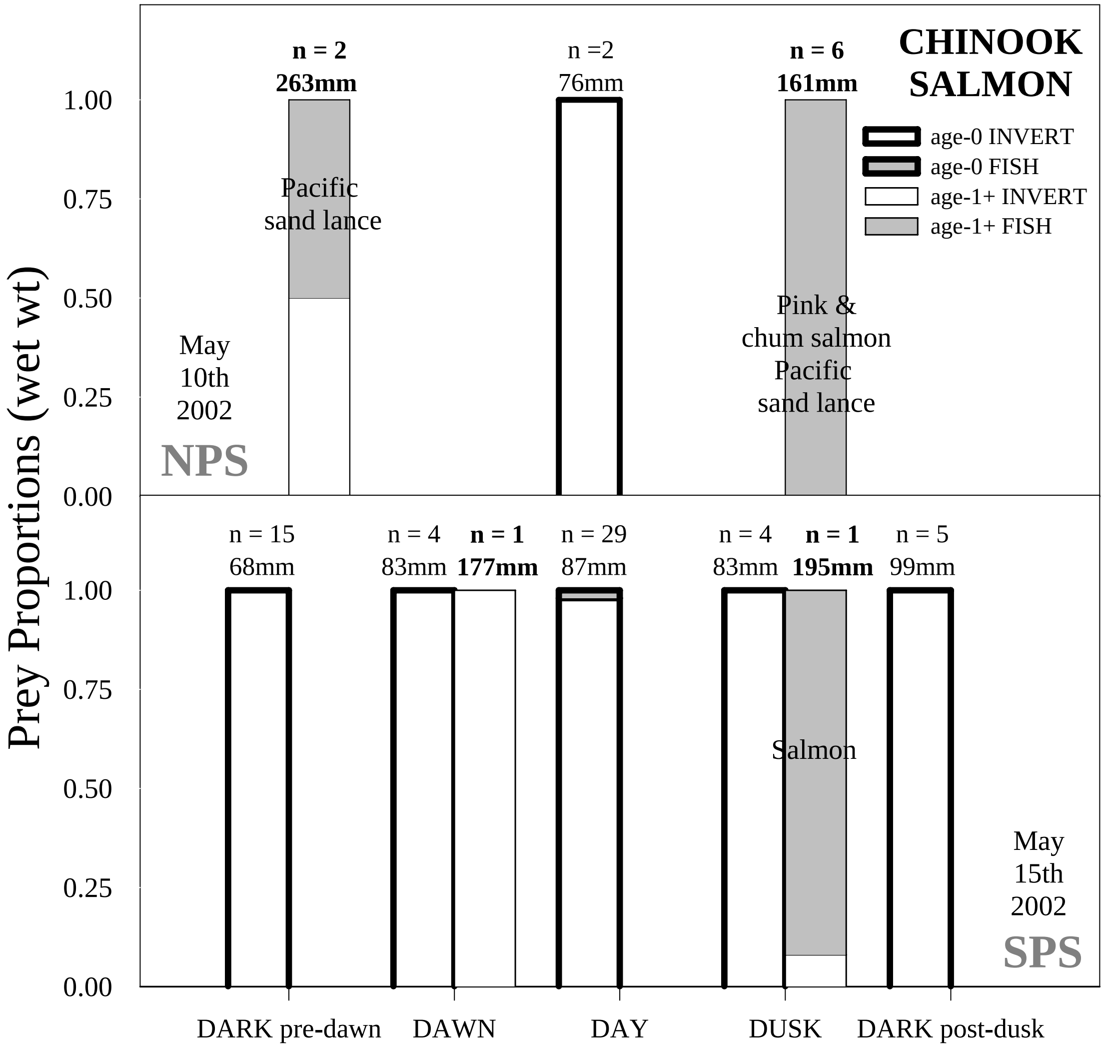

Figure 2.3. Wet weight proportions of invertebrate and fish prey items in juvenile age-0 (left bars) and older age-1+ (right bars) chinook salmon diets over diel sampling periods in May 2002 for NPS and SPS.

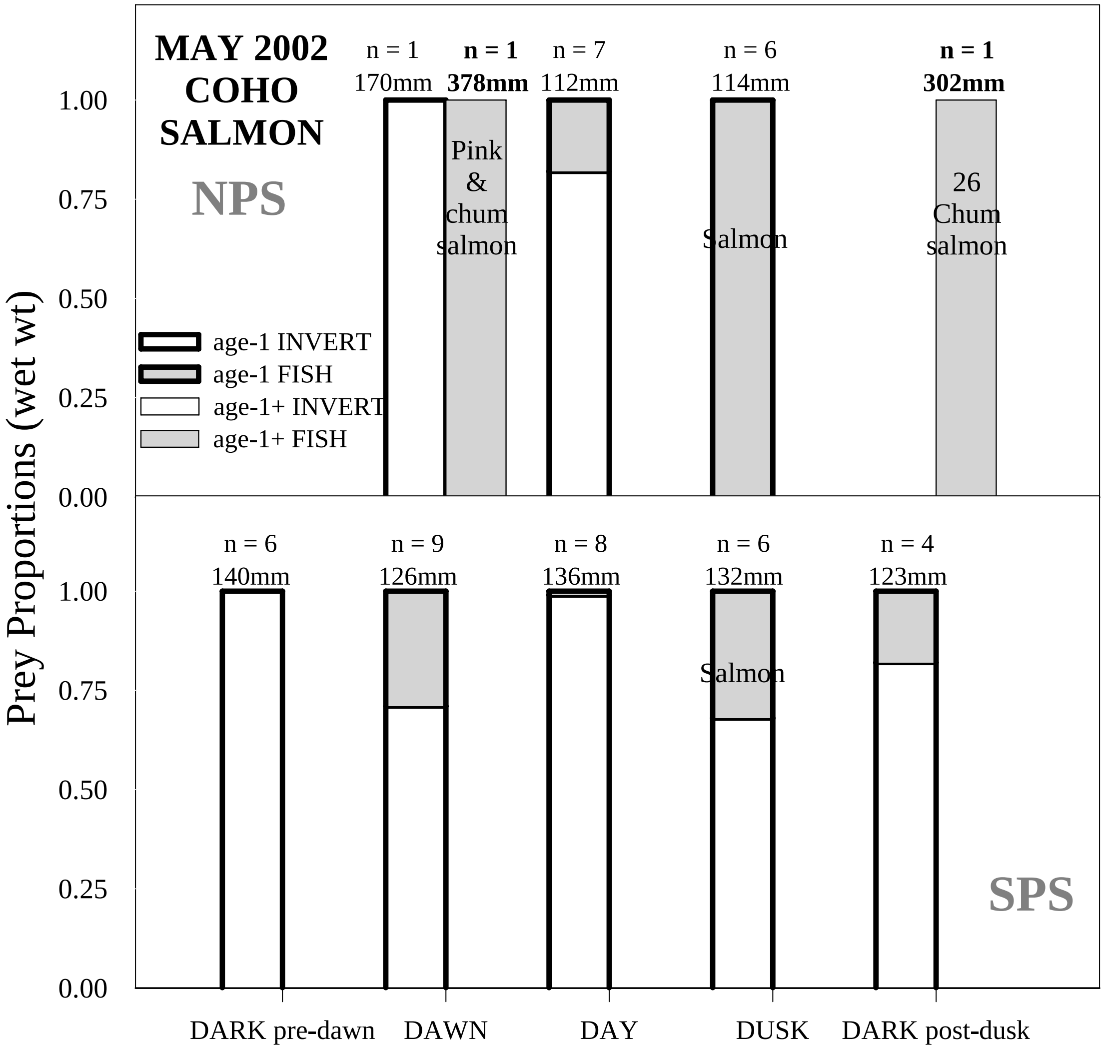

Figure 2.4. Wet weight proportions of invertebrate and fish prey items in juvenile age-1 (left bars) and age-1+ (right bars) coho salmon diets over diel sampling periods in May 2002 for NPS and SPS.

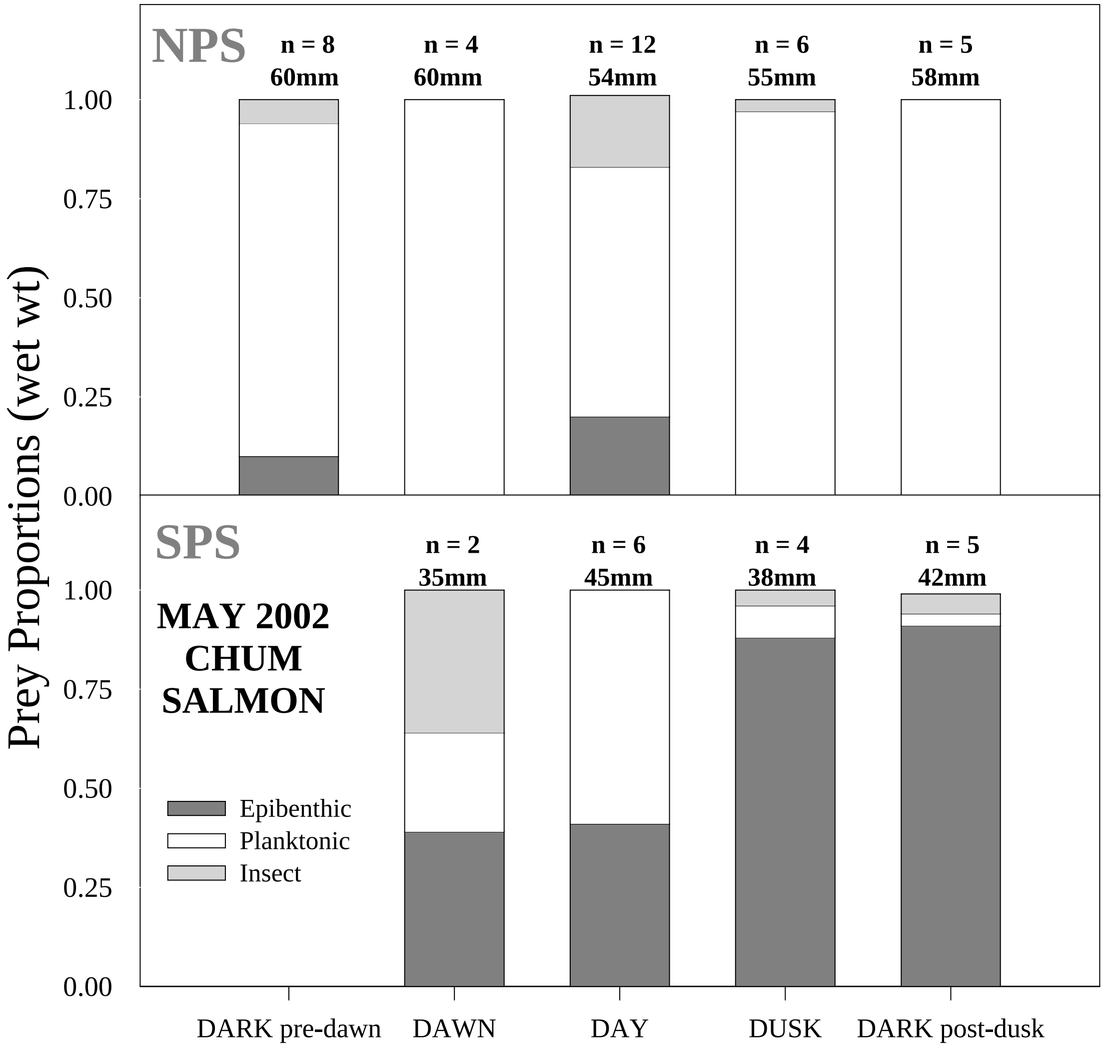

Figure 2.5. Wet weight proportions of invertebrate prey items in juvenile chum salmon diets over diel sampling periods in May 2002 for NPS and SPS.

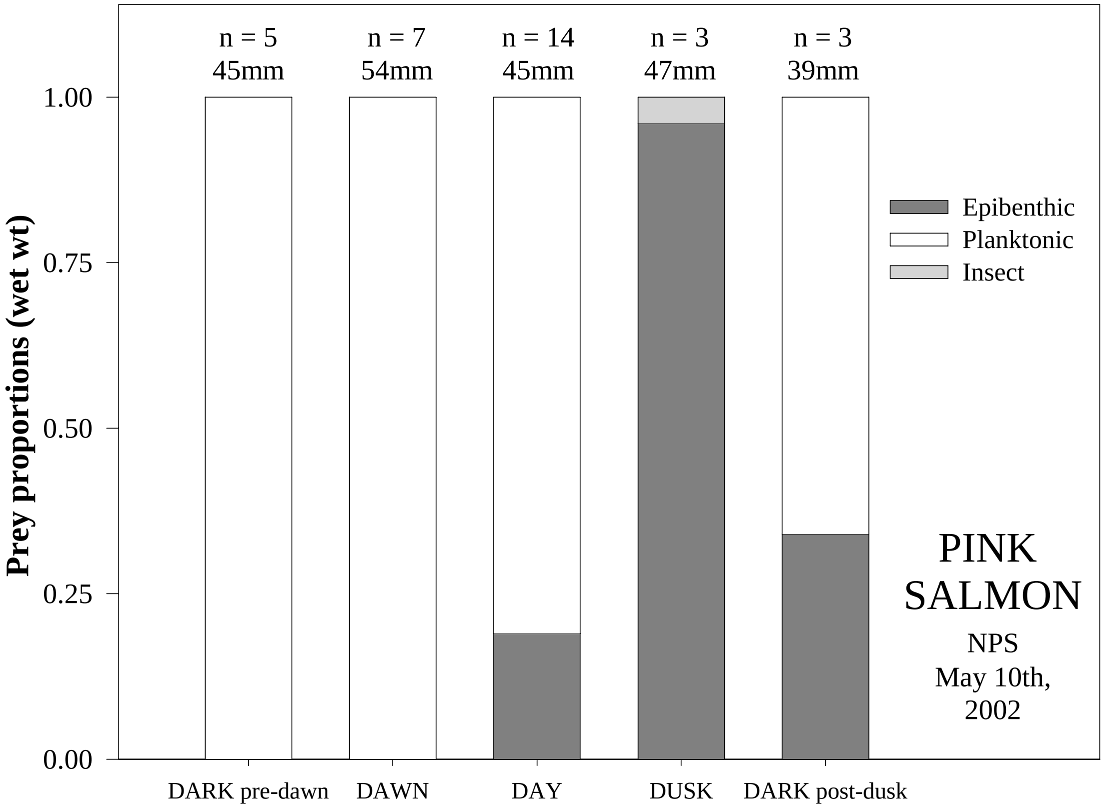

Figure 2.6. Wet weight proportions of invertebrate prey groups, organized into broad habitat based groups, in juvenile pink salmon diets over a diel sampling period in NPS on May 10, 2002.

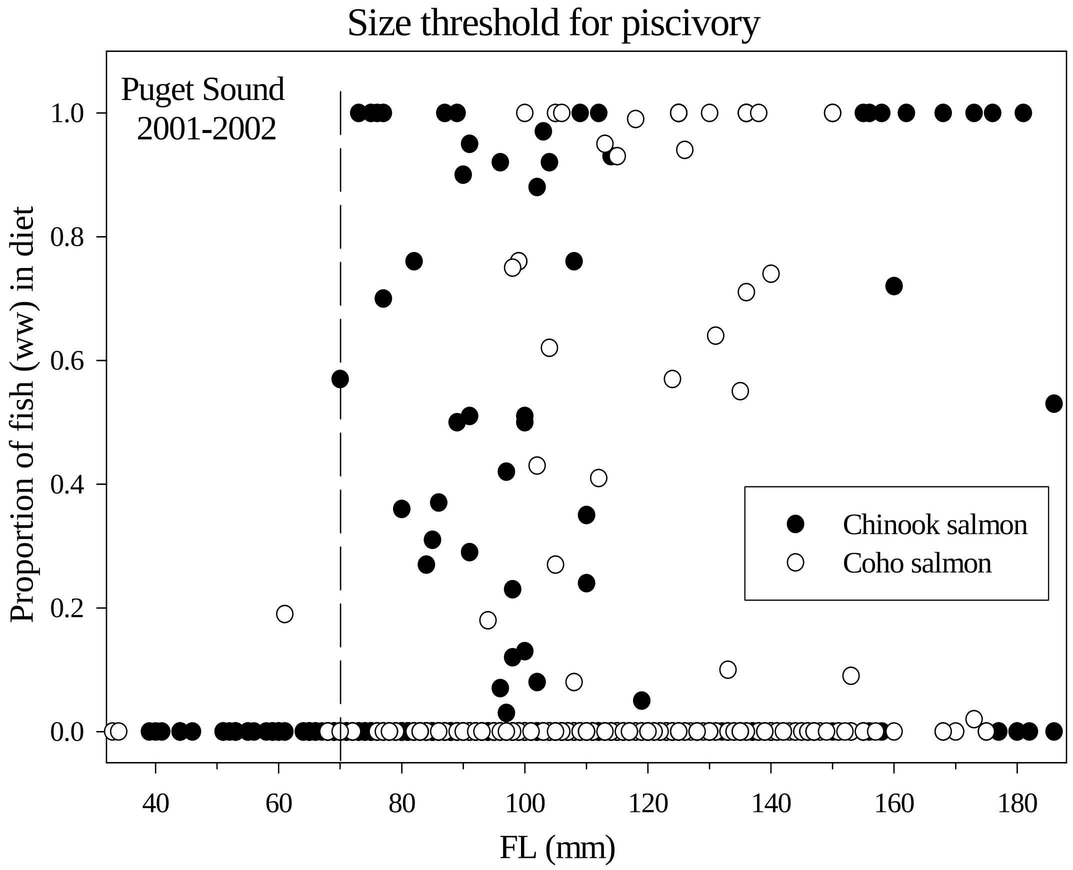

Figure 2.7. The fork length (FL) of juvenile chinook and coho salmon versus the wet weight proportions of fish prey consumed in stomachs sampled in Puget Sound during 2001-2002.

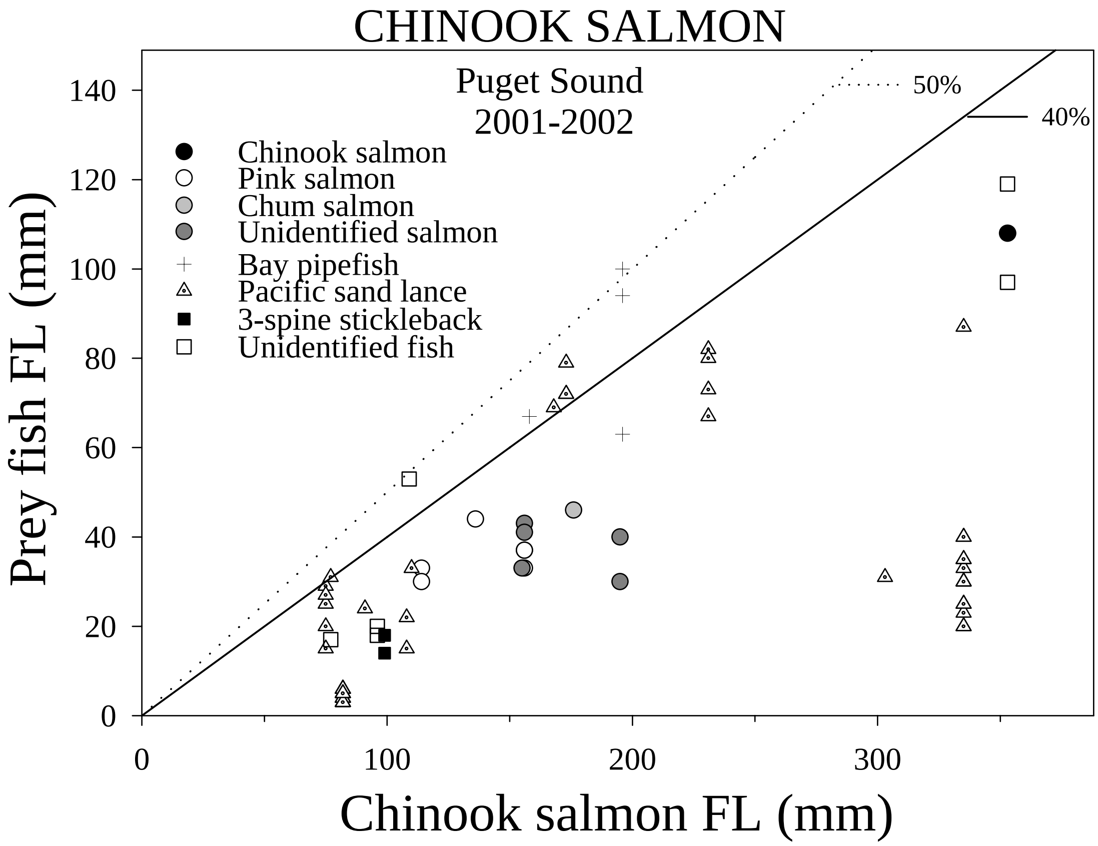

Figure 2.8. The fork length (FL) of chinook salmon versus the FL of different species of fish prey consumed in Puget Sound during 2001-2002. Lines indicate lengths that are 40% (black line) and 50% (dotted) of the piscivorous chinook salmon.

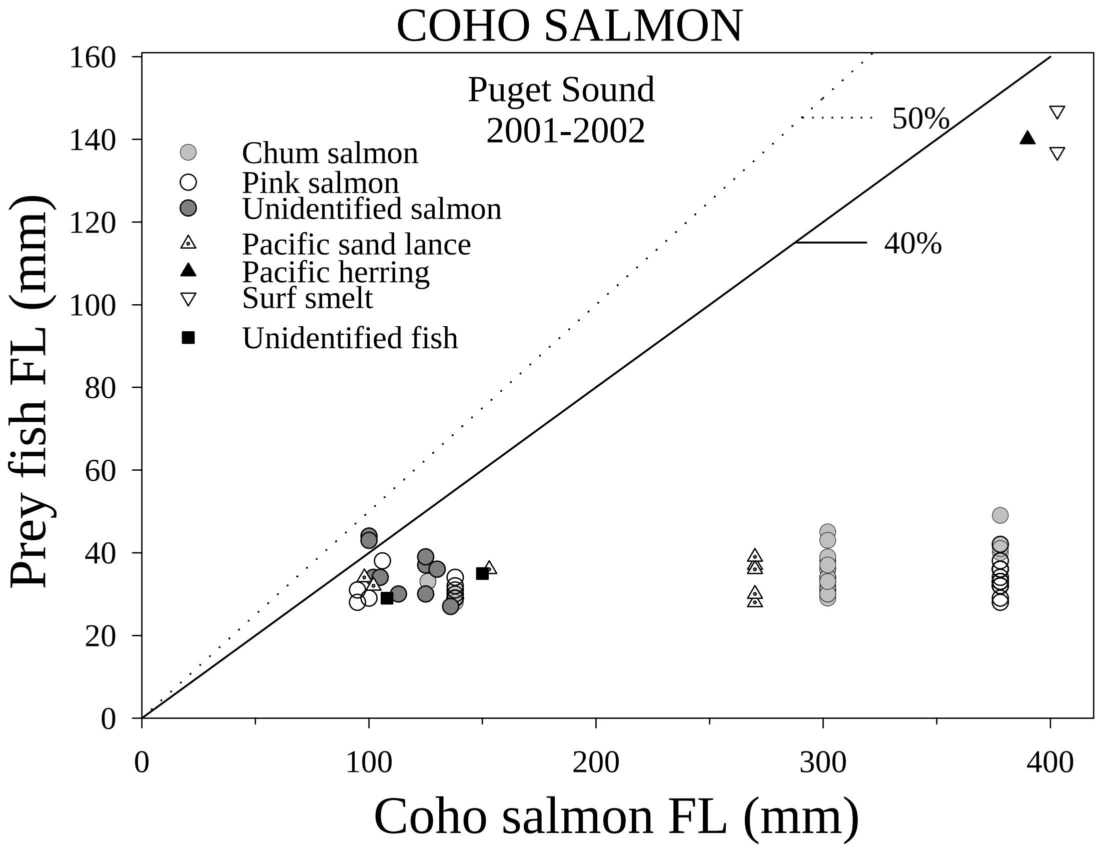

Figure 2.9. The fork length (FL) of coho salmon versus the FL of different species of fish prey consumed in Puget Sound during 2001-2002. Lines indicate lengths that are 40% (black line) and 50% (dotted) of the piscivorous coho salmon.

Table 2.1a. Wet weight proportions of major prey items for age-0 chinook salmon in Puget Sound 2001-2002. Prey proportions greater than or equal to 20% are in bold. Invertebrate prey items are organized alphabetically, followed by fish prey.

DATE	REGION	ZONE	n	Average FL (mm)	se	Barnacle larvae	Copepod	Crab larvae	Cumacean	Euphausiid	Gammarid amphipod	Hyperiid amphipod	Insect	Isopod	Other invertebrate	Polychate	Shrimp	Fish TOTAL	Salmon	Sand lance
19-Apr-01	NPS	delta	3	77.67	1.76	0%	0%	0%	0%	0%	**33%**	0%	**67%**	0%	0%	0%	0%	0%	0%	0%
03-May-01	NPS	delta	5	52.20	4.47	0%	0%	13%	0%	10%	**35%**	0%	**22%**	0%	**20%**	0%	0%	0%	0%	0%
22-May-01	NPS	delta	6	93.67	5.15	0%	0%	6%	0%	19%	4%	0%	**29%**	0%	6%	0%	**26%**	10%	0%	4%
26-Jun-01	NPS	delta	14	85.00	3.39	0%	0%	0%	0%	10%	**23%**	0%	**53%**	5%	4%	0%	5%	0%	0%	0%
10-Jul-01	NPS	delta	15	91.80	1.13	7%	0%	0%	0%	0%	13%	1%	13%	0%	**65%**	1%	0%	0%	0%	0%
24-Jul-01	NPS	delta	12	97.25	2.03	6%	0%	2%	0%	15%	**50%**	4%	18%	4%	1%	0%	0%	0%	0%	0%
07-Aug-01	NPS	delta	4	107.00	2.12	9%	0%	0%	0%	0%	**88%**	0%	3%	0%	0%	0%	0%	0%	0%	0%
18-Sep-01	NPS	delta	3	126.33	2.03	0%	0%	0%	0%	0%	14%	0%	**44%**	0%	0%	0%	**42%**	0%	0%	0%
19-Apr-01	NPS	nearshore	8	63.00	2.52	0%	1%	1%	0%	8%	0%	0%	**85%**	5%	0%	0%	0%	0%	0%	0%
03-May-01	NPS	nearshore	18	76.33	4.20	6%	0%	9%	1%	1%	**28%**	0%	**46%**	0%	0%	6%	1%	2%	0%	0%
22-May-01	NPS	nearshore	15	86.47	3.41	5%	0%	**32%**	1%	0%	12%	0%	**30%**	0%	13%	2%	0%	5%	0%	0%
29-May-01	NPS	nearshore	5	79.40	4.11	**33%**	0%	**27%**	0%	12%	10%	0%	13%	0%	5%	0%	0%	0%	0%	0%
26-Jun-01	NPS	nearshore	5	85.60	5.92	0%	0%	**21%**	0%	0%	0%	0%	**72%**	0%	7%	0%	0%	0%	0%	0%
10-Jul-01	NPS	nearshore	21	94.62	1.63	**27%**	0%	18%	0%	1%	0%	0%	**31%**	0%	8%	4%	0%	11%	0%	11%
24-Jul-01	NPS	nearshore	41	102.10	1.24	4%	0%	9%	0%	1%	5%	1%	**63%**	0%	11%	2%	0%	4%	0%	1%
07-Aug-01	NPS	nearshore	18	105.11	2.13	19%	0%	7%	0%	0%	7%	0%	**54%**	2%	5%	3%	3%	0%	0%	0%
08-May-01	SPS	delta	3	75.00	1.53	0%	0%	19%	17%	0%	14%	0%	0%	0%	0%	**50%**	0%	0%	0%	0%
17-May-01	SPS	delta	5	84.80	2.63	1%	1%	**33%**	0%	6%	**21%**	0%	9%	0%	8%	1%	0%	**20%**	0%	**20%**
31-May-01	SPS	delta	12	76.00	2.02	0%	1%	**29%**	6%	0%	11%	0%	**40%**	0%	5%	0%	0%	8%	0%	8%
14-Jun-01	SPS	delta	1	85.00		0%	0%	0%	0%	0%	15%	0%	**85%**	0%	0%	0%	0%	0%	0%	0%
28-Jun-01	SPS	delta	4	93.50	12.01	0%	0%	1%	0%	**52%**	7%	0%	15%	0%	0%	**25%**	0%	0%	0%	0%
12-Jul-01	SPS	delta	2	104.50	0.50	10%	0%	3%	0%	2%	0%	0%	**43%**	0%	0%	**42%**	0%	0%	0%	0%

Table 2.1a. (continued)

DATE	REGION	ZONE	n	Average FL (mm)	se	Barnacle larvae	Copepod	Crab larvae	Cumacean	Euphausiid	Gammarid amphipod	Hyperiid amphipod	Insect	Isopod	Other invertebrate	Polychate	Shrimp	Fish TOTAL	Salmon	Sand lance
20-Sep-01	SPS	delta	1	132.50	4.50	0%	0%	5%	0%	0%	**48%**	**43%**	4%	0%	0%	0%	0%	0%	0%	0%
08-May-01	SPS	nearshore	12	85.08	0.84	0%	0%	9%	3%	**22%**	**36%**	3%	2%	0%	13%	7%	5%	0%	0%	0%
17-May-01	SPS	nearshore	29	87.59	1.11	0%	8%	19%	0%	**20%**	4%	0%	4%	0%	**22%**	**22%**	1%	0%	0%	0%
31-May-01	SPS	nearshore	22	91.32	3.44	11%	8%	**28%**	0%	3%	0%	0%	9%	3%	2%	**32%**	0%	4%	0%	0%
14-Jun-01	SPS	nearshore	12	84.25	2.05	0%	1%	**40%**	2%	16%	7%	0%	6%	3%	18%	7%	0%	0%	0%	0%
28-Jun-01	SPS	nearshore	15	94.60	3.96	1%	11%	**26%**	1%	11%	8%	0%	11%	0%	12%	12%	5%	2%	0%	0%
12-Jul-01	SPS	nearshore	2	105.50	13.50	0%	0%	**50%**	0%	0%	**50%**	0%	0%	0%	0%	0%	0%	0%	0%	0%
26-Jul-01	SPS	nearshore	40	106.70	1.52	2%	3%	8%	0%	**44%**	4%	19%	5%	0%	8%	4%	3%	0%	0%	0%
09-Aug-01	SPS	nearshore	4	113.25	5.19	1%	0%	2%	0%	0%	19%	**49%**	4%	**25%**	0%	0%	0%	0%	0%	0%
20-Sep-01	SPS	nearshore	2	121.00	3.00	0%	0%	19%	0%	**39%**	0%	19%	**23%**	0%	0%	0%	0%	0%	0%	0%
20-Sep-01	SPS	nearshore	1	136.00		0%	0%	0%	0%	0%	**81%**	0%	19%	0%	0%	0%	0%	0%	0%	0%
23-Apr-02	NPS	delta	1	44.00		0%	4%	0%	0%	0%	0%	0%	0%	0%	0%	**96%**	0%	0%	0%	0%
10-May-02	NPS	delta	2	63.00	11.00	0%	**20%**	0%	11%	**45%**	19%	0%	0%	0%	0%	5%	0%	0%	0%	0%
21-May-02	NPS	delta	10	82.70	1.68	14%	0%	0%	4%	3%	**27%**	7%	**31%**	3%	8%	2%	1%	0%	0%	0%
05-Jun-02	NPS	delta	8	68.38	4.13	0%	0%	0%	0%	2%	12%	0%	**59%**	0%	5%	**22%**	0%	0%	0%	0%
02-Jul-02	NPS	delta	24	81.79	1.49	1%	0%	2%	0%	5%	**30%**	0%	**43%**	1%	13%	0%	5%	0%	0%	0%
17-Jul-02	NPS	delta	14	79.57	1.84	3%	0%	2%	1%	0%	2%	0%	**84%**	0%	0%	1%	0%	7%	0%	0%
30-Jul-02	NPS	delta	4	93.25	4.07	**25%**	0%	0%	0%	0%	2%	0%	**27%**	0%	0%	0%	0%	**46%**	0%	0%
20-Aug-02	NPS	delta	2	97.00	8.00	0%	0%	0%	0%	0%	0%	0%	0%	0%	**50%**	0%	0%	**50%**	0%	0%
10-Sep-02	NPS	delta	2	110.00	0.00	**25%**	0%	0%	0%	4%	0%	0%	**30%**	0%	**23%**	0%	0%	18%	18%	0%
10-May-02	NPS	nearshore	2	76.00	3.00	0%	0%	10%	0%	0%	0%	0%	5%	0%	**50%**	**35%**	0%	0%	0%	0%
21-May-02	NPS	nearshore	13	84.38	2.46	14%	0%	**26%**	0%	0%	7%	0%	**37%**	0%	8%	0%	0%	8%	0%	0%
05-Jun-02	NPS	nearshore	5	82.20	1.83	**36%**	10%	7%	0%	0%	3%	0%	17%	0%	**20%**	0%	7%	0%	0%	0%
02-Jul-02	NPS	nearshore	2	91.50	3.50	3%	0%	0%	0%	0%	0%	15%	**32%**	0%	**50%**	0%	0%	0%	0%	0%

Table 2.1a. (continued)

DATE	REGION	ZONE	n	Average FL (mm)	se	Barnacle larvae	Copepod	Crab larvae	Cumacean	Euphausiid	Gammarid amphipod	Hyperiid amphipod	Insect	Isopod	Other invertebrate	Polychate	Shrimp	Fish TOTAL	Salmon	Sand lance
17-Jul-02	NPS	nearshore	4	95.50	2.60	**27%**	0%	0%	0%	0%	0%	0%	**73%**	0%	0%	0%	0%	0%	0%	0%
30-Jul-02	NPS	nearshore	16	99.25	2.52	**21%**	0%	7%	0%	4%	11%	0%	**30%**	0%	**21%**	0%	0%	6%	0%	6%
20-Aug-02	NPS	nearshore	14	103.79	2.70	6%	0%	13%	0%	1%	**28%**	0%	**42%**	0%	6%	0%	0%	4%	0%	0%
10-Sep-02	NPS	nearshore	1	110.00		0%	0%	0%	0%	0%	2%	0%	**98%**	0%	0%	0%	0%	0%	0%	0%
25-Sep-02	NPS	NERITIC	1	124.00		0%	0%	0%	0%	0%	0%	0%	**100%**	0%	0%	0%	0%	0%	0%	0%
18-Apr-02	SPS	delta	1	69.00		0%	0%	0%	0%	0%	**100%**	0%	0%	0%	0%	0%	0%	0%	0%	0%
22-May-02	SPS	delta	2	96.50	1.50	0%	0%	**50%**	0%	0%	0%	0%	0%	0%	**50%**	0%	0%	0%	0%	0%
04-Jun-02	SPS	delta	10	90.90	2.00	0%	8%	**25%**	0%	1%	4%	0%	**20%**	0%	4%	**29%**	0%	9%	0%	0%
19-Jun-02	SPS	delta	5	85.20	2.78	2%	2%	16%	0%	3%	0%	0%	2%	7%	**20%**	**28%**	0%	**20%**	0%	0%
03-Jul-02	SPS	delta	1	120.00		0%	0%	0%	0%	0%	0%	0%	0%	0%	**100%**	0%	0%	0%	0%	0%
16-Jul-02	SPS	delta	5	85.00	2.32	0%	0%	0%	0%	0%	0%	0%	**43%**	6%	**31%**	**20%**	0%	0%	0%	0%
21-Aug-02	SPS	delta	3	104.00	4.16	0%	0%	0%	0%	0%	7%	**40%**	**27%**	**20%**	4%	0%	0%	2%	0%	0%
25-Apr-02	SPS	nearshore	4	77.00	3.94	0%	11%	0%	0%	13%	**36%**	0%	8%	0%	0%	0%	0%	**32%**	0%	0%
06-May-02	SPS	nearshore	5	95.60	7.36	2%	0%	12%	0%	0%	10%	0%	0%	0%	2%	**36%**	1%	**37%**	19%	0%
15-May-02	SPS	nearshore	29	87.07	2.00	2%	11%	**27%**	5%	**36%**	11%	0%	1%	0%	2%	3%	0%	2%	0%	0%
22-May-02	SPS	nearshore	11	93.09	2.36	8%	0%	**62%**	0%	18%	9%	0%	0%	0%	3%	0%	0%	0%	0%	0%
04-Jun-02	SPS	nearshore	9	92.67	3.09	0%	3%	**47%**	1%	1%	7%	1%	10%	0%	11%	16%	0%	3%	0%	0%
19-Jun-02	SPS	nearshore	17	90.71	2.89	8%	2%	15%	0%	8%	**21%**	0%	5%	1%	**22%**	13%	0%	5%	0%	0%
03-Jul-02	SPS	nearshore	2	107.50	10.50	**22%**	0%	**41%**	0%	0%	2%	0%	10%	2%	**23%**	0%	0%	0%	0%	0%
31-Jul-02	SPS	nearshore	4	102.00	3.72	17%	0%	16%	0%	2%	7%	12%	17%	2%	0%	**20%**	0%	7%	0%	0%
21-Aug-02	SPS	nearshore	9	115.22	2.39	0%	0%	16%	0%	**35%**	**31%**	0%	5%	2%	9%	2%	0%	0%	0%	0%
11-Sep-02	SPS	nearshore	3	120.67	4.67	0%	0%	1%	0%	2%	18%	4%	**51%**	0%	0%	0%	**24%**	0%	0%	0%
12-Jun-02	SPS	NERITIC	28	99.11	2.01	0%	9%	**48%**	0%	17%	0%	0%	**24%**	0%	2%	0%	0%	0%	0%	0%
11-Jul-02	SPS	NERITIC	13	102.69	2.32	6%	1%	**32%**	0%	2%	1%	8%	**23%**	0%	12%	8%	7%	0%	0%	0%
13-Aug-02	SPS	NERITIC	5	105.80	2.31	0%	0%	**38%**	0%	0%	1%	0%	**42%**	0%	19%	0%	0%	0%	0%	0%

Table 2.1b. Wet weight proportions of major prey items for age-1+ chinook salmon in Puget Sound 2001-2002.

DATE	REGION	ZONE	n	Average FL (mm)	se	Barnacle larvae	Copepod	Crab larvae	Cumacean	Euphausiid	Gammarid amphipod	Hyperiid amphipod	Insect	Isopod	Other invertebrate	Polychate	Shrimp	Fish TOTAL	Salmon	Sand lance
19-Apr-01	NPS	delta	1	332.00		0%	0%	0%	0%	0%	**100%**	0%	0%	0%	0%	0%	0%	0%	0%	0%
19-Apr-01	NPS	nearshore	3	328.33	3.33	0%	0%	8%	0%	0%	7%	0%	**34%**	0%	0%	0%	0%	**51%**	0%	**51%**
26-Jun-01	NPS	nearshore	1	353.00		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	**100%**	**66%**	0%
24-Jul-01	NPS	nearshore	1	150.00		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	**100%**	0%	0%
07-Aug-01	NPS	nearshore	2	156.00	12.00	**31%**	0%	0%	0%	0%	0%	0%	0%	0%	0%	19%	0%	**50%**	0%	**50%**
07-Aug-01	NPS	nearshore	1	231.00		0%	0%	0%	0%	0%	0%	0%	0%	0%	2%	0%	0%	**98%**	0%	**98%**
18-Sep-01	NPS	nearshore	5	168.20	7.59	0%	0%	0%	0%	0%	0%	**25%**	11%	4%	0%	0%	0%	**60%**	0%	**20%**
08-May-01	SPS	nearshore	5	146.00	9.26	0%	0%	11%	12%	9%	**44%**	0%	18%	0%	3%	2%	1%	0%	0%	0%
17-May-01	SPS	nearshore	1	186.00		0%	0%	0%	0%	0%	0%	0%	**47%**	0%	0%	0%	0%	**53%**	0%	0%
31-May-01	SPS	nearshore	2	163.00	23.00	0%	0%	**88%**	0%	0%	0%	0%	0%	0%	0%	12%	0%	0%	0%	0%
14-Jun-01	SPS	nearshore	2	193.50	0.50	**41%**	**50%**	6%	0%	0%	0%	0%	0%	3%	0%	0%	0%	0%	0%	0%
14-Jun-01	SPS	nearshore	2	203.00	1.00	**50%**	0%	14%	0%	0%	12%	0%	0%	0%	0%	0%	**24%**	0%	0%	0%
28-Jun-01	SPS	nearshore	3	161.67	12.81	0%	0%	**77%**	0%	0%	**23%**	0%	0%	0%	0%	0%	0%	0%	0%	0%
26-Jul-01	SPS	nearshore	3	135.33	2.19	0%	0%	**34%**	0%	**33%**	0%	0%	0%	0%	0%	**33%**	0%	0%	0%	0%
09-Aug-01	SPS	nearshore	1	177.00		0%	0%	3%	0%	0%	0%	**97%**	0%	0%	0%	0%	0%	0%	0%	0%
21-May-02	NPS	delta	1	189.00		0%	0%	0%	0%	0%	**96%**	0%	0%	0%	4%	0%	0%	0%	0%	0%
21-May-02	NPS	delta	2	216.00	6.00	0%	0%	0%	0%	0%	**88%**	0%	0%	12%	0%	0%	0%	0%	0%	0%
05-Jun-02	NPS	delta	1	137.00		0%	0%	0%	0%	**30%**	**70%**	0%	0%	0%	0%	0%	0%	0%	0%	0%
10-Sep-02	NPS	nearshore	2	165.00	10.00	1%	0%	0%	0%	10%	2%	5%	**69%**	0%	13%	0%	0%	0%	0%	0%
04-Jun-02	SPS	nearshore	3	143.00	3.51	0%	0%	**100%**	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
19-Jun-02	SPS	nearshore	1	153.00		0%	0%	0%	0%	**100%**	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
11-Sep-02	SPS	nearshore	3	157.00	11.50	0%	0%	0%	0%	**22%**	**23%**	0%	**22%**	4%	0%	0%	**29%**	0%	0%	0%

Table 2.2. Wet weight proportions of major prey items for juvenile coho salmon in Puget Sound during 2001 and 2002. Prey proportions greater than or equal to 20% are in bold.

DATE	REGION	ZONE	n	Average FL (mm)	se	Barnacle larvae	Copepod	Crab larvae	Euphausiid	Gammarid amphipod	Hyperiid amphipod	Insect	Isopod	Mysid/ shrimp	Ostracod	Other invertebrate	Polychaete	Fish TOTAL
5/29/01	NPS	delta	20	110.5	3.8	0%	0%	0%	0%	**67%**	0%	5%	14%	0%	0%	14%	0%	0%
5/22/01	NPS	nearshore	2	129.0		0%	0%	0%	**23%**	0%	0%	**77%**	0%	0%	0%	0%	0%	0%
5/29/01	NPS	nearshore	16	105.3	3.8	19%	0%	**31%**	0%	1%	2%	17%	3%	0%	4%	**23%**	0%	0%
6/26/01	NPS	nearshore	2	147.0	1.0	0%	0%	**95%**	3%	1%	0%	0%	0%	0%	1%	0%	0%	0%
8/7/01	NPS	nearshore	3	103.7	2.4	0%	0%	**22%**	0%	**33%**	0%	**36%**	0%	0%	0%	0%	0%	9%
6/14/01	SPS	delta	1	140.0		0%	0%	14%	0%	0%	0%	0%	0%	0%	0%	0%	**86%**	0%
5/8/01	SPS	nearshore	1	123.0		3%	0%	0%	0%	**26%**	5%	0%	0%	0%	0%	0%	**66%**	0%
5/17/01	SPS	nearshore	12	79.4	1.9	0%	1%	0%	8%	0%	0%	0%	0%	**83%**	0%	8%	0%	0%
5/31/01	SPS	nearshore	5	142.2	5.2	0%	0%	**100%**	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
6/14/01	SPS	nearshore	2	106.5	16.5	4%	0%	**54%**	0%	6%	0%	4%	1%	**23%**	8%	0%	0%	0%
6/28/01	SPS	nearshore	4	130.0	15.9	0%	0%	**45%**	0%	**20%**	0%	8%	0%	17%	2%	0%	8%	0%
7/26/01	SPS	nearshore	5	112.6	7.2	0%	0%	1%	**41%**	2%	18%	1%	0%	0%	2%	1%	0%	**34%**
8/9/01	SPS	nearshore	1	168.0		0%	0%	**26%**	0%	0%	0%	0%	0%	0%	0%	0%	**74%**	0%
4/9/02	NPS	delta	1	135.0		0%	0%	0%	3%	**38%**	0%	2%	2%	0%	0%	0%	0%	**55%**
5/10/02	NPS	delta	7	111.9	4.6	0%	0%	0%	0%	**53%**	0%	0%	0%	3%	0%	15%	11%	18%
5/21/02	NPS	delta	14	130.4	4.9	2%	0%	0%	0%	**52%**	0%	3%	0%	0%	0%	9%	**33%**	1%
6/5/02	NPS	delta	8	112.0	9.6	0%	0%	0%	0%	**86%**	0%	5%	1%	0%	0%	0%	8%	0%
7/30/02	NPS	delta	1	61.0		0%	0%	0%	0%	0%	**58%**	**23%**	0%	0%	0%	0%	0%	19%
4/23/02	NPS	nearshore	3	68.3	34.8	0%	0%	0%	0%	**44%**	0%	**23%**	0%	0%	0%	0%	0%	**33%**
5/21/02	NPS	nearshore	3	97.3	5.9	0%	0%	0%	0%	0%	0%	**33%**	0%	0%	0%	0%	0%	**67%**
6/5/02	NPS	nearshore	4	115.0	7.9	0%	3%	1%	0%	**20%**	0%	8%	0%	0%	0%	**25%**	0%	**43%**
6/11/02	NPS	nearshore	3	100.3	5.9	**20%**	0%	3%	0%	0%	0%	**43%**	0%	0%	0%	**20%**	0%	14%

Table 2.2. (continued)

DATE	REGION	ZONE	n	Average FL (mm)	se	Barnacle larvae	Cospepd	Crab larvae	Euphausiid	Gammarid amphipod	Hyperiid amphipod	Insect	Isopod	Mysid/ shrimp	Ostracod	Other invertebrate	Polychaete	Fish TOTAL
7/30/02	NPS	nearshore	2	154.5	5.5	7%	0%	**82%**	0%	11%	0%	0%	0%	0%	0%	0%	0%	0%
7/10/02	NPS	NERITIC	1	113.0		0%	0%	0%	**50%**	0%	**23%**	**23%**	0%	0%	0%	4%	0%	0%
4/25/02	SPS	delta	6	136.2	3.1	0%	0%	9%	0%	**40%**	0%	**33%**	10%	0%	0%	8%	0%	0%
5/22/02	SPS	delta	6	122.0	4.8	15%	9%	**36%**	0%	3%	0%	1%	0%	0%	0%	0%	9%	**27%**
6/4/02	SPS	delta	4	112.5	5.1	0%	1%	**47%**	0%	**23%**	0%	16%	0%	12%	1%	0%	0%	0%
7/16/02	SPS	delta	2	110.0	32.0	0%	0%	0%	0%	0%	0%	0%	0%	0%	7%	**43%**	**50%**	0%
7/31/02	SPS	delta	1	196.0		**67%**	0%	0%	0%	12%	0%	0%	**21%**	0%	0%	0%	0%	0%
4/18/02	SPS	nearshore	9	118.6	1.3	0%	**23%**	10%	0%	**58%**	0%	3%	0%	0%	0%	0%	6%	0%
4/25/02	SPS	nearshore	2	107.5	1.5	0%	0%	3%	**50%**	**47%**	0%	0%	0%	0%	0%	0%	0%	0%
5/6/02	SPS	nearshore	2	158.5	34.5	0%	0%	0%	**46%**	4%	0%	0%	0%	**50%**	0%	0%	0%	0%
5/15/02	SPS	nearshore	8	136.0	6.1	0%	5%	4%	**25%**	3%	0%	11%	0%	**51%**	0%	0%	0%	1%
5/22/02	SPS	nearshore	9	124.3	3.7	8%	2%	13%	**32%**	4%	0%	0%	0%	**33%**	0%	0%	0%	8%
6/4/02	SPS	nearshore	6	132.3	5.8	0%	1%	**76%**	1%	4%	0%	0%	0%	0%	0%	1%	17%	0%
6/19/02	SPS	nearshore	2	151.5	21.5	0%	0%	19%	**30%**	0%	0%	0%	0%	**50%**	0%	0%	0%	1%
7/16/02	SPS	nearshore	2	126.0	29.0	0%	0%	0%	0%	**76%**	0%	**24%**	0%	0%	0%	0%	0%	0%
8/21/02	SPS	nearshore	1	157.0		0%	0%	0%	0%	**92%**	0%	0%	0%	0%	8%	0%	0%	0%
9/11/02	SPS	nearshore	1	193.0		0%	0%	0%	0%	**99%**	1%	0%	0%	0%	0%	0%	0%	0%
6/12/02	SPS	NERITIC	5	118.6	2.5	0%	0%	**82%**	2%	8%	0%	0%	0%	8%	0%	0%	0%	0%
7/11/02	SPS	NERITIC	1	128.0		0%	0%	**81%**	0%	0%	0%	0%	0%	0%	19%	0%	0%	0%
4/19/01	NPS	nearshore	3	311.3	23.1	0%	0%	**24%**	0%	8%	0%	0%	0%	0%	0%	10%	0%	**58%**
5/3/01	NPS	nearshore	2	267.0	1.0	1%	0%	**53%**	0%	0%	0%	0%	0%	0%	0%	0%	0%	**46%**
5/6/02	SPS	delta	1	390.0		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	**100%**
5/22/02	SPS	nearshore	1	235.0		0%	0%	0%	**100%**	0%	0%	0%	0%	0%	0%	0%	0%	0%

Table 2.3. Wet weight proportions of major prey items for chum salmon in Puget Sound during 2001-2002. Prey proportions greater than or equal to 20% are in bold.

DATE	REGION	ZONE	n	Average FL (mm)	se	Barnacle larvae	Calanoid copepod	Crab larvae	Euphausiid	Gammarid amphipod	Harpacticoid copepod	Insect	Larvacean	Mysid/ Shrimp	Ostracod	Other invertebrate	Other prey
4/19/01	NPS	delta	5	42.00	1.10	0%	0%	0%	0%	2%	0%	0%	0%	0%	0%	**98%**	
5/3/01	NPS	nearshore	1	77.00		0%	0%	0%	**35%**	**62%**	0%	3%	0%	0%	0%	0%	
5/22/01	NPS	nearshore	8	58.75	5.03	0%	0%	0%	0%	6%	0%	**69%**	0%	0%	0%	**25%**	caprellid amphipod
5/29/01	NPS	nearshore	6	82.00	4.16	0%	0%	**67%**	0%	0%	0%	0%	17%	0%	0%	16%	
6/12/01	NPS	nearshore	3	77.33	4.18	0%	8%	0%	**80%**	9%	0%	0%	0%	0%	0%	3%	hyperiid
7/10/01	NPS	nearshore	3	78.33	4.81	0%	0%	**30%**	0%	0%	0%	**59%**	10%	0%	0%	1%	
5/8/01	SPS	delta	5	64.40	0.75	0%	0%	**20%**	**20%**	13%	**27%**	0%	0%	0%	0%	**20%**	polychaete
5/17/01	SPS	delta	7	60.86	4.42	3%	**23%**	3%	0%	0%	**21%**	0%	**48%**	0%	0%	2%	cladoceran
5/31/01	SPS	delta	5	60.00	2.37	0%	0%	0%	0%	0%	0%	2%	**80%**	0%	0%	18%	
6/14/01	SPS	delta	5	66.20	2.91	0%	**30%**	0%	0%	0%	**36%**	13%	12%	0%	0%	9%	
6/28/01	SPS	delta	1	92.00		0%	15%	**80%**	0%	0%	5%	0%	0%	0%	0%	0%	
9/20/01	SPS	delta	1	125.00		0%	0%	15%	0%	0%	0%	12%	**25%**	0%	**48%**	0%	
5/8/01	SPS	nearshore	12	56.83	7.40	0%	9%	0%	**41%**	0%	**50%**	0%	0%	0%	0%	0%	
5/17/01	SPS	nearshore	10	73.50	5.45	0%	17%	0%	**68%**	0%	3%	0%	12%	0%	0%	0%	
5/31/01	SPS	nearshore	9	72.80	3.63	0%	**83%**	17%	0%	0%	0%	0%	0%	0%	0%	0%	
6/14/01	SPS	nearshore	10	68.90	3.68	0%	**23%**	0%	0%	0%	**36%**	0%	**41%**	0%	0%	0%	
6/28/01	SPS	nearshore	2	67.00	2.00	0%	**25%**	0%	0%	17%	0%	2%	0%	**56%**	0%	0%	
7/12/01	SPS	nearshore	1	60.00		0%	5%	0%	0%	**95%**	0%	0%	0%	0%	0%	0%	
7/26/01	SPS	nearshore	9	107.44	6.54	0%	**13%**	10%	**42%**	0%	18%	0%	2%	15%	0%	0%	
4/9/02	NPS	delta	4	38.00	1.47	0%	**25%**	0%	0%	0%	**50%**	**25%**	0%	0%	0%	0%	
4/23/02	NPS	delta	5	39.00	0.32	10%	0%	0%	0%	0%	19%	**70%**	1%	0%	0%	0%	
5/10/02	NPS	delta	9	46.67	3.93	0%	0%	0%	0%	**28%**	**41%**	**25%**	2%	0%	0%	4%	cumacean, isopod
6/5/02	NPS	delta	1	37.00		0%	0%	14%	0%	0%	0%	**86%**	0%	0%	0%	0%	

Table 2.3. (continued)

DATE	REGION	ZONE	n	Average FL (mm)	se	Barnacle larvae	Calanoid copepod	Crab larvae	Euphausiid	Gammarid amphipod	Harpacticoid copepod	Insect	Larvacean	Mysid/ Shrimp	Ostracod	Other invertebrate	Other prey
7/2/02	NPS	delta	1	71.00		0%	0%	0%	0%	**100%**	0%	0%	0%	0%	0%	0%	
4/9/02	NPS	nearshore	3	39.00	0.00	0%	0%	0%	0%	0%	**21%**	**57%**	0%	0%	0%	**21%**	
4/23/02	NPS	nearshore	10	38.10	1.26	0%	**34%**	**33%**	0%	0%	**20%**	2%	1%	0%	0%	10%	
5/10/02	NPS	nearshore	12	53.83	2.85	0%	0%	17%	0%	1%	18%	18%	**20%**	0%	0%	**26%**	cladoceran
5/21/02	NPS	nearshore	1	60.00		0%	0%	0%	0%	0%	0%	**100%**	0%	0%	0%	0%	
6/5/02	NPS	nearshore	1	64.00		0%	0%	0%	0%	0%	0%	**100%**	0%	0%	0%	0%	
7/30/02	NPS	nearshore	1	134.00		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	**100%**	
7/10/02	NPS	NERITIC	1	142.00		0%	0%	0%	0%	0%	**33%**	0%	**67%**	0%	0%	0%	
4/25/02	SPS	delta	8	41.75	2.51	0%	5%	0%	0%	7%	**74%**	9%	5%	0%	0%	0%	
5/6/02	SPS	delta	7	57.57	5.52	0%	**17%**	0%	0%	10%	**32%**	5%	**23%**	14%	0%	0%	
5/15/02	SPS	delta	6	45.17	3.24	0%	**25%**	0%	0%	0%	**39%**	0%	**32%**	0%	0%	4%	
5/22/02	SPS	delta	6	62.83	3.91	2%	11%	0%	0%	2%	13%	0%	**60%**	0%	0%	12%	
6/4/02	SPS	delta	6	61.67	4.38	0%	**46%**	0%	0%	0%	**25%**	0%	**28%**	0%	0%	1%	
6/19/02	SPS	delta	5	60.40	2.11	0%	**61%**	2%	0%	0%	0%	3%	**32%**	1%	0%	2%	
4/18/02	SPS	nearshore	4	38.50	2.40	0%	3%	0%	0%	0%	**45%**	**20%**	2%	0%	0%	**29%**	
4/25/02	SPS	nearshore	10	57.90	4.54	0%	15%	0%	18%	0%	**34%**	1%	**32%**	0%	0%	0%	
5/6/02	SPS	nearshore	6	50.33	1.96	0%	**69%**	0%	10%	0%	4%	0%	16%	1%	0%	0%	
5/15/02	SPS	nearshore	17	61.41	5.58	0%	9%	0%	**23%**	1%	**26%**	0%	**24%**	10%	0%	7%	
5/22/02	SPS	nearshore	6	46.83	2.40	0%	**47%**	0%	**26%**	3%	10%	14%	0%	0%	0%	0%	
6/4/02	SPS	nearshore	10	58.20	2.29	1%	**45%**	0%	0%	0%	**25%**	1%	8%	6%	2%	12%	cladoceran, cumacean
6/19/02	SPS	nearshore	9	67.11	3.10	0%	**46%**	0%	16%	1%	**27%**	0%	0%	10%	0%	0%	
7/3/02	SPS	nearshore	10	74.10	3.05	0%	8%	10%	0%	0%	5%	**20%**	**32%**	4%	0%	**21%**	
6/12/02	SPS	NERITIC	26	64.88	1.07	0%	6%	0%	7%	0%	4%	0%	**82%**	0%	0%	1%	
7/11/02	SPS	NERITIC	2	96.50	1.50	1%	2%	0%	0%	0%	1%	0%	**96%**	0%	0%	0%	
8/13/02	SPS	NERITIC	2	108.50	20.50	0%	2%	**56%**	0%	0%	0%	0%	0%	**43%**	0%	0%	

Table 2.4. 2002 Wet weight proportions of major prey items for pink salmon in Puget Sound. Prey proportions greater than or equal to 20% are in bold.

DATE	REGION	ZONE	n	Average FL (mm)	se	Barnacle larvae	Calanoid copepod	Cumacean	Euphausiid	Gammarid amphipod	Harpacticoid copepod	Insect	Larvacean	Mysid	Ostracod	Other inverterate
4/9/02	NPS	delta	10	34.3	0.6	10%	15%	0%	0%	2%	**44%**	**24%**	0%	0%	0%	5%
4/23/02	NPS	delta	7	33.6	0.5	19%	0%	0%	0%	0%	**39%**	**38%**	0%	0%	0%	4%
5/10/02	NPS	delta	8	35.1	0.7	5%	16%	0%	0%	0%	**65%**	8%	6%	0%	0%	0%
5/21/02	NPS	delta	1	36.0		0%	**20%**	0%	0%	0%	0%	**20%**	0%	0%	**60%**	0%
4/9/02	NPS	nearshore	3	37.0	1.5	0%	**34%**	0%	0%	0%	0%	0%	0%	**33%**	0%	**33%**
4/23/02	NPS	nearshore	9	35.4	0.6	0%	**27%**	0%	0%	0%	**50%**	3%	**20%**	0%	0%	0%
5/10/02	NPS	nearshore	14	44.9	2.9	3%	**57%**	0%	0%	0%	19%	0%	0%	0%	0%	**21%**
5/21/02	NPS	nearshore	1	108.0		0%	**53%**	0%	0%	**27%**	0%	0%	0%	0%	**20%**	0%
6/5/02	NPS	nearshore	3	75.3	6.8	0%	0%	0%	0%	0%	0%	**97%**	0%	0%	0%	3%
6/11/02	NPS	NERITIC	2	82.5	4.5	0%	0%	0%	0%	0%	0%	0%	**100%**	0%	0%	0%
5/22/02	SPS	delta	6	67.5	7.0	0%	6%	0%	1%	0%	**89%**	0%	0%	0%	0%	4%
6/4/02	SPS	delta	6	77.3	6.0	0%	**24%**	12%	6%	0%	19%	4%	**33%**	0%	0%	2%
6/19/02	SPS	delta	9	70.2	2.6	0%	**35%**	0%	0%	0%	**31%**	1%	**21%**	0%	0%	12%
7/16/02	SPS	delta	2	80.5	1.5	0%	0%	0%	11%	0%	**88%**	2%	0%	0%	0%	0%
4/25/02	SPS	nearshore	10	48.7	4.0	0%	**27%**	3%	3%	0%	**48%**	0%	0%	10%	0%	9%
5/6/02	SPS	nearshore	4	50.5	1.2	0%	1%	0%	19%	0%	**76%**	4%	0%	0%	0%	0%
5/15/02	SPS	nearshore	9	75.7	2.4	0%	5%	0%	**86%**	0%	9%	0%	0%	0%	0%	0%
5/22/02	SPS	nearshore	9	85.1	3.1	0%	**24%**	0%	**27%**	0%	13%	0%	**37%**	0%	0%	0%
6/4/02	SPS	nearshore	13	78.6	3.8	0%	**52%**	12%	0%	0%	11%	0%	**24%**	0%	0%	1%
6/19/02	SPS	nearshore	9	80.0	6.8	0%	**32%**	0%	8%	0%	**29%**	0%	**22%**	10%	0%	0%
7/3/02	SPS	nearshore	3	96.0	10.0	4%	0%	0%	0%	**32%**	2%	0%	**30%**	0%	0%	**33%**
6/12/02	SPS	NERITIC	18	73.1	3.2	0%	2%	0%	4%	0%	0%	6%	**87%**	0%	0%	1%

Chapter III: Simulated prey consumption and growth performance of juvenile salmon in Puget Sound

ABSTRACT

I used the Wisconsin bioenergetics model to compare spatially and seasonally relevant quantitative estimates of consumption demand and growth performance between juvenile chinook, coho, chum and pink salmon, and between hatchery and wild (unmarked) chinook salmon emigrating through nearshore environments in Puget Sound during the spring and summer of 2001-2002. Foraging conditions for juvenile salmon were dynamic, varying spatially, annually, and seasonally. Weekly consumption demand for each salmon species was higher at southern Puget Sound (SPS) sites than at northern Puget Sound (NPS) sites. In NPS simulations, individual pink salmon consumed 0.3-0.4 g of prey, chum salmon consumed 0.6-0.9 g of prey, chinook salmon consumed 3.2-5.0 g of prey, and coho salmon consumed 6.0-6.5 g of prey per week to satisfy estimated growth rates in April-June. In simulations at SPS sites, pink salmon consumed 1.7-1.8 g of prey, chum salmon consumed 0.8-2.3 g of prey, chinook salmon consumed 4.0-6.6 g of prey per week, and coho salmon consumed 3.4-8.4 g of prey per week to satisfy estimated growth rates in April-June. During July-August simulations, individual chinook salmon consumed 6.4-8.5 g of prey per week at NPS sites and 8.4-12.3 g of prey per week at SPS sites to satisfy estimated growth rates. During periods of peak abundance for juvenile salmon cohorts, growth performance was higher at sites in NPS but less constant than at sites in SPS, and was higher in 2002 than 2001, driven primarily by the higher proportions of energy rich insects consumed in NPS both years and in SPS during 2002. In NPS, growth efficiency was highest in April for pink and chum salmon, and during mid to late May for coho salmon. Modeled chinook salmon cohorts experienced variable feeding conditions with peaks in growth efficiencies both in May and July. Simulated growth efficiencies were lower for chinook salmon than for other salmon, particularly in May when catches of the other salmon species were highest. While there were no differences in SPS, unmarked chinook salmon in NPS experienced higher growth rates and efficiency than hatchery chinook salmon. Diet quality for

chinook and pink salmon appeared to be more favorable in neritic environments as nearshore foraging conditions declined. In a preliminary examination of intrageneric predation by coho and chinook salmon on pink and chum salmon (33-43mm FL), I estimated that an individual juvenile coho salmon (100-130mm FL) consumed 1-2 pink or chum salmon per day, while a chinook salmon (80-90mm FL) consumed one pink or chum salmon every 2.5-5 days. Increasing spring water temperatures, which approached the upper thermal tolerances for salmon in NPS, potentially reduced growth efficiencies for salmon nearshore, particularly during highest temperatures in July. Spatial and temporal differences in environmental conditions and the forage base may significantly influence the potential for growth and ultimately the survival of juvenile salmon entering different areas of Puget Sound.

INTRODUCTION

Estuarine and coastal marine environments provide important foraging and rearing habitat for juvenile anadromous Pacific salmon (*Oncorhynchus* spp.; Simenstad et al. 1982; Thorpe 1994; Aitken 1998). While juvenile salmon in coastal and estuarine waters experience some of the most rapid growth rates of all life history stages (LeBrasseur and Parker 1964; Healey 1979; Healey 1982; Mortensen et al. 2000), they are also subject to the highest mortality rate during the period between seaward migration and adult return (Parker 1962; Royal 1962; Furnell and Brett 1986). There is evidence that growth during this period determines overall marine survival trends (Holtby et al. 1990; Hargreaves 1997; Murphy et al. 1998; Tovey 1999). In Puget Sound, chinook salmon (*O. tshawytscha*) and Hood Canal summer-run chum salmon (*O. keta*) are listed as threatened under the Endangered Species Act (ESA), while coho salmon (*O. kisutch*) are candidates for listing. While relatively little is currently known about the basic ecology of juvenile salmon in Puget Sound, recent results suggest that nearshore and neritic environments may be used extensively by chinook and chum salmon in specific regions of Puget Sound (Chapter 1; Beamish et al. 1998). Foraging conditions (including prey resources and water temperature) and food web dynamics may be contributing to declines in Puget Sound salmon stocks.

Juvenile salmon enter the nearshore marine environment at a size vulnerable to many potential predators (including fish, birds, and marine mammals), which are hypothesized to be responsible for much of the mortality in this phase (Parker 1971; Beamish and Mahnken 1998). Size at this stage is critical because it partially determines vulnerability to predation. According to size-spectrum theory, larger, fast-growing individuals are vulnerable to gape-limited predators for shorter periods than smaller, slower-growing conspecifics (Sogard 1997). Favorable foraging conditions enable fish to "outgrow" potential predators. In Puget Sound, hatchery production constitutes 70-75% of the salmon (mainly chinook and coho) population in Puget Sound (Hatchery Scientific Review Group 2002). There is concern that high densities of juvenile salmon created by coincident releases of hatchery chinook salmon and coho salmon during peak migrations of natural populations may deplete localized food supply and increase predation on smaller pink (*O. gorbuscha*), chum, and chinook salmon (Buckley 1999).

When food resources are limited, high densities and dietary overlaps among juvenile salmon species, and between hatchery and wild salmon, may also result in intra- and inter-specific competition that would negatively affect growth rates and overall smolt size (Fisher and Pearcy 1996; Sturdevant 1999). In addition, seasonal shifts in prey resources and water temperature may affect the potential growth rates of juvenile salmon. Timing of arrival in estuaries have been positively correlated to survival (Blackbourn 1976; Parker 1971; Healey 1982; Ward et al. 1989; Henderson and Cass 1991), whereas high densities of juvenile salmon in estuaries have been linked to reduced growth (Reimers 1973) and survival (Blackbourn 1976). Poor quality feeding areas, which may vary over various time scales, may result in increased susceptibility to predation due to poorer condition and smaller sizes of fish (Brodeur et al. 1992; Perry et al. 1996). The quality of feeding areas can also affect migration rates and residence times, since salmon are believed to leave poor foraging habitats faster (Healey 1982; Simenstad et al. 1982; Orsi et al. 2001).

It is essential to take a food web perspective to understand the complicated array of potential processes and interactions affecting aquatic communities (Paine 1980 and 1988). Determining the strength of interactions and identifying which processes regulate populations give us insight into the underlying mechanisms and conditions that mediate them (Paine 1980; Brandt et al. 1993). Bioenergetically-based food web models, used in conjunction with directed field sampling, provide an effective method for quantifying trophic interactions in a temporal, spatial, and ontogenetic framework (Ney 1990; Hansen et al. 1993). The widely used Wisconsin bioenergetics model (Hanson et al. 1997) uses an energy-balance approach calculated on a daily time step, which allows for a fine-grained analysis of trophic interactions over various time scales. This sensitivity is particularly appropriate for dynamic conditions, like those experienced by emigrating juvenile salmon, where residence times are relatively short, but variable, and environmental factors (i.e., water temperature), diets, and sizes are rapidly changing.

The Wisconsin bioenergetics model has been used successfully to identify carrying capacity of systems, seasonal bottlenecks in food supply, and impacts of predation primarily in freshwater systems (Kitchell et al. 1977; Stewart et al. 1981; Stewart and Ibarra 1991; Beauchamp et al. 1995; Rand et al. 1995; Cartwright 1998; Baldwin et al. 2000). The model has also been used to estimate temporal consumption demand and growth in estuarine and marine waters (Brandt et al. 1992; Brodeur et al. 1992; Ciannelli et al. 1998; Davis et al. 1998; Holsman et al. in press). In coastal marine waters, the bioenergetics model has yielded consumption estimates within 5-10% of independently generated field estimates for juvenile chinook and coho salmon (Brodeur et al. 1992). Other applications of the model include estimating mortality due to predation, and evaluating growth performance under differing conditions like water temperature, prey quality and availability, and consumer density.

In this paper, I examine the feeding conditions and growth performance of juvenile salmon (chinook, coho, chum, and pink) during their emigration through Puget Sound by using bioenergetics modeling to synthesize information on their early marine trophic dynamics during April-September, 2001-2002. I use growth efficiency, which incorporates both daily growth and consumption rates, as a measure of growth performance. Focusing on ESA-listed chinook salmon, I compare spatially and seasonally relevant quantitative estimates of consumption demand and growth efficiency between hatchery and wild (unmarked) chinook salmon and between different salmon species. I also investigate how seasonal, annual, and regional shifts in diet, temperature, and structure and sizes of the salmon community affect prey consumption and salmon growth performance and potential. A better understanding of their foraging conditions may provide insight into factors influencing the residence, growth and survival of salmon stocks in Puget Sound.

METHODS

STUDY AREA

Puget Sound is a deep, elongated glacial fjord in western Washington. For this study I focused on two regions: a northern Puget Sound (NPS) region encompassing Possession Sound/Port Susan/Port Gardner, and a southern Puget Sound (SPS) region encompassing Cormorant Passage/Wollochet Bay/south of the Narrows (Figure 3.1). These two regions are the first areas of Puget Sound used by both wild juvenile salmon and those from several major hatchery-based stock enhancement programs. Within each sampling region, I chose five to six comparable shallow sublittoral sites both near freshwater inputs, “delta” sites, and “nearshore” sites along exposed beaches, at increasing distances from “delta” sites, and three offshore “neritic” transects. This design targeted likely salmon emigration routes. Sites were located in regions with significant wild salmon production (Snohomish and Nisqually Rivers), but in close proximity to release sites for hatchery salmon (Tulalip Bay and Snohomish River, Chambers Creek and Nisqually River) along suspected emigration corridors.

FISH SAMPLING

Field sampling was designed to characterize migration timing, size structure, and diet in both NPS and SPS. I conducted biweekly beach seining (two sets per site) at each site in both regions from April through September 2001 and 2002 using a floating beach seine (37.0m length x 2.0m height, with mesh grading from 3 cm in the wings to 6 mm at the cod end) according to standard estuarine fish sampling protocol (Simenstad et al. 1991). In 2002, I sampled fish from neritic (offshore surface waters; three tows per site) sites monthly during May-September in NPS and June-September in SPS) using a

Kvichak two-boat surface trawl ("tow net," 3.1m height x 6.1m width x 15.0m length with mesh grading from 76.0 mm in the mouth to 6.4 mm at the cod end).

Counts of all fish were recorded by species. Hatchery chinook and coho salmon were identified by adipose fin-clips or coded-wire-tag (cwt) detectors (in 2002 only). Unmarked chinook and coho salmon were assumed to be wild fish, however, the total (and regional) proportions of hatchery chinook and coho salmon that are mass-marked with adipose fin-clips (used by WDFW since 1996) are not accurately known, and marking success rates may differ by hatchery facility. Individual fork lengths (FL, to the nearest 1mm) and wet weights (Wt, to the nearest 0.1g) were recorded for sub-samples (at least 30 fish per species, when available).

Stomach contents were analyzed from a subset of juvenile salmon. Using a dissecting microscope, invertebrate prey were separated into broad taxonomic categories, and fish prey were identified to species where possible. Blotted wet weights of all prey categories and each prey fish were recorded to the nearest 0.0001g using an electronic scale. The proportional wet weight contribution of each prey category was calculated individually for all non-empty stomachs.

BIOENERGETICS MODELING

I modeled consumption of emigrating juvenile chinook, coho, chum and pink salmon using the Wisconsin bioenergetics model (Hanson et al. 1997). The Wisconsin bioenergetics model uses an energy-balance approach in which total energy consumption (C), over a particular time frame, equals the sum of growth (G, positive or negative), metabolic costs (M), and waste losses (W).

$$C = G + M + W$$

Typically the model, which operates on a daily time step, is used estimate consumption rates by individuals of a species at a given life history stage. The primary model inputs are thermal experience (temperature experienced by the predator), diet, prey and predator energy densities, and growth. I used the model's default physiological parameters specific to chinook, coho, and pink salmon, and used the pink/sockeye salmon parameters for chum salmon.

Thermal experience

I used water temperatures that had been recorded for nearshore sampling sites at a depth of 0.5 – 1.0m using the YSI Model 55 Handheld Dissolved Oxygen and Temperature System (Table 3.1). Water was consistently warmer and less saline in NPS than at SPS sites (Chapter 1). The model interpolated temperature values between sampling dates.

Diet composition

I used average proportional (wet weight) diet composition data, obtained from age-0 juvenile salmon (except age-1 for coho salmon) caught during daylight sampling in the spring and summer of 2001 and 2002, to model simulations of specific pulses (also termed cohorts) (Table 3.2a-d; Chapter 2) of salmon. Diet composition differed markedly between sampling regions and seasonally between April and September. The potential for dietary overlap was greatest between juvenile pink and chum salmon, between chinook and coho salmon of similar sizes, and between hatchery and wild chinook salmon, especially during large hatchery releases which tended to coincide with peak outmigration of wild salmon. A small proportion of juvenile chinook and coho salmon (100-160mm FL) consumed smaller juvenile salmon (primarily pink and chum salmon) during peak outmigration pulses in April and May (Chapter 2).

Energy density

I used literature energy density values for prey items that were most comparable to organisms found in Puget Sound and used averages of similar prey types when specific values were unavailable (Table 3.3). Predator energy density values for pink and chum salmon were manually entered into the model as 4171 J/g (Boldt and Haldorson 2002). For predator energy density of chinook and coho salmon, I used the model’s default equation which changes as a function of body weight.

I used bomb calorimetry to determine the energy density of 25-40mm larval Pacific sand lance (*Ammodytes hexapterus*), the most common prey fish consumed by juvenile salmon in Puget Sound (Chapter 2). A sample of 25 fish was collected during sampling activities at neritic sites in June 2002. The sample was frozen on dry ice in the field, and the thawed (blotted) wet weight was measured to the nearest 0.0001g using an electronic balance in the laboratory. The sample was re-measured after being dried at 70^o Celsius. The dried material was ground, homogenized, and pressed into 0.1-0.2g pellets. Individual pellets (2 per sample) were combusted in a Parr 1425 Semi-micro Bomb calorimeter to determine the gross energy content. Dry to wet weight ratio was assumed to be 0.24, an average of values reported for larval fish (Davis 1993). Energy value was determined using weighted averages and reported as joules/gram (J/g) wet weight (Table 3.3).

Growth

For model simulations, I constructed growth cohorts partly from seasonal increases in mean and modal lengths and residence time for pulses of fish while I could track them in the catch data. I used delta sites to derive starting sizes for juvenile salmon entering Puget Sound. In 2002, I also used sizes of chinook salmon measured in the Nisqually River (Hodgson and Brakensiek 2003) to estimate starting sizes for selected wild and hatchery cohorts entering SPS. Ending sizes were taken from nearshore sites. Puget Sound growth was assumed to be the difference between the fish size at these nearshore sites versus the delta sites over a set time interval (nearshore residence time). This measure, the “apparent growth,” assumes that fish caught in consecutive sampling weeks were the same fish and that they had been resident to that area over the elapsed time. This method may either underestimate actual growth if smaller fish are continually cycling through the region or overestimate growth if larger fish are newly entering, or smaller fish are experiencing higher size-selective mortality.

More specific information recovered from coded-wire-tags (cwt), including release date, location, and average size, was used to help determine residence time of individual hatchery chinook and coho salmon. The coded-wire-tags were read by the Washington Department of Fish and Wildlife (L. Anderson, WDFW, unpublished data). In 2002, chinook and coho salmon released from Snohomish River hatcheries resided in

NPS waters for 20 and 18 days, respectively, while those released from hatcheries on the Nisqually River spent 15 and 16 days in SPS waters before they were captured (Chapter 1). These estimates of residence time were used to run simulations comparing concurrent hatchery and wild cohorts of chinook salmon.

Fork lengths (FL) were converted to wet weights (Wt) using regressions derived from this study (Chapter 1):

Chinook salmon $Wt\ (g) = 0.000006 * FL(mm)^{3.1068}$ $r^2 = 0.9526$; n = 532; 51-203 mm FL
Coho salmon $Wt\ (g) = 0.000006 * FL(mm)^{3.0926}$ $r^2 = 0.9162$; n = 242; 77-196 mm FL
Chum salmon $Wt\ (g) = 0.000003 * FL(mm)^{3.2506}$ $r^2 = 0.9786$; n = 425; 31-145 mm FL
Pink salmon $Wt\ (g) = 0.000002 * FL(mm)^{3.3689}$ $r^2 = 0.9804$; n = 185; 31-97 mm FL

Simulations

I ran simulations of the most likely growth scenarios for juvenile salmon pulses (or cohorts) based on peak catches in both NPS and SPS, 2001-2002 (2002 only for pink salmon; Table 3.4). In 2001-2002, the majority of juvenile salmon were caught in pulses between April and June in nearshore waters (pink and chum salmon generally peaking earlier than chinook and coho salmon), with most peak catches in May. In NPS, a second peak for chinook salmon occurred during July. Peak catches and timing of juvenile salmon differed between the two sampling regions, and between 2001 and 2002. Overall, salmon in SPS were slightly larger than in NPS, and a higher proportion of the salmon caught in SPS were produced by hatcheries. Hatchery chinook and coho salmon were, on average, larger than concurrent unmarked fish (Chapter 1) in both regions.

In each year, simulation days 1-170 corresponded to the period from April 9th - September 25th. In most simulations, called “fit to end wt.,” I used the bioenergetics model to quantify prey consumption needed by a juvenile salmon to achieve the estimated growth over a specified time interval (the estimated residence time). I estimated consumption for the main cohorts of each species, and a hatchery and unmarked cohort for chinook salmon, using both nearshore and neritic diets. In 2002, peak pulses of pink salmon appeared in NPS earlier in the season and at smaller sizes than those in SPS, which were likely all hatchery fish (Chapter 1). Therefore, I modeled estimates of apparent growth for each of these cohorts within their identified region, but I also ran simulations using the sizes (apparent growth) and diets from the other region.

In additional modeling, I performed simulations of chinook salmon at a constant p value of 0.68, the average for realistic cohorts in 2001-2002, and used either a constant temperature regime to examine the effects of a particular diet composition, or used a constant diet regime to examine the effects of different temperature regimes. For coho salmon, I used p values determined for 2002 cohorts (“constant p”) to run simulations of hatchery coho salmon using the residence time determined for cwt fish. I also simulated the potential effect of predation by juvenile chinook and coho salmon on pink and chum salmon. I ran simulations for peak cohorts using diets of 90-105 mm fish with maximum measured proportions of salmon prey (Table 3.2a-b) and representative proportions of invertebrates and insects (Table 3.5). I ran simulations to 67% of their maximum consumption rate for chinook salmon and 55% for coho salmon, the average for realistic spring cohorts, at in situ NPS and SPS temperatures.

RESULTS

GROWTH PERFORMANCE

Chinook salmon

Chinook fed at 49-86% of their maximum consumption rate in all simulations (Table 3.4). The estimated growth rates of chinook were higher in 2002 than in 2001. Cohorts of chinook salmon emigrating through Puget Sound in July during both 2001 and 2002, experienced greater growth efficiencies and fed at a higher proportion of maximum consumption than fish during May simulations (Figure 3.2, Table 3.4). Growth efficiencies were consistently higher and total consumption lower for chinook salmon in NPS than in SPS, and growth efficiencies were generally higher in 2002 than in 2001, although this difference was more pronounced in SPS.

To satisfy estimated growth rates, individual chinook salmon consumed more total prey (by weight in grams) per week in July than in May simulations in both 2001 and 2002 (Table 3.4). In 2001, individual chinook salmon at NPS sites consumed 0.13-

0.93 g of amphipods, 0.01-0.26 g of euphausiids, 0.35-1.33 g of crab larvae, 0.73-4.70 g of insects, 0.06-0.80 g of fish, and 0.50-2.83 g of other invertebrate prey per week during May and July. At SPS sites in 2001, individual chinook salmon in SPS consumed 0.06-6.86 g of amphipods, 0.29-4.04 g of euphausiids, 0.38-1.67 g of crab larvae, 0.27-0.58 g of insects, 0.00-0.37 g of fish, and 1.51-2.90 g of other invertebrate prey per week during May-June and July-August in order to satisfy the estimated growth rates (Figure 3.3a).

In 2002, individual chinook salmon at NPS sites consumed 0.16-1.24 g of amphipods, 0.00-0.25 g of euphausiids, 0.06-0.71 g of crab larvae, 1.12-4.94 g of insects, 0.00-0.38 g of fish, and 1.00-3.14 g of other invertebrate prey per week during May-June and July. At SPS sites in 2002, individual chinook salmon in SPS consumed 0.07-1.71 g of amphipods, 0.00-0.96 g of euphausiids, 1.40-3.38 g of crab larvae, 0.02-2.55 g of insects, 0.00-0.62 g of fish, and 1.04-4.53 g of other invertebrate prey per week during May-June and July in order to satisfy the estimated growth rates (Figure 3.3b). Insects consumed by chinook salmon included mainly adult terrestrial and aquatic forms, mostly from the orders hymenoptera and diptera, but also from orders lepidoptera, homoptera, and hemiptera. Spiders were also consumed, and included with insects in the diet.

In model simulations of hatchery and unmarked chinook salmon, initial and final sizes of cohorts differed (unmarked chinook salmon were always smaller than hatchery conspecifics) and proportional consumption of key prey items were slightly different. In SPS, daily growth and consumption rates were nearly identical for hatchery and wild fish, while unmarked fish in NPS experienced higher growth rates and efficiency than hatchery conspecifics (Figure 3.4, Table 3.4) due to a diet with higher energy density (more insects and fish). In SPS, hatchery fish ate more energetically rich insects than unmarked fish, but unmarked fish consumed more fish, seemingly balancing the overall energy contributions of the two diets.

Growth efficiencies and daily growth rates were consistently higher but more variable with diets from NPS than SPS (Figure 3.5). This was likely due to the predominance of high-energy prey items, like adult insects, in NPS. In NPS, overall growth efficiencies were higher and increased over the season in 2002. In 2001, rates declined rapidly from an April peak to a minimum in June, then slowly increased throughout the summer. In SPS, growth efficiencies peaked episodically throughout the spring and summer. Consumption and growth rates for chinook salmon were similar between nearshore and neritic diets in SPS. In NPS, the neritic diet, based on a September sampling event, consisted solely of insects, which produced peak growth rates and efficiencies when extended back over the sampling season. At nearshore sites in NPS, chinook salmon also fed almost solely on insects during September.

In the colder waters of SPS, growth efficiencies were consistently higher than in NPS, and gradually decreased over the sampling period until values leveled off in August (Figure 3.6). In NPS, growth efficiencies dropped more drastically as the waters approached the upper limits of thermal tolerances for salmon in July and began to improve as waters cooled in the late summer and early autumn.

Coho Salmon

Apparent growth rates of coho salmon (1.3-2.0% body wt/day) were higher in 2002 than 2001, although low relative abundances and duration at sampling sites made estimates of growth more difficult for this species. Coho salmon fed at approximately 50% of maximum consumption in all simulations and growth efficiencies were highest in May (Figure 3.7, Table 3.4). Whereas growth efficiencies were very similar between regions in 2001, growth efficiencies were higher in NPS than SPS in 2002. In NPS, hatchery coho salmon grew at a higher rate, 0.76mm/day, than those in SPS (0.60mm/day).

In 2001, individual coho salmon in NPS consumed 0.13-1.97 g of amphipods, 0.00-0.08 g of euphausiids, 1.20-3.63 g of crab larvae, 0.56-0.76 g of insects, and 1.63-2.56 g of other invertebrate prey per week during May-June in order to satisfy the growth rates estimated during this period. Individual coho salmon in SPS consumed 0.00-0.33 g of amphipods, 0.08-0.18 g of euphausiids, 0.28-2.41 g of crab larvae, and 0.93-2.76 g of other invertebrate prey per week during May in order to satisfy the estimated growth rates. In 2002, coho salmon in NPS consumed 0.52-3.10 g of amphipods, 0.24-1.70 g of insects, 0.73-3.52 g of fish, and 0.48-2.26 g of other invertebrate prey to satisfy estimated growth rates in May. Individual coho salmon in SPS consumed 3.64-4.28 g of amphipods, 0.23-3.14 g of euphausiids, 0.33-0.78 g crab larvae, 0.05-1.17 g of insects, and 0.75-1.97 g of other invertebrate prey per week during April to early May in order to satisfy the estimated growth rates (Figure 3.8). Insects consumed by coho salmon included adult terrestrial and aquatic forms, mostly from the orders hymenoptera and diptera.

Chum Salmon

Model simulations for chum salmon were run 2-3 weeks earlier in the season and apparent growth rate estimates were higher both in NPS than SPS, and in 2002 than 2001. Chum salmon fed at 36-53% of their maximum consumption rate in all simulations (Table 3.4 Figure 3.9). In both 2001 and 2002, their overall growth efficiency (40%) at sites in NPS was higher than in SPS as well as all other simulations in this study. This appeared to be driven by extremely high growth efficiencies in April, likely a result of the high proportion of adult insects in the diet. Growth efficiency in SPS was greater in 2002 than 2001, which may be due, in part, to the larger size and slower growth rate estimated for the chum salmon modeled in 2001.

To satisfy estimated growth rates, individual chum salmon in NPS consumed mainly amphipods, insects and other invertebrates in April-May of 2001 and copepods, crab larvae, insects, and other invertebrates in May of 2002 (Figure 3.10). Weekly consumption rates were similar between years. In May, the insect prey included adult terrestrial and aquatic forms, mostly from the orders hymenoptera and diptera, and in April, chum salmon also ate chironomid pupae. At SPS sites, chum salmon consumed twice the weight of prey in May-June 2001 than in 2002 and more than in NPS. Dominant prey items, by weight, were copepods, larvaceans, and other invertebrates.

Pink Salmon

Growth efficiencies for the “realistic” cohorts were lower but more constant in SPS than in NPS (Table 3.4, Figure 3.11). The pink salmon caught at SPS sites were likely of hatchery origin, based on the timing, fish size, and proximity of the capture location to the Carr Inlet release point (Chapter 1, Table 1.1). The lower growth rate (percent body weight per day) estimated for pink salmon in SPS versus NPS, as well as the relatively lower energetic quality of their diet, contributed to the discrepancy in growth efficiencies between the two areas. When these simulations were run with neritic diets consisting predominately of larvaceans, growth efficiencies were similar and more constant in both NPS and SPS (Figure 3.11).

Pink salmon fed at 30-37% of maximum consumption, the lowest of all simulations run in this study. Individual pink salmon in NPS consumed 0.21-0.27 g of copepods, 0.01-0.05 g of insects, 0.03-0.04 g of larvaceans, and 0.03-0.04 g of other invertebrate prey per week during April-May in order to satisfy the growth rates estimated during this period. At SPS sites, pink salmon consumed 1.02-1.08 g of copepods, 0.40-0.50 g of larvaceans, 0.03 g of insects, and 0.18-0.24g of other invertebrates to satisfy estimated growth rates (Figure 3.12). The insect prey included adult, largely terrestrial forms, mostly from the orders hymenoptera and diptera.

INTRAGENERIC PREDATION

I simulated the potential effect of predation by juvenile age-0 chinook salmon and age-1 coho salmon on age-0 pink and chum salmon that were 30-43mm FL, the average size range measured during peak catches (Table 3.5). Assuming that the pink and chum salmon were most vulnerable to predation at these sizes (0.3-0.6g), I estimated that juvenile coho salmon (100-130mm FL) consumed 1-2 pink/chum salmon per day, and juvenile chinook salmon (80-90mm FL) consumed 1 pink/chum salmon every 2.5-5 days, based on observed diet information. More data are needed to get a realistic idea of the extent of juvenile salmon predation by chinook and coho salmon.

DISCUSSION

Foraging conditions for juvenile salmon are dynamic in Puget Sound, varying spatially, annually, and seasonally. Overall growth performance for all juvenile salmon species was lower at sites in SPS than in NPS, and better in 2002 versus 2001. Weekly individual consumption demand for each salmon species in the spring (April-June) was higher at SPS than at NPS sites, and for individual chinook salmon, weekly consumption demand was higher in July than in May in both 2001 and 2002. This was primarily due to diet differences, driven by the higher proportions of energy rich insects in NPS diets overall and in SPS diets in 2002. Increasing water temperatures, which approached the upper limits of thermal tolerances for salmon in NPS, led to decreasing growth efficiencies for salmon, particularly in July when water was warmest. The variability in water temperatures and greater proportion of neustonic drift insects (terrestrial and aquatic adults mainly, and aquatic pupae) in NPS was likely a result of substantially greater freshwater flow into that region (Chapters 1 and 2). Temperatures and energetic content of diets were less variable at sites in SPS, which generated more consistent growth efficiencies. Growth efficiencies for all species but chinook salmon tended to decline over time, suggesting that growth conditions nearshore may be most favorable for relatively short intervals (1-2 weeks).

Chinook salmon are believed to be the most dependent (Healey 1982) on estuarine environments and the diverse life history strategies of chinook salmon result in migrations of juveniles into estuaries throughout much of the year (Reimers 1973; Iwamoto and Salo 1977). Cwt recoveries from hatchery chinook salmon in Puget Sound revealed individual residence times of up to 18 weeks, while the average time spent in a single sampling region was 1-3 weeks (Chapter 1). Modeled chinook salmon cohorts experienced variable feeding conditions, with peaks in growth efficiencies both in May and July. Based on diets alone, peak growth efficiencies vary considerably over a season and between years, and can be very favorable not only in the spring but into September as well. The diversity of life history strategies may help chinook salmon to maximize chances of experiencing peak growth conditions.

Whereas growth conditions were nearly identical for hatchery and unmarked chinook salmon in SPS, unmarked fish in NPS consumed a higher energy diet (rich in insects and a greater proportion of fish) and experienced higher growth rates and efficiency than hatchery counterparts during July. This may reflect the relative dominance of hatcheries which produced at least 98% of the chinook salmon caught in SPS but only 44% of the chinook salmon caught in NPS during 2002 (Chapter 1). It may also reflect the available prey resource, which appears to be more consistently based on more energetically constant planktonic and epibenthic production in SPS. The supply and distribution of neustonic insects, on the other hand, can be very patchy and dynamic. The dominance of neustonic drift insects in NPS chinook diets was likely a combination of high freshwater inflow (Chapter 2), fallout (Simenstad et al. 1982) and transport by wind (Cheng and Birch 1978) from vegetation in wetlands and uplands. Hatchery and unmarked chinook salmon in NPS may have experienced different prey resources due to slight differences in timing and spatial orientation; alternatively hatchery fish may have targeted different prey than unmarked fish, especially at delta sites, a trend observed in hatchery fish shortly after release (Myers 1980).

Pink and chum salmon usually arrive in estuarine waters earliest (February-April) and at the smallest size (pink salmon often the smallest). While chum salmon are highly dependent (Healey 1982) on estuarine environments (second to chinook salmon), pink salmon migrate rapidly to marine habitats, and are considered the least dependent on estuaries (Bostick 1955; Stober et al. 1973; Shepard 1981; Healey 1982; Simenstad et al. 1982). Rapid migrations with continual cycling of small fish would have produced underestimates of apparent growth, which may explain why pink salmon fed at the lowest proportion of maximum consumption of all the simulations I ran. Apparent growth rates estimated for pink salmon (1.8-3.1% body wt/day) were on the lower end of rates measured in British Columbia and Alaska estuaries (LeBrasseur and Parker 1964; Healey 1980b; Willette 1996; Mortensen et al. 2000). Estimated growth rates for chum salmon (2.6-5.8% body wt/day) were also generally lower than rates in Hood Canal (5.7-8.6% body wt/day; Salo et al. 1980) and British Columbia (5.7% body wt/day; Healey 1979), but similar to rates in the Gulf of Alaska (2.3-4.1% body wt/day; Orsi et al. 2001). In NPS, both pink and chum salmon experienced the highest growth efficiencies in April, likely a result of favorable temperatures and a diet rich in adult insects. Future study should examine foraging conditions in late winter and early spring, a time which may be more important to a larger proportion of the pink and chum salmon in these areas.

Estimates of apparent growth rates for coho salmon in this study (1.3-2.0% body wt/day) were similar to those measured in British Columbia estuaries (1.5-1.9% body wt/day; Healey 1982). However, growth rate estimates for chinook salmon in Puget

Sound (1.0-3.5% body wt/day) were generally lower than rates measured in British Columbia estuaries (3.5-5.5% body wt/day; Healey 1982). In model simulations, growth efficiencies for chinook salmon at NPS and SPS sampling sites were lower than for the other salmon, particularly in May when relative abundances of the other salmon species were highest. This suggests that chinook salmon entering Puget Sound in May could experience relatively poor growth at a time when extremely high growth rates may be favorable to survival. Slowing of apparent growth for chinook salmon has been attributed to inter- or intra-specific competition in other estuaries (Reimers 1973; Levy et al. 1978). The greatest potential for dietary overlap and competition for chinook salmon was found between hatchery and unmarked conspecifics, and minorly between coho and chinook salmon of similar sizes (Chapter 2).

If the food supply were limited, competition among and between pink and chum salmon, which had exhibited potentially high dietary overlap (Chapter 2), may also have been responsible for declining growth efficiencies observed for chum and pink salmon in April-May. In Hood Canal, it was estimated that during peak densities in spring, chum salmon might experience lower growth and poorer foraging conditions, depleting supplies of harpacticoid copepod prey (Wissmar and Simenstad 1988). In order to adequately address this as a question of carrying capacity, future sampling is needed to quantify supply and availability of planktonic, epibenthic and neustonic prey resources, as well as to determine other potential competitors beyond juvenile salmon species.

I assumed that juvenile salmon remained in the sampling regions for consistent residence intervals, and that they primarily utilized shallow nearshore habitats. In reality, juvenile salmon experience a wide variety of residence times in estuarine waters and are also found in offshore neritic and pelagic habitats. Salmon are hypothesized to move from shallow nearshore habitats to offshore surface waters after either achieving a certain size threshold (at least 50-60mm for chum salmon; Simenstad et al. 1982) or after a certain amount of time (LeBrasseur and Parker 1964; Wetherall 1970; Blackbourn 1976; Healey 1980a; Dawley et al. 1986). In parts of Puget Sound, a portion (presumed to be small) of the juveniles move offshore immediately and at very small sizes, likely due to strong currents prevailing during the ebb tide (Tyler 1963; 2002, C. Rice, NOAA-

Fisheries, Mukilteo, WA, pers. comm.). Although based on simulations using very limited data, it appeared that diet quality for chinook and pink may be more consistently favorable in neritic environments, especially as nearshore foraging conditions decline. Diet, thermal experience, and potential growth may be affected if salmon are more widely dispersed and residence times vary from those I estimated. To gain more accurate estimates of residence times and growth, future sampling should include tracking groups of fish in the field and use of scales and/or otoliths for relative measures of growth rates.

In Puget Sound, the majority of reported intrageneric salmon predation is minimal and occurs during the spring (Mathews and Buckley 1976; Cardwell and Fresh 1979; Fresh et al. 1981; Simenstad et al. 1982; Chapter 1). Chinook and coho salmon are able to consume other salmon up to 50% of their length (Pearsons and Fritts 1999; Brodeur 1990; Chapter 2). In 2001-2002, the minimal predation by juvenile chinook salmon on other salmon was likely due to gape-limitation, since most pink and chum salmon present in Puget Sound during peak age-0 chinook salmon abundances were 36-61% of their FL (Chapter 1). Age-1 coho salmon were at least 10-50mm larger than chinook salmon during peak emigrations, and were more piscivorous on salmon.

Based on piscivory rates observed in 2002, I estimated that an individual juvenile coho, 100-130mm, consumed 1-2 pink/chum per day, while an 80-90mm chinook consumed one pink/chum every 2.5-5 days. However, it is the larger-sized salmonids, including coastal cutthroat trout (*Oncorhynchus clarki clarki*, Jauquet 2002; E. Duffy, University of Washington, unpublished data 2001-2002) and large juvenile and subadult chinook and coho salmon (Introduction; Chapter 2) that have the potential to be more significant individual predators on juvenile salmon. In order to infer the potential predation impact at a population level, diet data must be collected at the appropriate spatial and temporal scales and used in conjunction with predator abundances (Beauchamp et al. 1995). This will require intensive sampling during crepuscular hours (Chapter 2) and peak densities of potential prey and predators. Even low apparent rates of predation could produce significant impacts if the predator abundance is high.

The validity of estimates derived from bioenergetics modeling depends on the accuracy of its inputs. Any errors in these inputs will propagate throughout the model, and consequently, consumption estimates risk losing accuracy (Ney 1990). In this study, I made many assumptions that could affect the accuracy of the consumption and growth efficiency estimates. I used estimated, not measured, growth scenarios which directly affect the consumption estimates and growth efficiencies produced by the model. I also used water temperatures measured in shallow waters very close to shore, which may not necessarily reflect the actual thermal experience for the highly motile juvenile salmon that may target preferred temperatures. I primarily used literature values of energy densities for prey that were often sampled in different geographical areas, and I occasionally used individual or average values from comparable species. Future studies that aim to target these key uncertainties are needed to increase the accuracy of these estimates.

The values from simulations in this study reflect potential, not necessarily precise quantitative estimates of consumption in the field, and therefore they should not be used to make quantitative predictions of impact on specific prey populations. However, they are useful for making general estimates and relative comparisons of fish consumption rate and growth efficiency (Kitchell et al. 1977; Bartell et al. 1986; Ney 1993). In this study, simulations suggest that juvenile salmon occupying sites in the NPS sampling region may experience relatively high growth rates, due to the availability of high quality prey resources (especially insects). However, growth conditions for juvenile salmon at these sites appear to be variable, as diet quality and water temperatures fluctuate on a weekly to monthly scale. Therefore, the timing of juvenile salmon encountering these sites may greatly affect their potential for growth. Juvenile salmon occupying sites in the SPS sampling region, on the other hand, may experience more moderate growth rates but a greater consistency of foraging conditions and water temperatures at sites in SPS may translate to a more constant potential for growth. Therefore the seasonal migration timing may not be as important for the growth performance of salmon encountering these sites. Timing, however, may impact other critical factors, including the vulnerability of these juveniles to potential predators.

This study examined relatively small, localized areas of Puget Sound and results cannot be extrapolated to make broad regional generalizations. Future efforts are needed to synthesize results from current and ongoing studies in order to expand the spatial coverage and facilitate a more comprehensive understanding of the ecology of juvenile salmon in Puget Sound. Comparisons between different Puget Sound areas may help to determine whether juvenile salmon face spatial and temporal differences in the forage base and environmental conditions that could affect their early marine growth potential. In addition, a focus on potential predators will help to determine the proximate causes of mortality in Puget Sound. Ultimately, understanding which factors affect the early marine survival of juvenile salmon in Puget Sound may help us to ameliorate current declines faced by some Puget Sound salmon populations.

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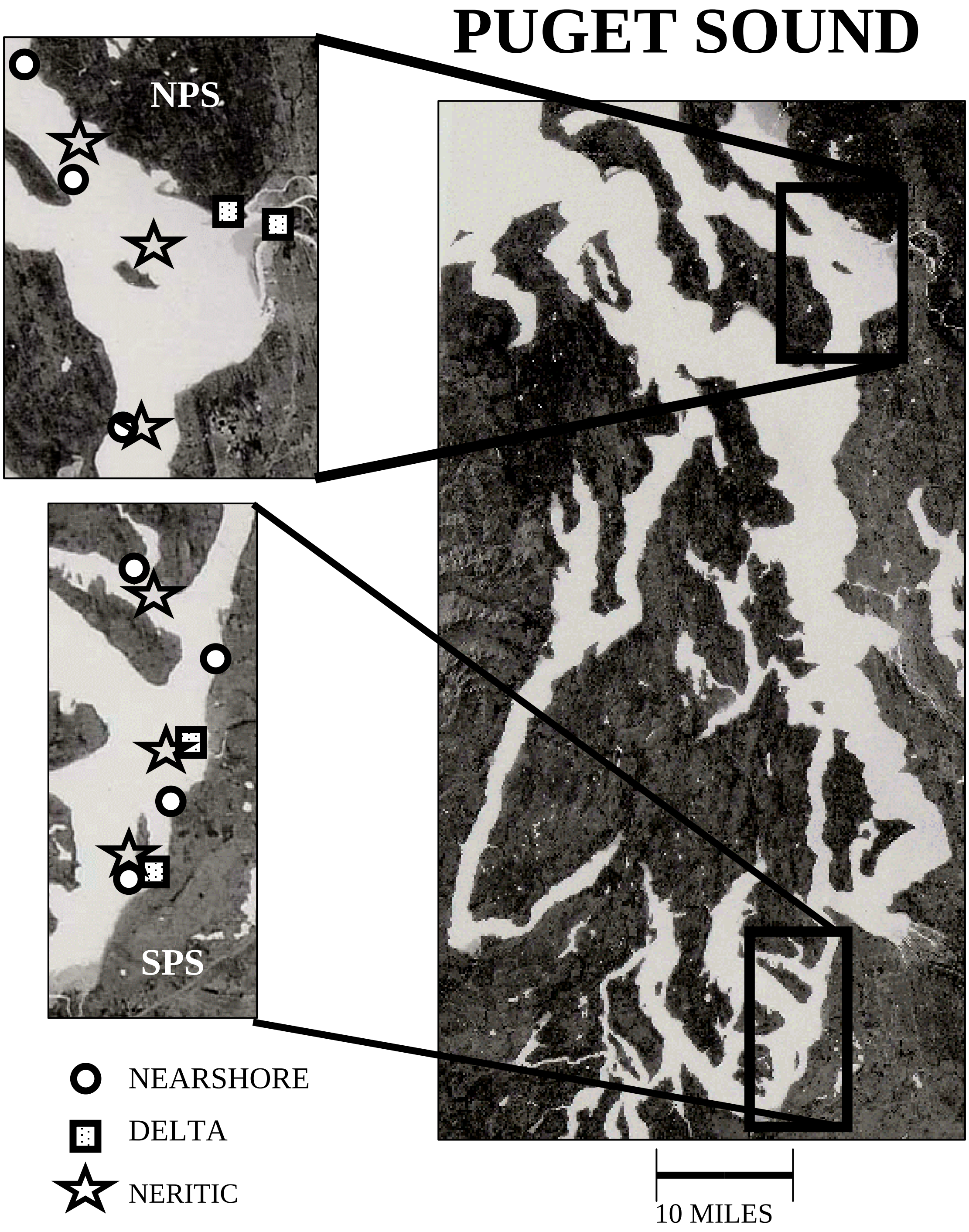

Figure 3.1. Puget Sound study regions and sampling locations. Circles and squares indicate nearshore and delta beach seine locations. Stars indicate neritic tow net locations.

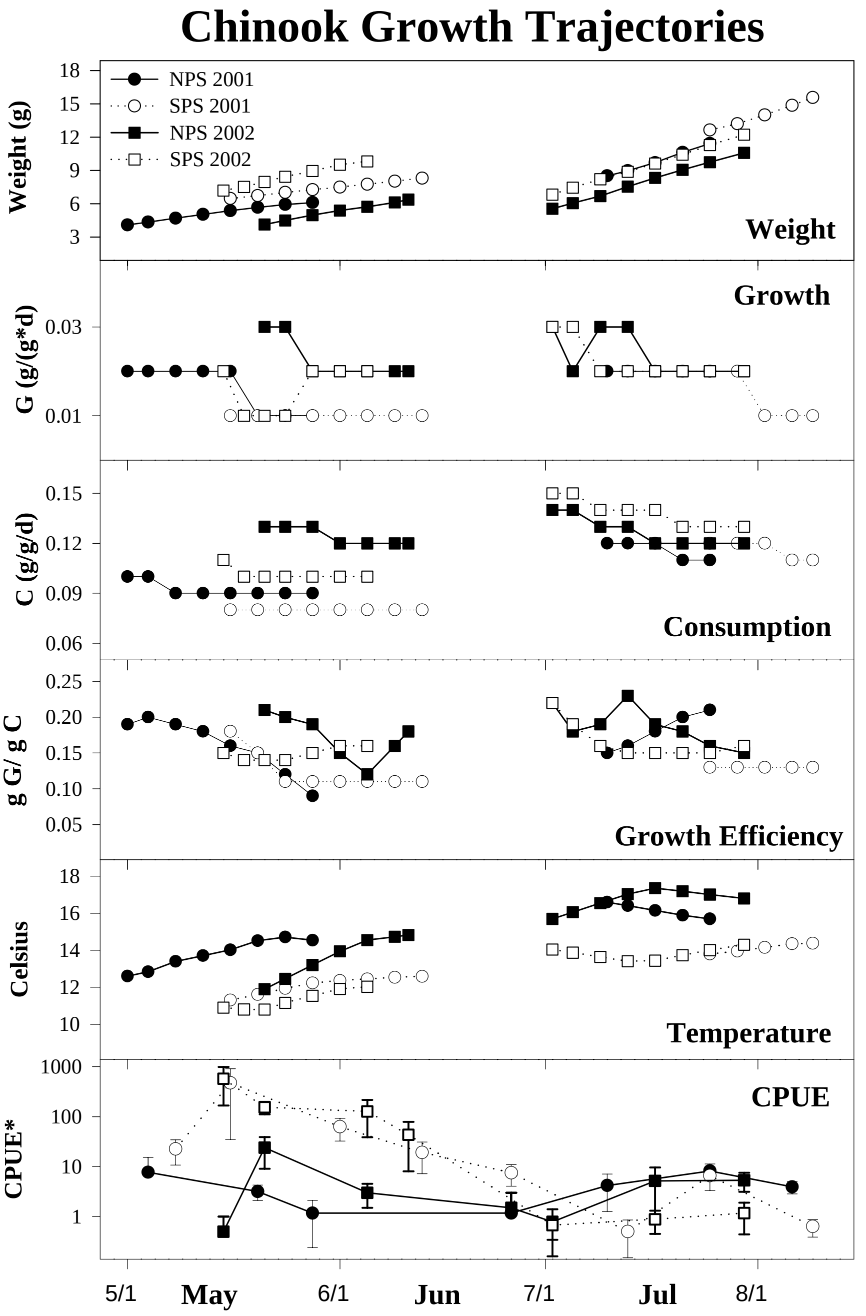

Figure 3.2. Bioenergetics model run growth performance for peak juvenile chinook salmon outmigrants in NPS and SPS during May and July, 2001-2002 (see Table 3.4). *Y-axis of CPUE is in log10 scale.

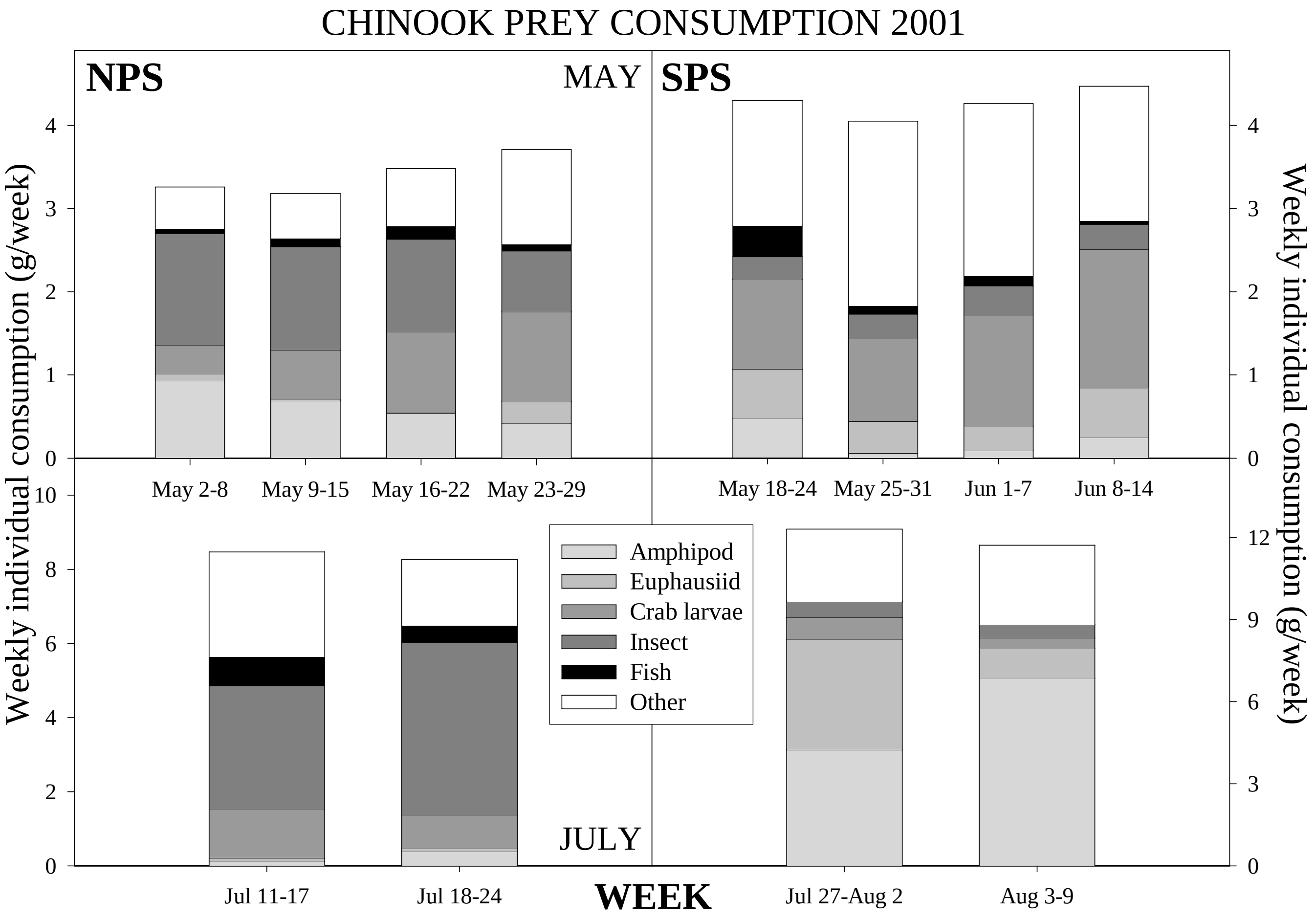

Figure 3.3a. Simulated weekly individual consumption estimates (g/week) of major prey categories in diets of juvenile chinook salmon in NPS and SPS during May and July, 2001.

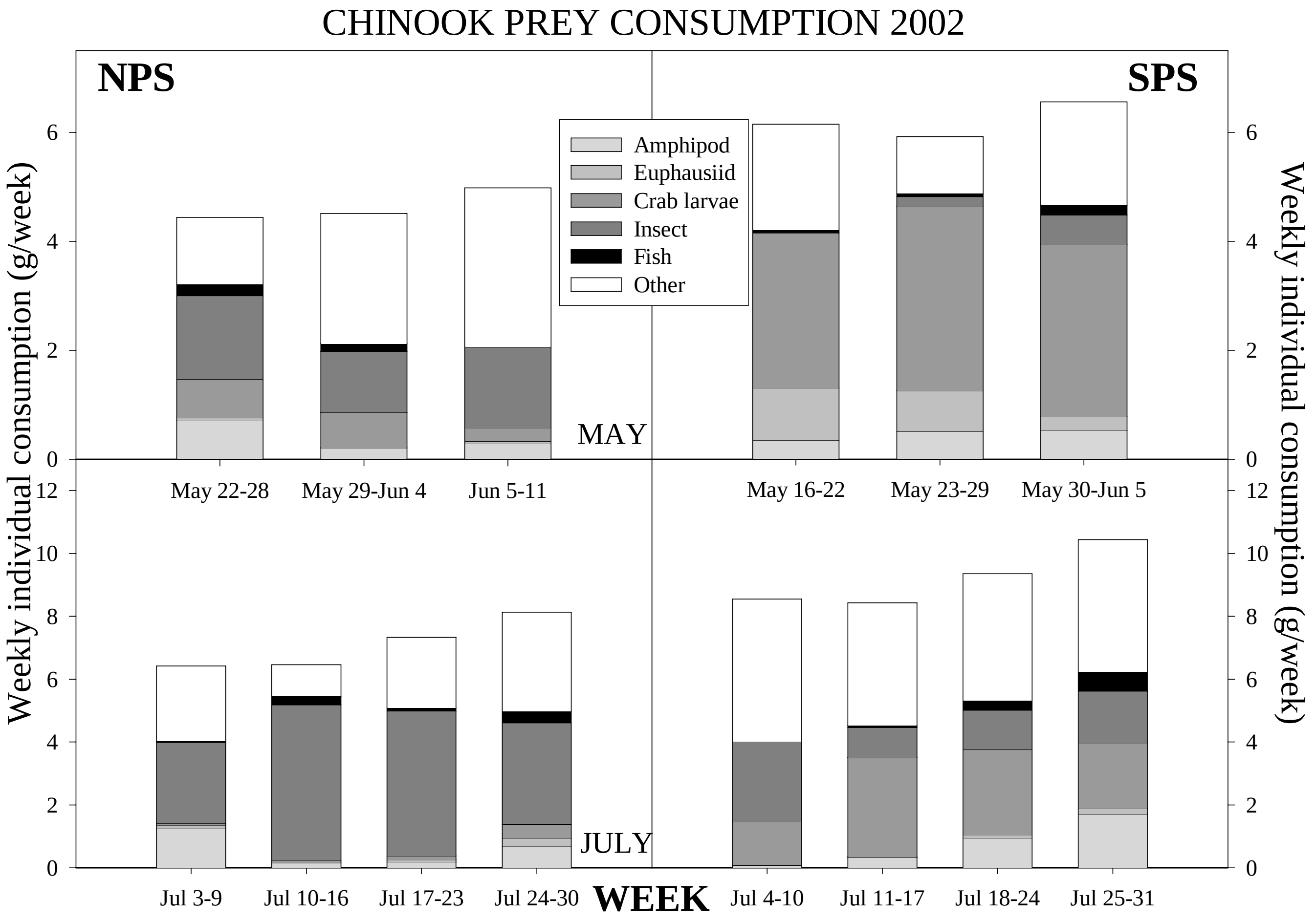

Figure 3.3b. Simulated weekly individual consumption estimates (g/week) of major prey categories in diets of juvenile chinook salmon in NPS and SPS during May and July, 2002.

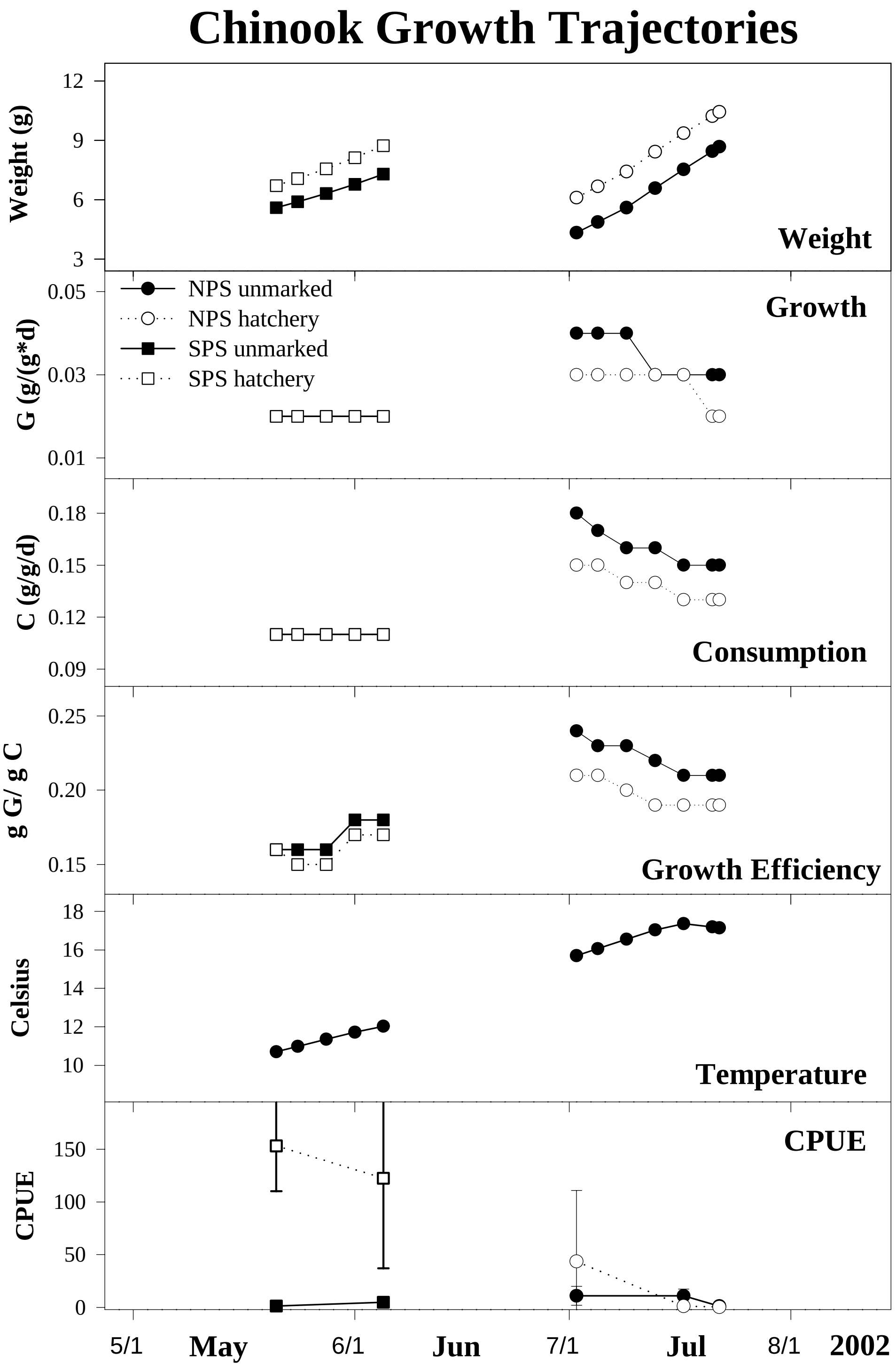

Figure 3.4. Bioenergetics model run growth performance for peak juvenile hatchery (cwt) and unmarked chinook salmon outmigrants in NPS and SPS 2002.

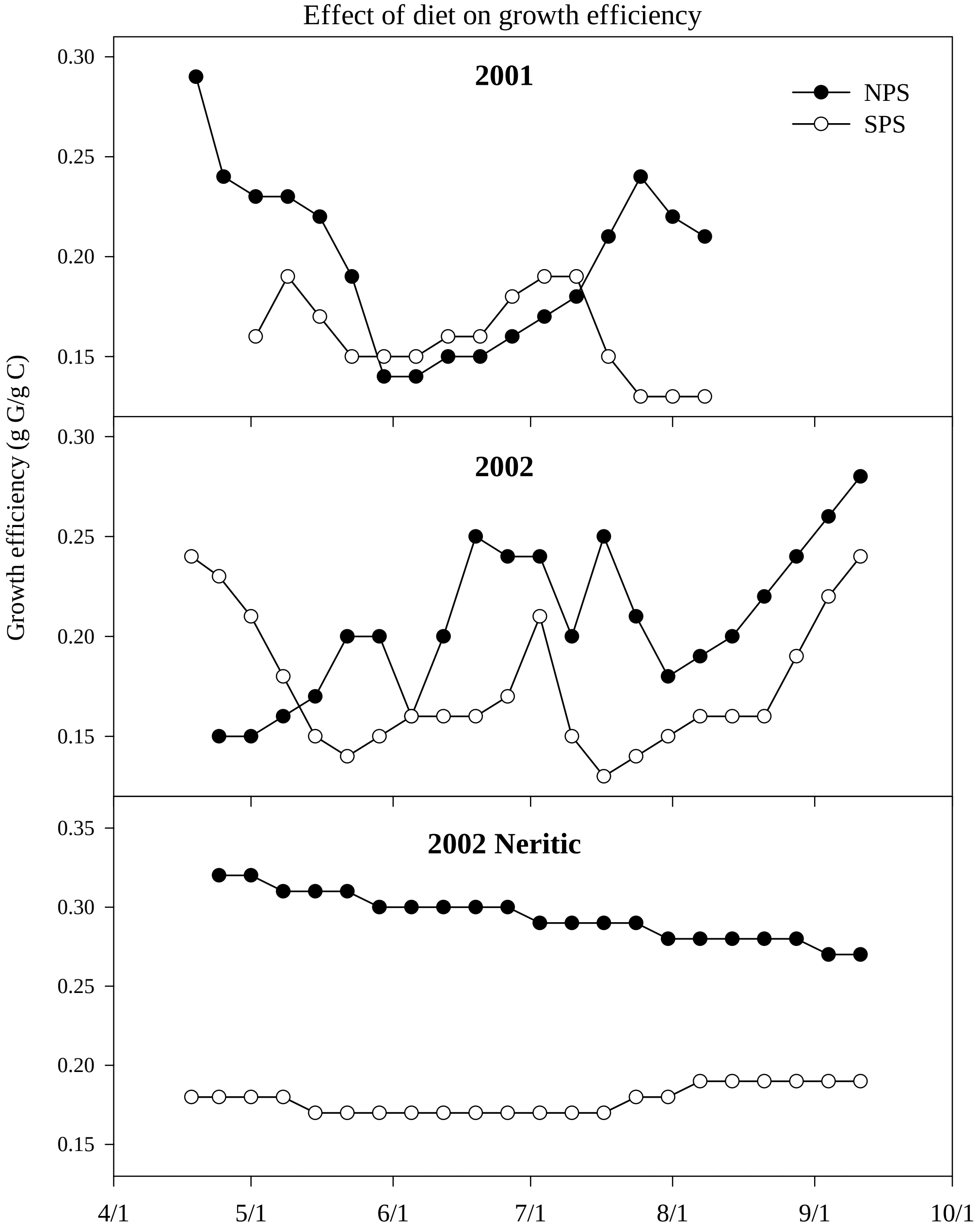

Figure 3.5. Modeled growth efficiency of chinook salmon between April and September fed diets determined at northern Puget Sound (NPS) and southern Puget Sound (SPS) sampling sites in 2001 and 2002. In all simulations, chinook were fed at 68% of maximum consumption in waters 11 degrees Celsius (see Table 3.4).

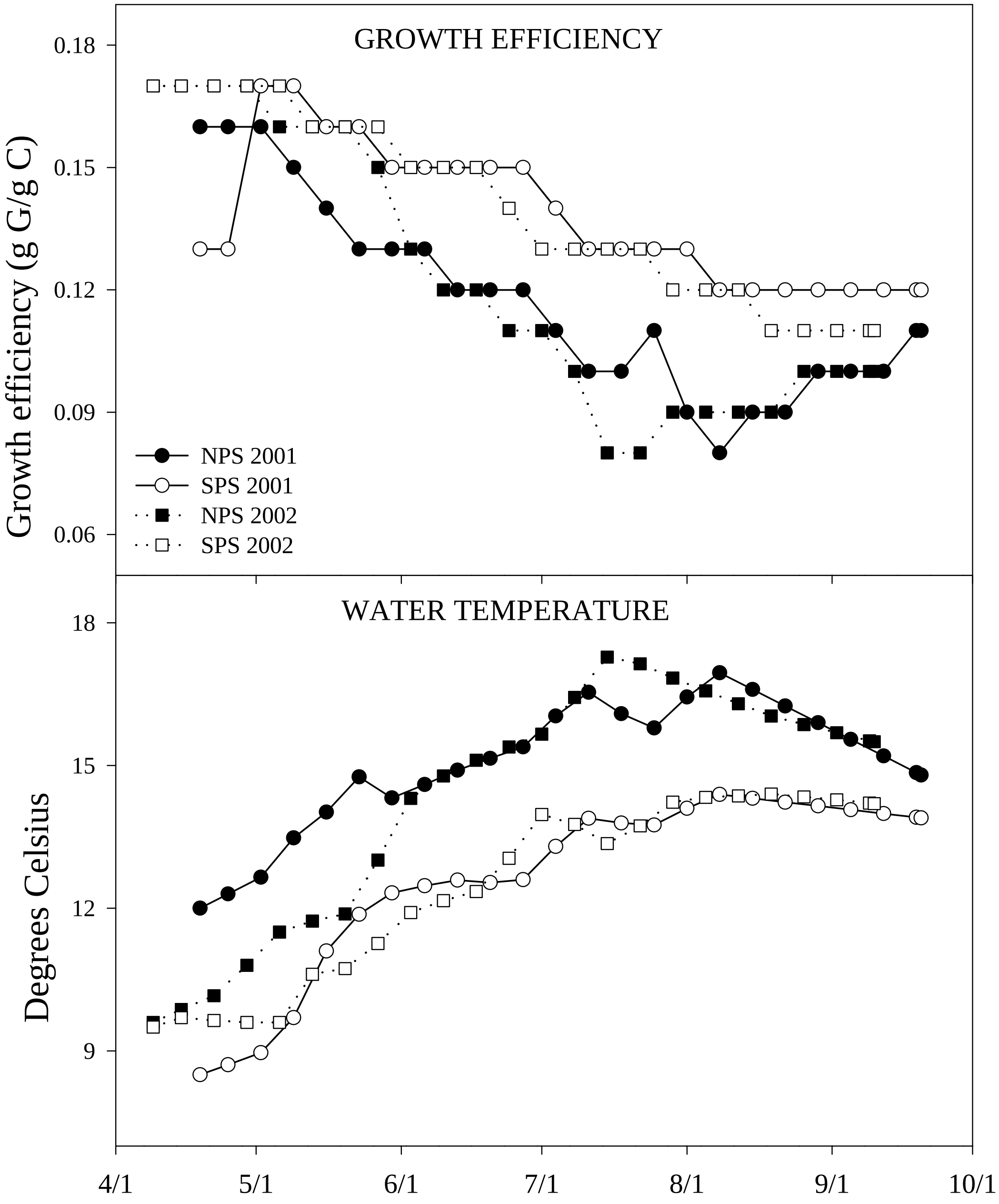

Figure 3.6. Modeled growth efficiency (upper panel) of chinook salmon between April and September in water temperatures (lower panel) measured at nearshore northern Puget Sound (NPS) and southern Puget Sound (SPS) sites in 2001 and 2002. In all simulations, chinook were fed at 68% maximum consumption on a constant diet (see Table 3.4).

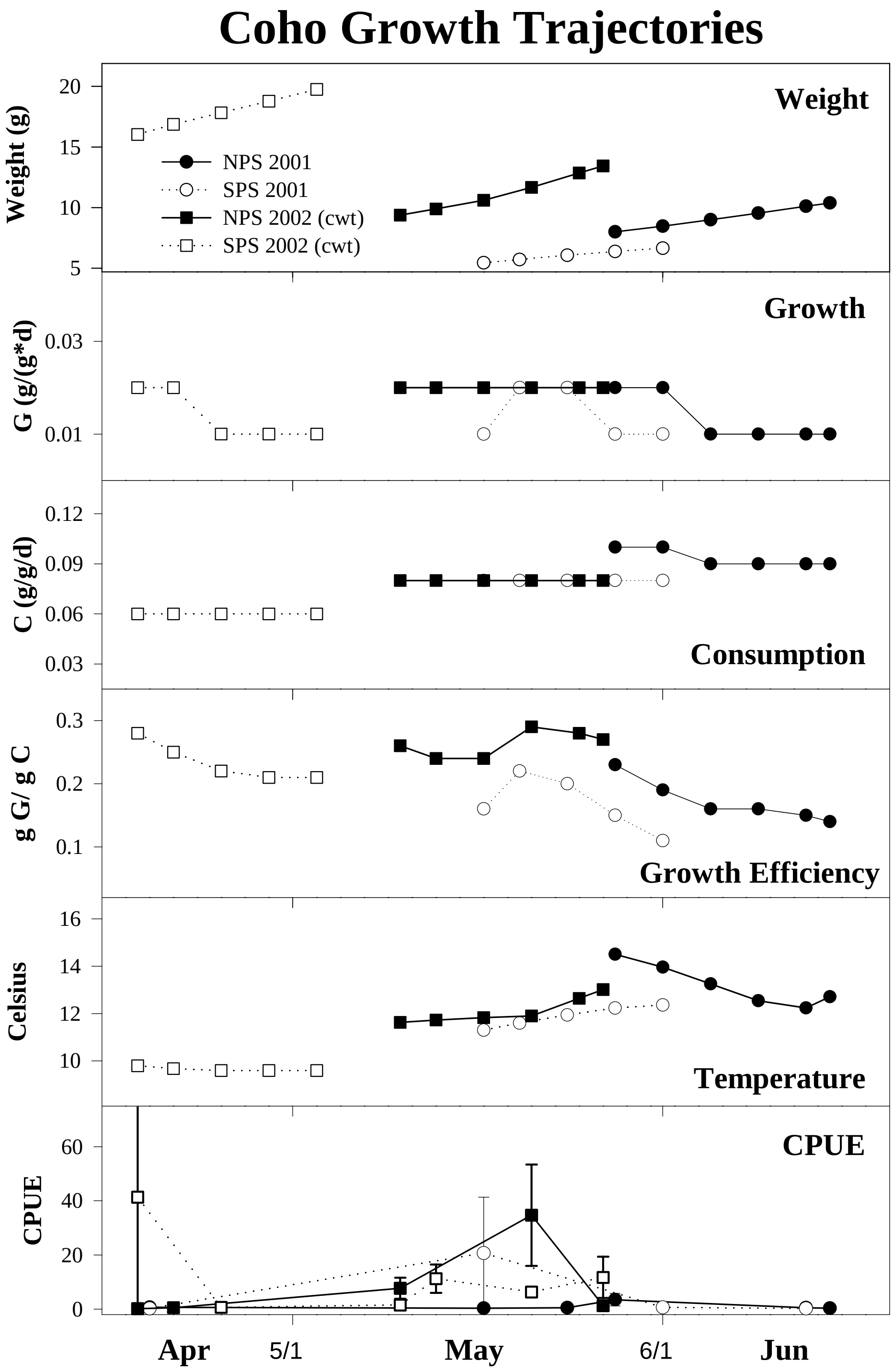

Figure 3.7. Bioenergetics model run growth performance for peak juvenile coho salmon outmigrants in NPS and SPS 2001-2002 (see Table 3.4).

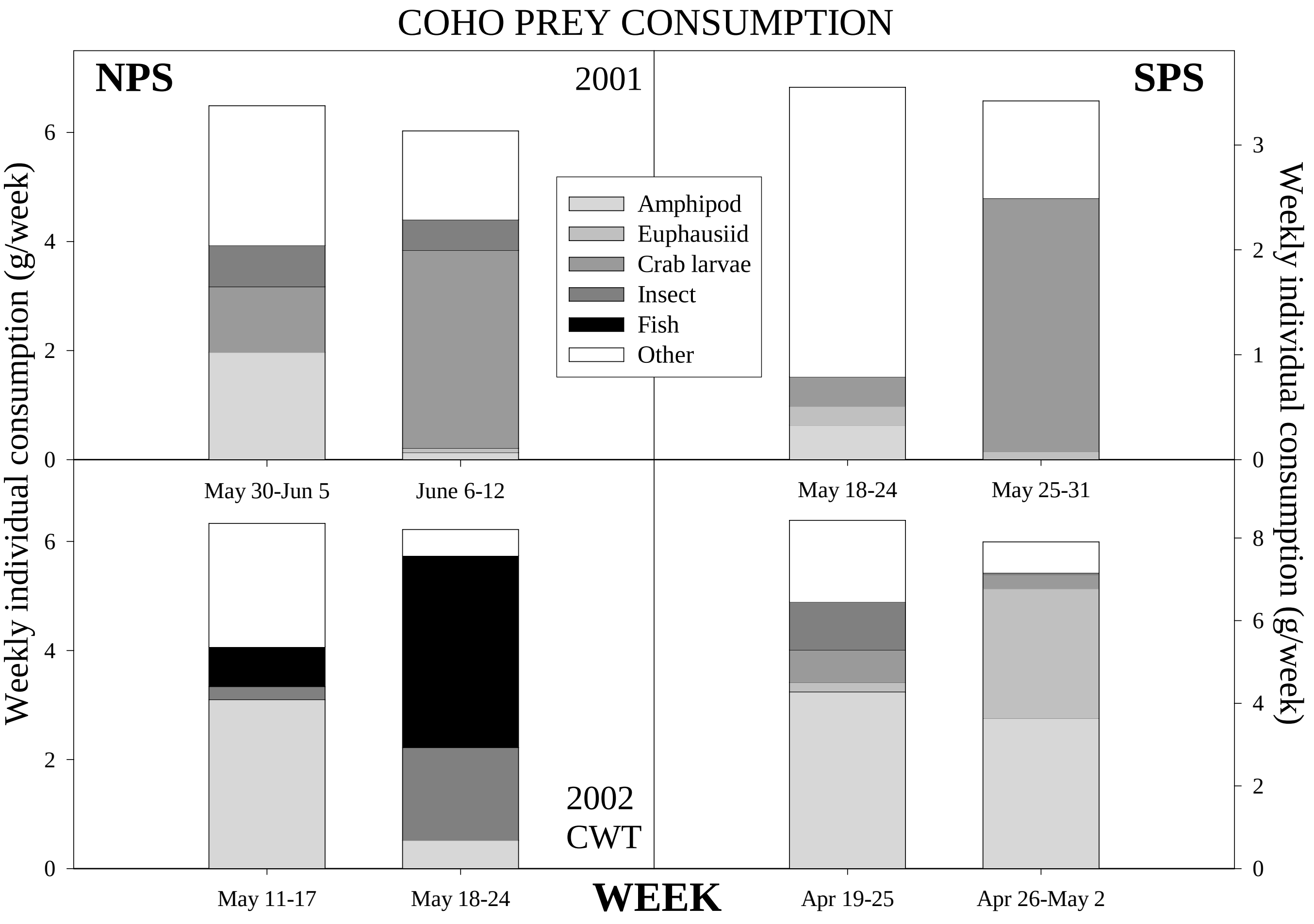

Figure 3.8. Simulated weekly consumption estimates of major prey categories in diets of juvenile coho salmon in NPS and SPS during spring 2001 and 2002.

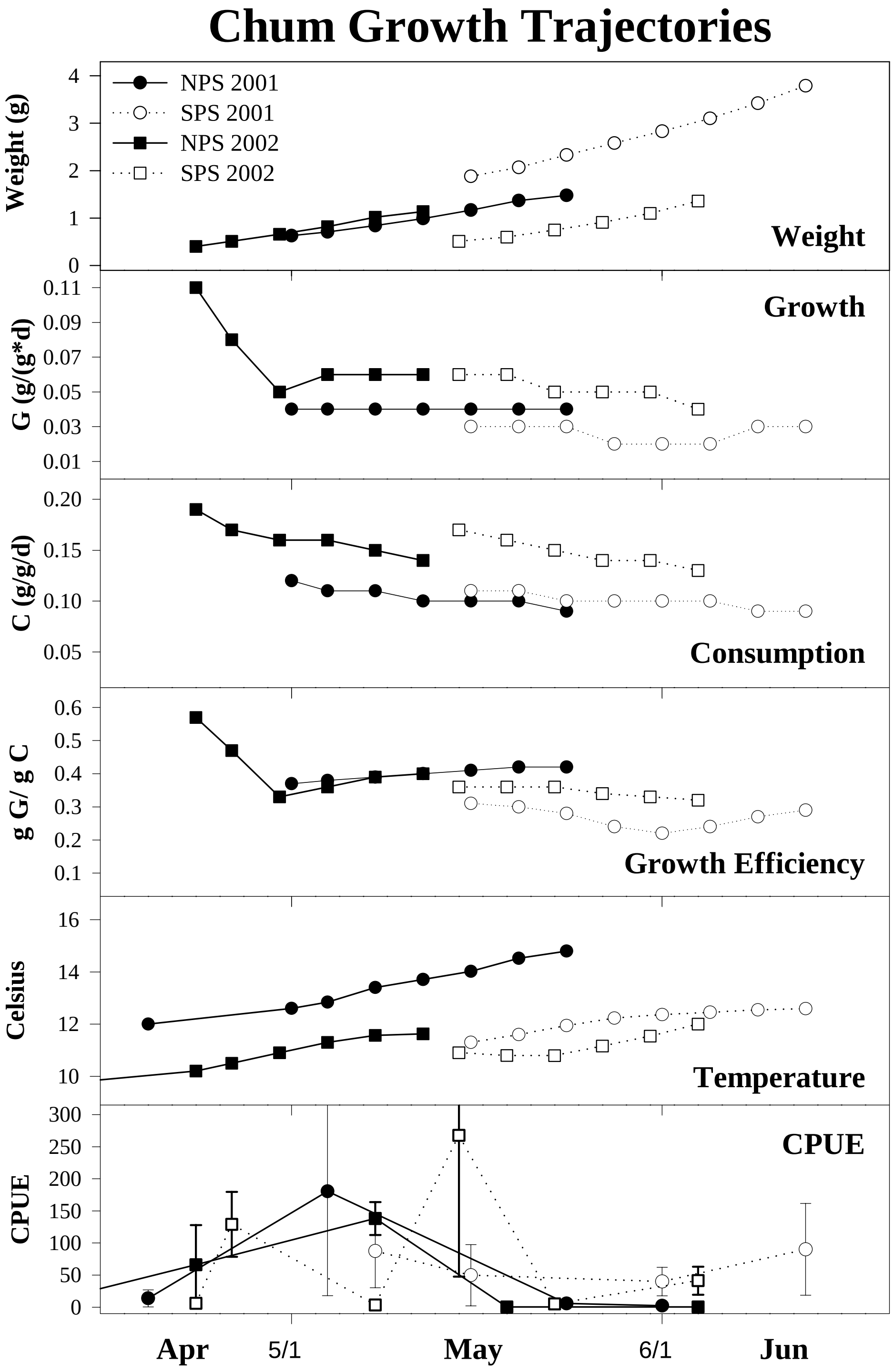

Figure 3.9. Bioenergetics model run growth performance for peak juvenile chum salmon outmigrants in NPS and SPS 2001-2002 (see Table 3.4).

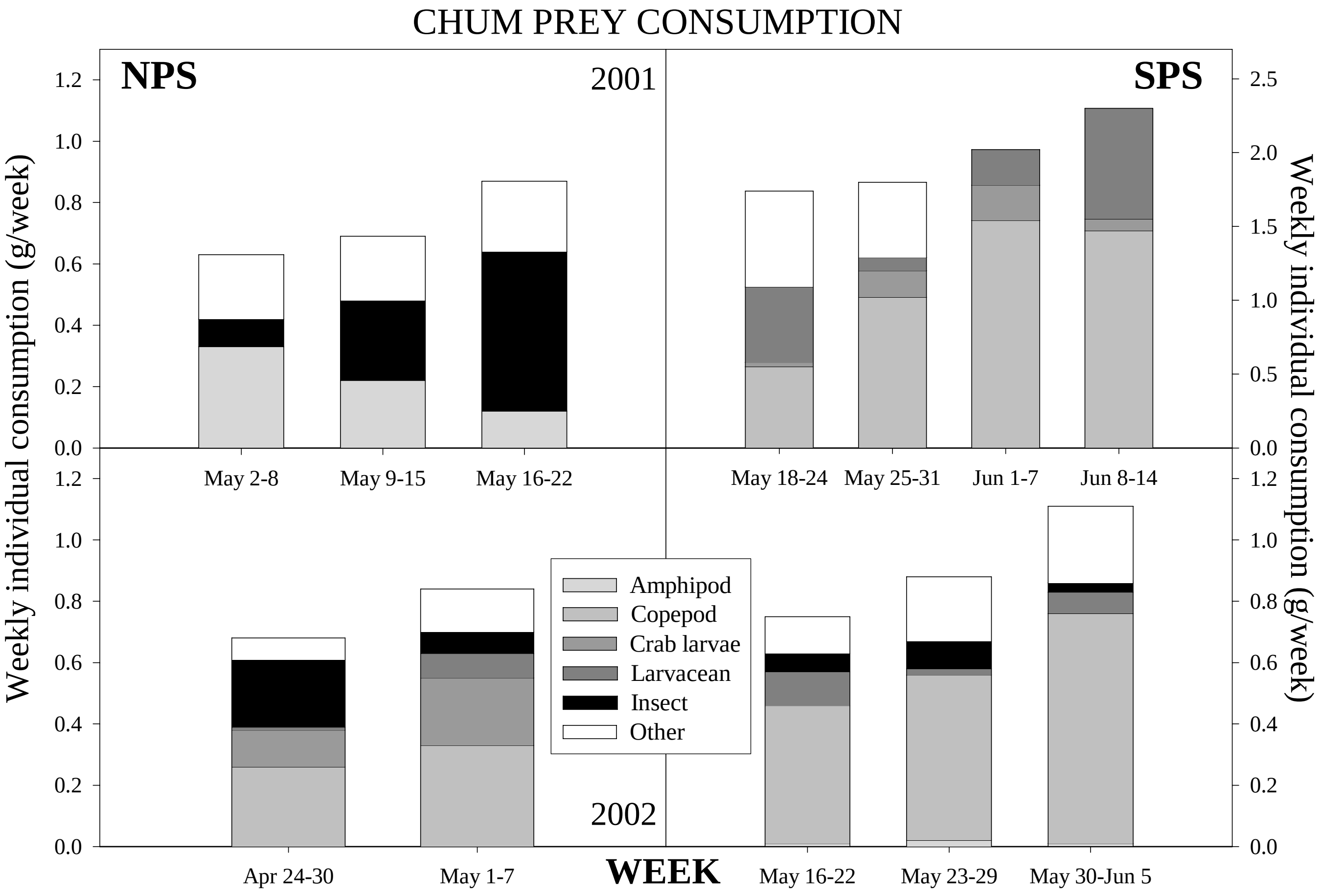

Figure 3.10. Simulated weekly individual consumption estimates (g/week) of major prey categories in diets of juvenile chum salmon in NPS and SPS during spring 2001 and 2002.

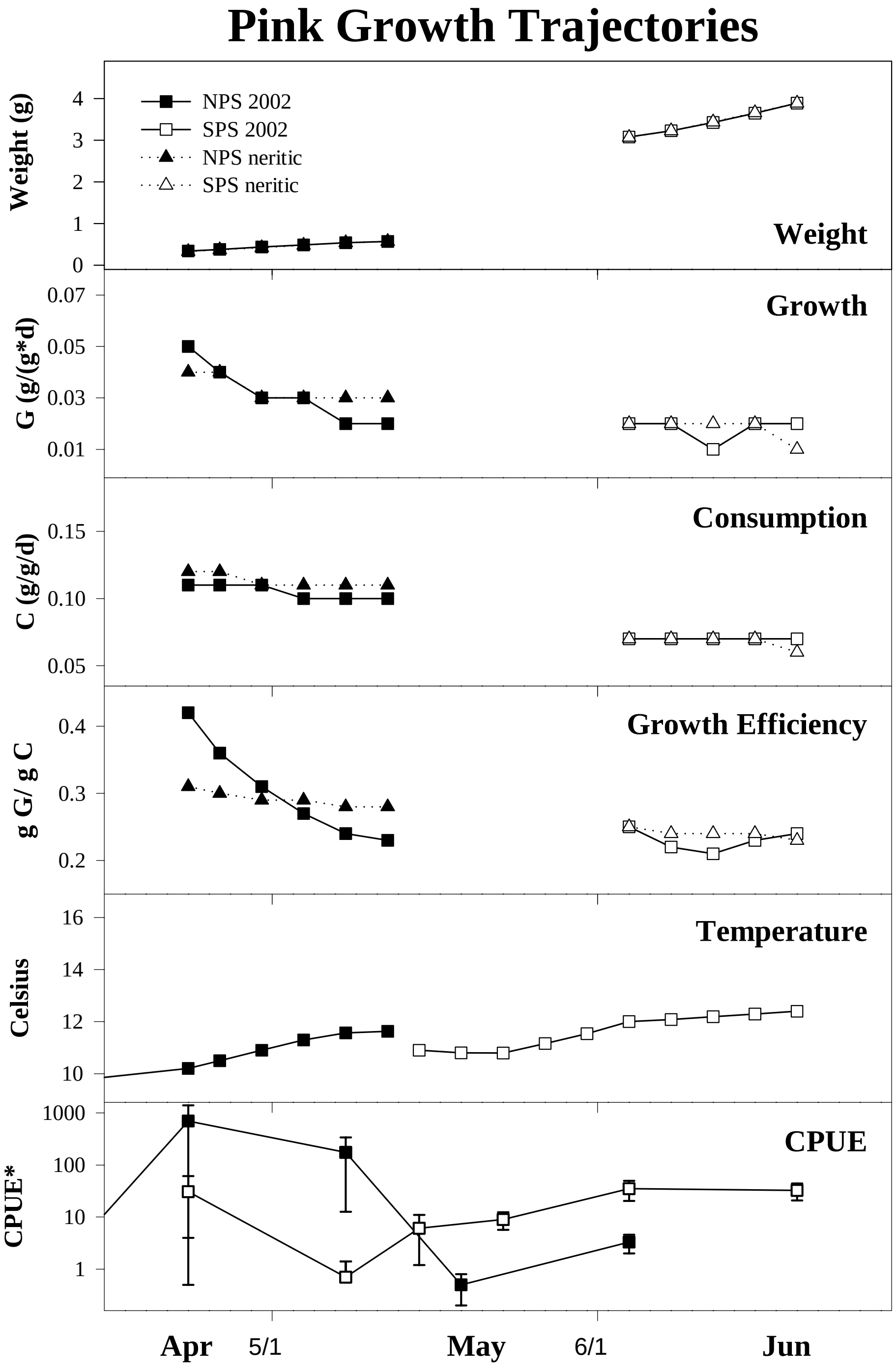

Figure 3.11. Bioenergetics model run growth performance for peak juvenile pink salmon outmigrants in NPS and SPS 2001-2002 (see Table 3.4).
*Y-axis of CPUE is in log10 scale.

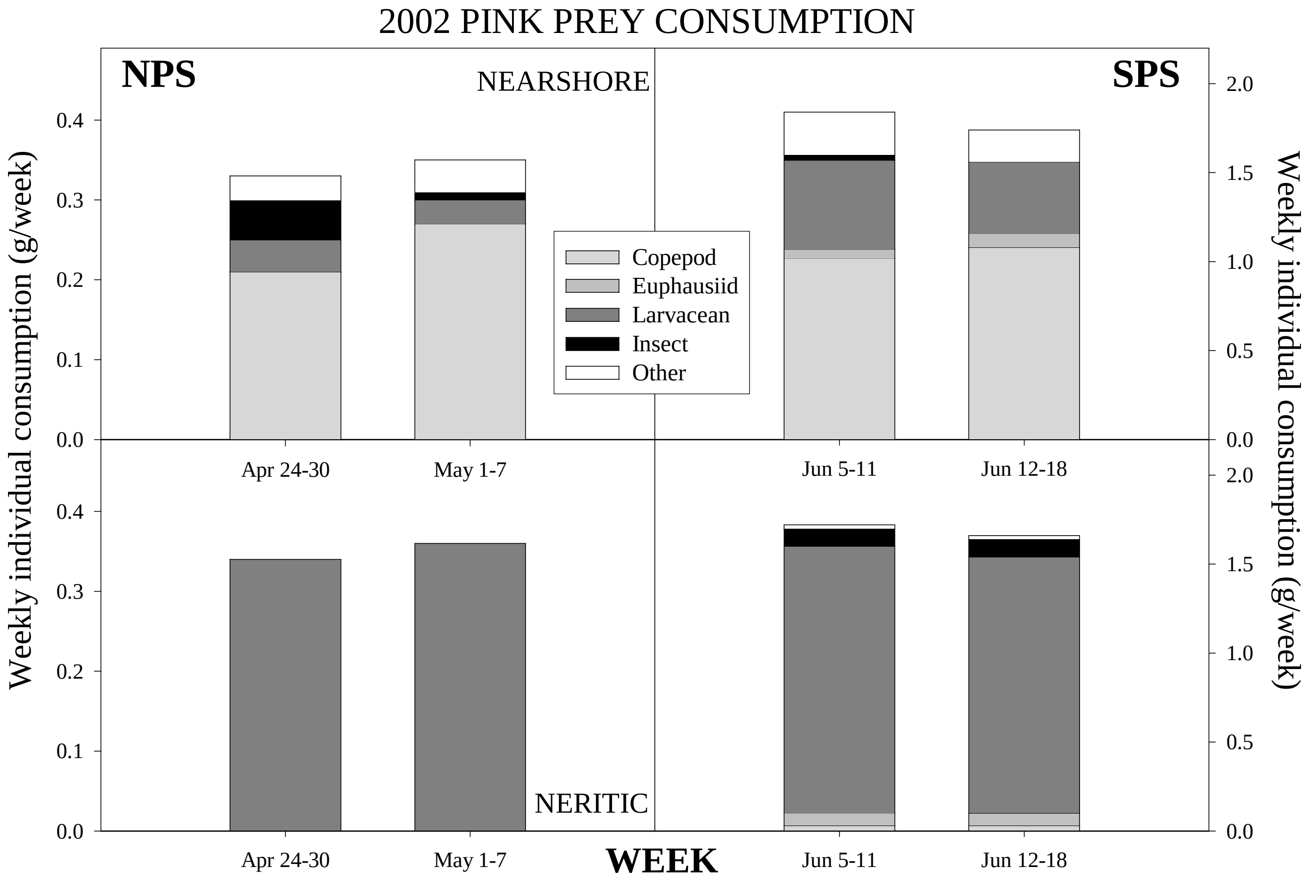

Figure 3.12. Simulated weekly individual consumption estimates (g/week) of major prey categories in nearshore and neritic diets of

juvenile pink salmon in NPS and SPS during spring 2002.

Table 3.1. Water temperature values (in degrees Celsius at 1m depth) are averages from sampling sites.

Date	Sim Day	NPS Nearshore	s.d.	SPS nearshore	s.d.
19-Apr-01	11	12.0	1.0		
3-May-01	25	12.7	1.2		
8-May-01	30			9.5	0.7
17-May-01	39			11.3	1.9
22-May-01	44	14.8	1.3		
29-May-01	51	14.5	0.5	12.3	1.6
12-Jun-01	65			12.6	0.8
26-Jun-01	79	15.3	1.0	12.5	0.4
10-Jul-01	93	16.6	2.3	13.9	0.9
24-Jul-01	107	15.7	0.8	13.7	0.7
7-Aug-01	121	17.0	1.1	14.4	0.6
20-Sep-01	165	14.8	0.2	13.9	0.7
9-Apr-02	1	9.6	0.6		
18-Apr-02	10			9.8	0.67
23-Apr-02	15	10.2	0.5	9.6	0.44
6-May-02	28	11.5	1.4	9.6	0.6
15-May-02	37			10.9	0.92
21-May-02	43	11.9	0.4	10.7	0.61
4-Jun-02	57	14.5	1.0	12.0	0.55
19-Jun-02	72	15.2	1.2	12.4	1.16
2-Jul-02	85	15.7	0.3	14.1	0.45
16-Jul-02	99	17.4	0.1	13.3	0.71
30-Jul-02	113	16.8	0.9	14.3	0.87
20-Aug-02	134	16.0	0.2	14.4	0.21
10-Sep-02	155	15.5	0.9	14.2	0.78

Table 3.2a. Diet composition (wet weight proportions) for chinook salmon cohorts.

DATE	REGION	ZONE	SIM DAY	Barnacle larvae	Copepod	Crab larvae	Cumacean	Euphausiid	Gammarid amphipod	Hyperiid amphipod	Insect	Isopod	Mysid/ Shrimp	Polychate	Other invertebrate	Salmon	Sand lance	Other fish
NPSchk-May2001			23-51															
03-May-01	NPS	delta	20	0%	0%	13%	0%	10%	**35%**	0%	**22%**	0%	0%	0%	**20%**	0%	0%	0%
03-May-01	NPS	nearshore	27	6%	0%	9%	1%	1%	**28%**	0%	**46%**	0%	1%	6%	0%	0%	0%	2%
22-May-01	NPS	nearshore	44	5%	0%	**32%**	1%	0%	13%	0%	**29%**	0%	0%	2%	13%	0%	0%	5%
29-May-01	NPS	nearshore	51	**33%**	0%	**27%**	0%	12%	10%	0%	13%	0%	0%	0%	5%	0%	0%	0%
NPSchk-July2001			93-107															
10-Jul-01	NPS	nearshore	93	**27%**	0%	18%	0%	1%	0%	0%	**31%**	0%	0%	4%	8%	0%	11%	0%
24-Jul-01	NPS	nearshore	107	4%	0%	9%	0%	1%	5%	1%	**63%**	0%	0%	2%	11%	0%	1%	3%
SPSchk-May2001			39-67															
17-May-01	SPS	delta	39	1%	1%	**33%**	0%	6%	**21%**	0%	9%	0%	0%	1%	9%	0%	**20%**	0%
17-May-01	SPS	nearshore	45	0%	8%	19%	0%	**20%**	4%	0%	4%	0%	1%	**22%**	**22%**	0%	0%	0%
31-May-01	SPS	nearshore	53	11%	8%	**28%**	0%	3%	0%	0%	9%	3%	0%	**32%**	3%	0%	0%	4%
14-Jun-01	SPS	nearshore	67	0%	1%	**40%**	2%	16%	7%	0%	6%	3%	0%	7%	19%	0%	0%	0%
SPSchk-July2001			109-123															
26-Jul-01	SPS	nearshore	109	2%	3%	8%	0%	**44%**	4%	19%	5%	0%	3%	4%	8%	0%	0%	0%
09-Aug-01	SPS	nearshore	125	1%	0%	2%	0%	0%	19%	**49%**	4%	**25%**	0%	0%	0%	0%	0%	0%
NPSchk-May2002			43-64															
21-May-02	NPS	delta	43	14%	0%	0%	4%	3%	**26%**	7%	**32%**	3%	1%	2%	8%	0%	0%	0%
21-May-02	NPS	nearshore	48	14%	0%	**26%**	0%	0%	7%	0%	**37%**	0%	0%	0%	8%	0%	0%	8%
05-Jun-02	NPS	nearshore	58	**36%**	10%	7%	0%	0%	3%	0%	17%	0%	7%	0%	**20%**	0%	0%	0%
05-Jun-02	NPS	delta	68	0%	0%	0%	0%	2%	13%	0%	**59%**	0%	0%	**22%**	4%	0%	0%	0%
NPSchk-July2002			85-113															
02-Jul-02	NPS	delta	85	1%	0%	2%	0%	5%	**30%**	0%	**43%**	1%	5%	0%	13%	0%	0%	0%
02-Jul-02	NPS	nearshore	90	3%	0%	0%	0%	0%	0%	15%	**32%**	0%	0%	0%	**50%**	0%	0%	0%

17-Jul-02	NPS	delta	95	3%	0%	2%	1%	0%	2%	0%	**84%**	0%	0%	1%	0%	0%	0%	7%

Table 3.2a. (continued)

DATE	REGION	ZONE	SIM DAY	Barnacle larvae	Copepod	Crab larvae	Cumacean	Euphausiid	Gammarid amphipod	Hyperiid amphipod	Insect	Isopod	Mysid/ Shrimp	Polychate	Other invertebrate	Salmon	Sand lance	Other fish
17-Jul-02	NPS	nearshore	100	**27%**	0%	0%	0%	0%	0%	0%	**73%**	0%	0%	0%	0%	0%	0%	0%
30-Jul-02	NPS	nearshore	113	**21%**	0%	7%	0%	4%	11%	0%	**30%**	0%	0%	0%	**21%**	0%	6%	0%
SPSchk-May2002			37-58															
15-May-02	SPS	nearshore	37	2%	11%	**27%**	5%	**36%**	11%	0%	1%	0%	0%	3%	2%	0%	0%	2%
22-May-02	SPS	delta	41	0%	0%	**50%**	0%	0%	0%	0%	0%	0%	0%	0%	**50%**	0%	0%	0%
22-May-02	SPS	nearshore	44	8%	0%	**62%**	0%	18%	9%	0%	0%	0%	0%	0%	3%	0%	0%	0%
04-Jun-02	SPS	nearshore	57	0%	3%	**46%**	1%	1%	7%	1%	10%	0%	0%	16%	12%	0%	0%	3%
19-Jun-02	SPS	delta	67	2%	2%	16%	0%	3%	0%	0%	2%	7%	0%	**28%**	20%	0%	0%	**20%**
NPSchk-July2002			86-114															
16-Jul-02	SPS	delta	86	0%	0%	0%	0%	0%	0%	0%	**43%**	6%	0%	**20%**	**31%**	0%	0%	0%
03-Jul-02	SPS	nearshore	95	**22%**	0%	**41%**	0%	0%	2%	0%	10%	2%	0%	0%	**23%**	0%	0%	0%
31-Jul-02	SPS	nearshore	114	17%	0%	16%	0%	2%	7%	12%	17%	2%	0%	**20%**	0%	0%	0%	7%
NPS unmarked			85-105															
July 2002	NPS	unmarked	83-114	9%	0%	4%	0%	3%	12%	1%	**55%**	0%	7%	0%	3%	0%	0%	6%
NPS hatchery			85-105															
July 2002	NPS	hatchery	83-114	11%	0%	2%	0%	3%	18%	0%	**44%**	1%	18%	0%	0%	0%	0%	3%
SPS unmarked			43-58															
May 2002	SPS	unmarked	25-53	6%	0%	**20%**	0%	**33%**	18%	0%	1%	0%	18%	1%	0%	0%	0%	3%
June 2002	SPS	unmarked	54-80	8%	1%	6%	0%	0%	**23%**	0%	4%	4%	15%	**22%**	0%	0%	0%	17%
SPS hatchery			43-58															
May 2002	SPS	hatchery	25-53	3%	9%	**38%**	0%	**25%**	8%	0%	1%	0%	3%	7%	0%	0%	0%	6%
June 2002	SPS	hatchery	54-80	1%	7%	**40%**	0%	11%	3%	0%	18%	0%	9%	9%	0%	0%	0%	2%
NPS diet 2001			11-121															
19-Apr-01	NPS	delta	11	0%	0%	0%	0%	0%	**33%**	0%	**67%**	0%	0%	0%	0%	0%	0%	0%

Table 3.2a. (continued)

DATE	REGION	ZONE	SIM DAY	Barnacle larvae	Copepod	Crab larvae	Cumacean	Euphausiid	Gammarid amphipod	Hyperiid amphipod	Insect	Isopod	Mysid/ Shrimp	Polychate	Other invertebrate	Salmon	Sand lance	Other fish
03-May-01	NPS	delta	20	0%	0%	13%	0%	10%	**35%**	0%	**22%**	0%	**20%**	0%	0%	0%	0%	0%
03-May-01	NPS	nearshore	27	6%	0%	9%	1%	1%	**28%**	0%	**46%**	0%	0%	6%	1%	0%	0%	2%
22-May-01	NPS	nearshore	44	5%	0%	**32%**	1%	0%	13%	0%	**29%**	0%	13%	2%	0%	0%	0%	5%
29-May-01	NPS	nearshore	51	**33%**	0%	**27%**	0%	12%	10%	0%	13%	0%	5%	0%	0%	0%	0%	0%
10-Jul-01	NPS	delta	85	7%	0%	0%	0%	0%	13%	1%	13%	0%	**65%**	1%	0%	0%	0%	0%
10-Jul-01	NPS	nearshore	93	**27%**	0%	18%	0%	1%	0%	0%	**31%**	0%	8%	4%	0%	0%	11%	0%
24-Jul-01	NPS	nearshore	107	4%	0%	9%	0%	1%	5%	1%	**63%**	0%	11%	2%	0%	0%	1%	3%
07-Aug-01	NPS	nearshore	121	19%	0%	6%	0%	0%	7%	0%	**54%**	2%	5%	3%	3%	0%	0%	1%
SPS diet 2001			30-125															
08-May-01	SPS	delta	30	0%	0%	19%	17%	0%	14%	0%	0%	0%	0%	**50%**	0%	0%	0%	0%
08-May-01	SPS	nearshore	35	0%	0%	9%	3%	**22%**	**36%**	3%	2%	0%	13%	7%	5%	0%	0%	0%
17-May-01	SPS	delta	39	1%	1%	**33%**	0%	6%	**21%**	0%	9%	0%	8%	1%	0%	0%	**20%**	0%
17-May-01	SPS	nearshore	45	0%	8%	19%	0%	**20%**	4%	0%	4%	0%	**22%**	**22%**	1%	0%	0%	0%
31-May-01	SPS	nearshore	53	11%	8%	**28%**	0%	3%	0%	0%	9%	3%	2%	**32%**	0%	0%	0%	4%
14-Jun-01	SPS	nearshore	67	0%	1%	**40%**	1%	16%	7%	0%	6%	3%	19%	7%	0%	0%	0%	0%
28-Jun-01	SPS	nearshore	81	1%	11%	**26%**	1%	11%	8%	0%	11%	0%	12%	12%	5%	0%	0%	2%
12-Jul-01	SPS	delta	95	10%	0%	4%	0%	2%	0%	0%	**42%**	0%	0%	**42%**	0%	0%	0%	0%
12-Jul-01	SPS	nearshore	102	0%	0%	**50%**	0%	0%	**50%**	0%	0%	0%	0%	0%	0%	0%	0%	0%
26-Jul-01	SPS	nearshore	109	2%	3%	8%	0%	**44%**	4%	19%	5%	0%	8%	4%	3%	0%	0%	0%
09-Aug-01	SPS	nearshore	125	1%	0%	2%	0%	0%	19%	**49%**	4%	**25%**	0%	0%	0%	0%	0%	0%
NPS diet 2002			15-155															
23-Apr-02	NPS	delta	15	0%	4%	0%	0%	0%	0%	0%	0%	0%	0%	**96%**	0%	0%	0%	0%
10-May-02	NPS	delta	32	0%	**20%**	0%	11%	**45%**	19%	0%	0%	0%	0%	5%	0%	0%	0%	0%
21-May-02	NPS	delta	43	14%	0%	0%	4%	3%	**26%**	7%	**32%**	3%	8%	2%	1%	0%	0%	0%
21-May-02	NPS	nearshore	48	14%	0%	**26%**	0%	0%	7%	0%	**37%**	0%	8%	0%	0%	0%	0%	8%

Table 3.2a. (continued)

DATE	REGION	ZONE	SIM DAY	Barnacle larvae	Copepod	Crab larvae	Cumacean	Euphausiid	Gammarid amphipod	Hyperiid amphipod	Insect	Isopod	Mysid/ Shrimp	Polychate	Other invertebrate	Salmon	Sand lance	Other fish
05-Jun-02	NPS	nearshore	58	**36%**	10%	7%	0%	0%	3%	0%	17%	0%	**20%**	0%	7%	0%	0%	0%
05-Jun-02	NPS	delta	68	0%	0%	0%	0%	2%	13%	0%	**59%**	0%	4%	**22%**	0%	0%	0%	0%
02-Jul-02	NPS	delta	85	1%	0%	2%	0%	5%	**30%**	0%	**43%**	1%	13%	0%	5%	0%	0%	0%
02-Jul-02	NPS	nearshore	90	3%	0%	0%	0%	0%	0%	15%	**32%**	0%	**50%**	0%	0%	0%	0%	0%
17-Jul-02	NPS	delta	95	3%	0%	2%	1%	0%	2%	0%	**84%**	0%	0%	1%	0%	0%	0%	7%
17-Jul-02	NPS	nearshore	100	**27%**	0%	0%	0%	0%	0%	0%	**73%**	0%	0%	0%	0%	0%	0%	0%
30-Jul-02	NPS	nearshore	113	**21%**	0%	7%	0%	4%	11%	0%	**30%**	0%	**21%**	0%	0%	0%	6%	0%
20-Aug-02	NPS	nearshore	134	6%	0%	13%	0%	2%	**28%**	0%	**42%**	0%	5%	0%	0%	0%	0%	4%
10-Sep-02	NPS	nearshore	155	0%	0%	0%	0%	0%	2%	0%	**98%**	0%	0%	0%	0%	0%	0%	0%
SPS diet 2002			10-156															
18-Apr-02	SPS	delta	10	0%	0%	0%	0%	0%	**100%**	0%	0%	0%	0%	0%	0%	0%	0%	0%
25-Apr-02	SPS	nearshore	17	0%	10%	0%	0%	13%	**37%**	0%	8%	0%	0%	0%	0%	0%	0%	**32%**
06-May-02	SPS	nearshore	28	2%	0%	12%	0%	0%	10%	0%	0%	0%	2%	**36%**	1%	19%	0%	18%
15-May-02	SPS	nearshore	37	2%	11%	**27%**	5%	**36%**	11%	0%	1%	0%	2%	3%	0%	0%	0%	2%
22-May-02	SPS	delta	41	0%	0%	**50%**	0%	0%	0%	0%	0%	0%	**50%**	0%	0%	0%	0%	0%
22-May-02	SPS	nearshore	44	8%	0%	**62%**	0%	18%	9%	0%	0%	0%	3%	0%	0%	0%	0%	0%
04-Jun-02	SPS	nearshore	57	0%	3%	**46%**	1%	1%	7%	1%	10%	0%	12%	16%	0%	0%	0%	3%
19-Jun-02	SPS	delta	67	2%	2%	16%	0%	3%	0%	0%	2%	7%	20%	**28%**	0%	0%	0%	**20%**
19-Jun-02	SPS	nearshore	77	7%	2%	16%	0%	8%	**21%**	0%	5%	1%	**22%**	13%	0%	0%	0%	5%
16-Jul-02	SPS	delta	86	0%	0%	0%	0%	0%	0%	0%	**43%**	6%	**31%**	**20%**	0%	0%	0%	0%
03-Jul-02	SPS	nearshore	95	**22%**	0%	**41%**	0%	0%	2%	0%	10%	2%	**23%**	0%	0%	0%	0%	0%
31-Jul-02	SPS	nearshore	114	17%	0%	16%	0%	2%	7%	12%	17%	2%	0%	**20%**	0%	0%	0%	7%
21-Aug-02	SPS	delta	120	0%	0%	0%	0%	0%	7%	**40%**	**27%**	**20%**	4%	0%	0%	0%	0%	2%
21-Aug-02	SPS	nearshore	135	0%	0%	16%	0%	**35%**	**31%**	0%	5%	2%	9%	2%	0%	0%	0%	0%
11-Sep-02	SPS	nearshore	156	0%	0%	1%	0%	2%	18%	4%	**51%**	0%	0%	0%	**24%**	0%	0%	0%

Table 3.2a. (continued)

DATE	REGION	ZONE	SIM DAY	Barnacle larvae	Copepod	Crab larvae	Cumacean	Euphausiid	Gammarid amphipod	Hyperiid amphipod	Insect	Isopod	Mysid/ Shrimp	Polychate	Other invertebrate	Salmon	Sand lance	Other fish
NPS neritic diet			1-170															
25-Sep-02	NPS	NERITIC	1-170	0%	0%	0%	0%	0%	0%	0%	**100%**	0%	0%	0%	0%	0%	0%	0%
SPS neritic diet			1-170															
12-Jun-02	SPS	NERITIC	1-65	0%	9%	**48%**	0%	17%	0%	0%	**24%**	0%	0%	0%	2%	0%	0%	0%
11-Jul-02	SPS	NERITIC	94	6%	1%	**32%**	0%	2%	1%	8%	**23%**	0%	7%	8%	12%	0%	0%	0%
13-Aug-02	SPS	NERITIC	127-170	0%	0%	**38%**	0%	0%	1%	0%	**42%**	0%	0%	0%	19%	0%	0%	0%

Table 3.2b. Diet composition (wet weight proportions) for coho salmon cohorts.

DATE	REGION	ZONE	SIM DAY	Barnacle larvae	Copepod	Crab larvae	Euphausiid	Gammarid amphipod	Hyperiid amphipod	Insect	Isopod	Mysid/ Shrimp	Ostracod	Polychaete	Other invertebrate	Salmon	Sand lance	Other fish
NPS-2001coho			51-68															
5/29/01	NPS	delta	51	0%	0%	0%	0%	**67%**	0%	5%	14%	0%	0%	0%	14%	0%	0%	0%
5/29/01	NPS	nearshore	57	19%	0%	**31%**	0%	1%	2%	17%	3%	0%	4%	0%	**23%**	0%	0%	0%
6/26/01	NPS	nearshore	68	0%	0%	**95%**	3%	1%	0%	0%	0%	0%	1%	0%	0%	0%	0%	0%
SPS-2001coho			39-54															
5/8/01	SPS	nearshore	39	3%	0%	0%	0%	**26%**	5%	0%	0%	0%	0%	**66%**	0%	0%	0%	0%
5/17/01	SPS	nearshore	43	0%	1%	0%	8%	0%	0%	0%	0%	**83%**	0%	0%	8%	0%	0%	0%
5/31/01	SPS	nearshore	53	0%	0%	**100%**	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
6/14/01	SPS	nearshore	67	4%	0%	**54%**	0%	6%	0%	4%	1%	**23%**	8%	0%	0%	0%	0%	0%
NPS-2002coho/-cwt			32-49															
5/10/02	NPS	delta	32	0%	0%	0%	0%	**53%**	0%	0%	0%	3%	0%	11%	15%	2%	15%	1%
5/21/02	NPS	delta	37	2%	0%	0%	0%	**52%**	0%	3%	0%	0%	0%	**33%**	9%	1%	0%	0%
5/21/02	NPS	nearshore	43	0%	0%	0%	0%	0%	0%	**33%**	0%	0%	0%	0%	0%	**67%**	0%	0%
6/5/02	NPS	nearshore	58	0%	3%	1%	0%	**20%**	0%	8%	0%	0%	0%	0%	**25%**	0%	18%	**25%**
NPS-2002neritic																		
7/10/02	NPS	NERITIC	32-49	0%	0%	0%	**50%**	0%	**23%**	**23%**	0%	0%	0%	0%	4%	0%	0%	0%
SPS-2002coho/-cwt			10-37															
4/25/02	SPS	delta	10	0%	0%	9%	0%	**40%**	0%	**33%**	10%	0%	0%	0%	8%	0%	0%	0%
4/18/02	SPS	nearshore	15	0%	**23%**	10%	0%	**58%**	0%	3%	0%	0%	0%	6%	0%	0%	0%	0%
4/25/02	SPS	nearshore	22	0%	0%	3%	**50%**	**47%**	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
5/6/02	SPS	nearshore	28	0%	0%	0%	**46%**	4%	0%	0%	0%	**50%**	0%	0%	0%	0%	0%	0%
5/15/02	SPS	nearshore	37	0%	5%	4%	**25%**	3%	0%	11%	0%	**51%**	0%	0%	0%	0%	1%	0%
SPS-2002neritic																		
6/12/02	SPS	NERITIC	10-25	0%	0%	**82%**	2%	9%	0%	0%	0%	8%	0%	0%	0%	0%	0%	0%

Table 3.2c. Diet composition (wet weight proportions) for chum salmon cohorts.

DATE	REGION	ZONE	SIM DAY	Barnacle larvae	Calanoid copepod	Crab larvae	Euphausiid	Gammarid amphipod	Harpacticoid copepod	Insect	Larvacean	Mysid/ Shrimp	Other invertebrate
NPS-2001chum			23-44										
5/3/01	NPS	nearshore	23	0%	0%	0%	**35%**	**62%**	0%	3%	0%	0%	0%
5/22/01	NPS	nearshore	44	0%	0%	0%	0%	6%	0%	**69%**	0%	0%	**25%**
SPS-2001chum			39-67										
5/17/01	SPS	delta	39	3%	**23%**	3%	0%	0%	**21%**	0%	**48%**	0%	2%
5/17/01	SPS	nearshore	46	0%	17%	0%	**68%**	0%	3%	0%	12%	0%	0%
5/31/01	SPS	nearshore	53	0%	**83%**	17%	0%	0%	0%	0%	0%	0%	0%
6/14/01	SPS	nearshore	67	0%	**23%**	0%	0%	0%	**36%**	0%	**41%**	0%	0%
NPS-2002chum			15-32										
4/23/02	NPS	delta	15	10%	0%	0%	0%	0%	19%	**70%**	1%	0%	0%
4/23/02	NPS	nearshore	22	0%	**34%**	**33%**	0%	0%	**20%**	2%	1%	0%	10%
5/10/02	NPS	nearshore	32	0%	0%	17%	0%	1%	18%	18%	**20%**	0%	**26%**
NPS-2002neritic													
7/10/02	NPS	NERITIC	15-32	0%	0%	0%	0%	0%	**33%**	0%	**67%**	0%	0%
SPS-2002chum			37-57										
5/15/02	SPS	delta	37	0%	**25%**	0%	0%	0%	**39%**	0%	**32%**	0%	4%
5/22/02	SPS	nearshore	44	0%	**47%**	0%	**26%**	3%	10%	14%	0%	0%	0%
6/4/02	SPS	nearshore	57	1%	**45%**	0%	0%	0%	**25%**	1%	8%	6%	13%
SPS-2002neritic													
6/12/02	SPS	NERITIC	37-57	0%	6%	0%	7%	0%	4%	0%	**82%**	0%	1%

Table 3.2d. Diet composition (wet weight proportions) for pink salmon cohorts.

DATE	REGION	ZONE	SIM DAY	Barnacle larvae	Calanoid copepod	Euphausiid	Harpacticoid copepod	Insect	Larvacean	Mysid	Other inverterate
NPS-pink			15-32								
4/23/02	NPS	delta	15	19%	0%	0%	**39%**	**38%**	0%	0%	4%
4/23/02	NPS	nearshore	20	0%	**27%**	0%	**50%**	3%	**20%**	0%	0%
5/10/02	NPS	nearshore	32	3%	**58%**	0%	**18%**	0%	0%	0%	**21%**
NPS-neritic											
6/11/02	NPS	NERITIC	15-32	0%	0%	0%	0%	0%	**100%**	0%	0%
SPS-pink			57-72								
6/4/02	SPS	delta	57	0%	**24%**	6%	19%	4%	**33%**	0%	14%
6/4/02	SPS	nearshore	62	0%	**52%**	0%	11%	0%	**24%**	0%	13%
6/19/02	SPS	nearshore	72	0%	**32%**	8%	**29%**	0%	**22%**	10%	0%
SPS-neritic											
6/12/02	SPS	NERITIC	57-62	0%	2%	4%	0%	6%	**87%**	0%	1%

Table 3.3. Gross caloric density (J/g wet weight) values for salmonid prey organisms.

Prey (group)	**Energy density J/g (ww)**	**Indigestible fraction (%)**	**Sample Area**	**Reference**	**Comments**
Barnacle larvae/slough	2045	10	Newport River estuary, NC	Thayer et al. 1973	
Calanoid copepod	2625	9	N. Pacific and Bering Sea	Davis et al. 1998	*Neocalanus cristatus*
Crab larvae	2981	10	Bristol Bay	Davis 1993*	Crab zoea
Cumacean	3243	10			Average of crustacean prey
Euphausiid	3111	10	N. Pacific and Bering Sea	Davis et al. 1998	*Thysanoessa spp.*
Gammarid amphipod	4408	12	NW Atlantic	Davis 1993*	Average for gammaridea and amphipods
Harpacticoid copepod	3811	9	Bristol Bay	Boldt and Haldorson 2002*	
Hyperiid amphipod	2466	13	Bering Sea	from Davis et al. '98	July 1992-1995
Insect	5311	10	Salmon River estuary, OR	A. Gray, 2002, University of Washington, unpublished data	Average of adult insects eaten by salmon in a Pacific NW estuary
Isopod	3391	10	NW Atlantic	Davis 1993*	For lowest gammarid value
Larvacean	3233	10	N. Pacific	Davis et al. 1998; Boldt and Haldorson 2002*	For appendicularians
Ostracod	2586	10	NE Atlantic	Boldt and Haldorson 2002*	
Other fish	4743	9	WA; AK	this study; Boldt and Haldorson 2002	Average of juvenile salmon and larval sand lance
Other invertebrate	3115-3321	10			Average of other non-insect invertebrates in diets
Polychaete	3186	13	NW Atlantic	Davis 1993*	Mean of 2 reported values
Salmon - juvenile	4171	9	Prince WilliamSound, AK	Boldt and Haldorson 2002	Average of pink salmon fry and smolts sampled in 1998
Sand lance - larval	5315	5	N. Puget Sound[1]	this study	June 2002; 25-40mm FL
Shrimp/mysid	4352	10	NW Atlantic	Davis 1993*	Average for *Mysis stenoiepis* and Caridean shrimp

*literature values are summarized in this reference; this is not the original author

[1] N Puget Sound is Possession Sound/Port Susan

Table 3.4. Puget Sound growth simulations for chinook, coho, chum and pink salmon run using the bioenergetics model during 2001-2002 in NPS and SPS.

G is total growth, C is total consumption, p is the proportion of maximum consumption.

G (mm/d) refers to daily growth in FL and g.e. is the growth efficiency (g G/g C).

CHINOOK

Type of simulation	Cohort	Start date	Duration	Start wt.	End wt.	G (g)	G (mm/d)	p	C (g)	g.e.(%)
fit to end wt.	NPSchk-May2001	1-May-01	28 days	4.01	6.14	2.13	0.39	0.49	13.63	16%
fit to end wt.	NPSchk-July2001	10-Jul-01	14 days	8.37	11.42	3.05	0.71	0.72	16.75	18%
fit to end wt.	SPSchk-May2001	17-May-01	28 days	6.37	8.37	2.00	0.29	0.49	17.03	12%
fit to end wt.	SPSchk-July2001	26-Jul-01	14 days	12.46	15.56	3.10	0.57	0.81	24.04	13%
fit to end wt.	NPSchk-May2002	21-May-02	21 days	4.01	6.37	2.36	0.57	0.66	13.94	17%
fit to end wt.	NPSchk-July2002	2-Jul-02	28 days	5.38	10.59	5.21	0.72	0.74	28.34	18%
fit to end wt.	SPSchk-May2002	15-May-02	21 days	7.07	9.81	2.74	0.48	0.67	18.63	15%
fit to end wt.	SPSchk-July2002	3-Jul-02	28days	6.60	12.46	5.86	0.71	0.86	36.76	16%
fit to end wt.	NPS-unmarked diet	2-Jul-02	20 days	4.15	8.67	4.52	1.02	0.87	20.34	22%
fit to end wt.	NPS-hatchery diet	2-Jul-02	20 days	5.90	10.43	4.53	0.86	0.83	23.28	19%
fit to end wt.	SPS-unmarked diet	21-May-02	15 days	5.50	7.29	1.79	0.53	0.65	10.81	17%
fit to end wt.	SPS-hatchery diet	21-May-02	15 days	6.60	8.73	2.13	0.55	0.70	13.39	16%
constant p, 11ºC	NPS diet 2001	19-Apr-01	110 days	4.91	33.99	29.08	0.63	0.68	150.27	19%
constant p, 11ºC	NPS diet 2002	23-Apr-02	140 days	4.91	55.59	50.68	0.68	0.68	231.99	22%
constant p, 11ºC	NPS neritic diet	23-Apr-02	140 days	4.91	107.69	102.78	0.97	0.68	359.30	29%
constant p, 11ºC	SPS diet 2001	8-May-01	93 days	4.91	21.30	17.20	0.52	0.68	102.02	16%
constant p, 11ºC	SPS diet 2002	18-Apr-02	146 days	4.91	43.57	38.66	0.56	0.68	223.95	17%
constant p, 11ºC	SPS neritic diet	18-Apr-02	146 days	4.91	45.67	40.76	0.58	0.68	226.40	18%
constant p, diet	NPS temp 2001	19-Apr-01	154 days	4.91	29.73	24.82	0.41	0.68	226.17	11%
constant p, diet	NPS temp 2002	9-Apr-02	154 days	4.91	29.86	24.95	0.41	0.68	226.22	11%
constant p, diet	SPS temp 2001	19-Apr-01	154 days	4.91	33.29	28.38	0.44	0.68	215.81	13%
constant p, diet	SPS temp 2002	9-Apr-02	154 days	4.91	35.76	30.85	0.46	0.68	233.87	13%

Table 3.4. (continued)

COHO

Type of simulation	Cohort	Start date	Duration	Start wt.	End wt.	G (g)	G (mm/d)	p	C (g)	g.e.(%)
fit to end wt.	NPS-2001coho	29-May-01	18 days	7.84	10.38	2.54	0.53	0.59	15.22	17%
fit to end wt.	SPS-2001coho	17-May-01	16 days	5.36	6.64	1.28	0.40	0.45	7.48	17%
fit to end wt.	NPS-2002coho	10-May-02	12 days	9.19	11.66	2.47	0.73	0.54	9.77	25%
fit to end wt.	SPS-2002coho	18-Apr-02	28 days	15.74	23.25	7.51	0.59	0.55	33.12	23%
to p-value	NPS-2002coho-cwt	10-May-02	18 days	9.19	13.44	4.25	0.76	0.54	15.49	26%
to p-value	SPS-2002coho-cwt	18-Apr-02	16 days	15.74	19.75	4.01	0.60	0.55	17.52	23%
fit to end wt.	NPS-neritic	10-May-02	18 days	9.19	13.44	4.25	0.76	0.68	19.56	21%
fit to end wt.	SPS-neritic	18-Apr-02	16 days	15.74	19.75	4.01	0.60	0.67	21.22	19%

CHUM

Type of simulation	Cohort	Start date	Duration	Start wt.	End wt.	G (g)	G (mm/d)	p	C (g)	g.e.(%)
fit to end wt.	NPS-2001chum	1-May-01	22 days	0.60	1.48	0.88	0.63	0.36	2.18	40%
fit to end wt.	SPS-2001chum	17-May-01	28 days	1.82	3.89	2.07	0.55	0.48	7.86	26%
fit to end wt.	NPS-2002chum	23-Apr-02	18 days	0.36	1.14	0.78	0.94	0.54	1.97	40%
fit to end wt.	SPS-2002chum	15-May-02	21 days	0.48	1.36	0.88	0.79	0.52	2.58	34%
fit to end wt.	NPS-neritic	23-Apr-02	18 days	0.36	1.14	0.78	0.94	0.57	2.06	38%
fit to end wt.	SPS-neritic	15-May-02	21 days	0.48	1.36	0.88	0.79	0.53	2.62	34%

Table 3.4. (continued)

PINK

Type of simulation	Cohort	Start date	Duration	Start wt.	End wt.	G (g)	G (mm/d)	p	C (g)	g.e.(%)
fit to end wt.	NPS-pink	23-Apr-02	18 days	0.32	0.57	0.25	0.35	0.32	0.84	30%
fit to end wt.	SPS-pink	4-Jun-02	16 days	3.02	3.89	0.87	0.33	0.36	3.84	23%
fit to end wt.	NPS-sps-size	23-Apr-02	18 days	3.02	3.89	0.87	0.29	0.30	3.61	24%
fit to end wt.	SPS-nps-size	4-Jun-02	16 days	0.32	0.57	0.25	0.40	0.37	0.89	28%
fit to end wt.	NPS-spsdiet	23-Apr-02	18 days	0.32	0.57	0.25	0.35	0.34	0.88	28%
fit to end wt.	SPS-npsdiet	4-Jun-02	16 days	3.02	3.89	0.87	0.33	0.33	3.62	24%
fit to end wt.	NPS-neritic	23-Apr-02	18 days	0.32	0.57	0.25	0.35	0.33	0.86	29%
fit to end wt.	SPS-neritic	4-Jun-02	16 days	3.02	3.89	0.87	0.33	0.34	3.63	24%

Table 3.5. Simulated predation by juvenile coho and chinook salmon on juvenile pink and chum salmon in Puget Sound during 2002.

Diet for coho was 67% salmon, 33% other invertebrates.

Diet for chinook was 19% salmon, 21% insects, 60% other invertebrates.

Type of simulation	cohort	Start date	Duration	Start wt.	G (g)	G (mm/d)	C (g)	g.e.(%)o	C (g salmon/d)	# salmon*/d
to p=0.55	NPS coho	10-May-02	18 days	9.19	3.45	0.64	15.59	22%	0.61	1.0-2.0
to p=0.55	SPS coho	18-Apr-02	16 days	15.74	3.98	0.60	17.39	23%	0.78	1.3-2.6
to p=0.67	NPS chinook	1-May-02	14 days	4.91	1.95	0.65	9.90	20%	0.13	0.2-0.4
to p=0.67	SPS chinook	1-May-02	14 days	4.91	1.85	0.62	9.07	20%	0.12	0.2-0.4

*Assuming each salmon = 0.3-0.6g, the average size of pink and chum salmon during peak catches

SUMMARY AND CONCLUSIONS

SUMMARY

CATCH TIMING

- Water was consistently warmer and less saline at NPS sites than at SPS sites. Delta sites had lower salinities and more variable water temperatures than nearshore and neritic sites.
- The timing of peak catches was similar at delta and nearshore sites within sampling regions but differed between NPS and SPS sites.
- During April-September sampling seasons in 2001 and 2002, the majority of juvenile salmon were caught between April and June (pink and chum salmon generally peaking earlier than chinook and coho salmon), with most peak catches in May. A second peak for chinook salmon occurred during July in NPS.
- Peak catches of all juvenile salmon species in neritic waters occurred in June at SPS sites.
- Peak catches for chum and chinook salmon were greater at SPS than NPS sites in both years, whereas coho and pink salmon catches were greater at NPS sites.

  With the exception of NPS chum salmon, total and peak catches of each species were greater in 2002 than 2001.
- The proportions of hatchery coho and chinook salmon to unmarked conspecifics were much greater in SPS than NPS in both years.

SIZE

- Mean sizes of juvenile salmon were slightly but consistently smaller at NPS than at SPS sites and at delta versus nearshore and neritic sites.
- Overall, chinook and chum salmon were larger in 2001 than 2002, although there was no consistent difference in sizes between 2001 and 2002 for all species and between regions.

- Overall, hatchery coho and chinook salmon were larger than their unmarked counterparts.

DIET

- Prey composition differed markedly between NPS (predominately insects) and SPS (predominately planktonic crustaceans) sites, likely a result of substantially higher freshwater inputs to NPS.
- Diel feeding chronologies indicated that juvenile salmon fed most actively during daylight, but diet composition changed between light and dark periods.
- In general, juvenile salmon shifted from predominantly epibenthic feeding in April-May and at delta sites to more planktonic and neustonic feeding during June-July and at nearshore marine and neritic sites.
- Epibenthic and planktonic copepods and larvaceans were the primary prey for pink and chum salmon. Chum and pink salmon ate predominantly planktonic prey during daylight, but shifted to epibenthic prey during and after dusk.
- Epibenthic and planktonic crustaceans, including gammarid amphipods, crab larvae, euphausiids, and shrimp (primarily hippolyttid and pandalid), were the major prey for coho salmon, whereas insects and fish prey were episodically important.
- Chinook salmon fed mainly on insects in NPS, and on crab larvae, euphausiids and hyperiid amphipods in SPS.
- Fish constituted only 5-10% of the diet for chinook and coho salmon <200mm FL, but piscivory increased with size. Larger chinook and coho salmon became more piscivorous at crepuscular and post-dusk hours, feeding mainly on sand lance and juvenile salmon (pink and chum) in April-June.
- For chinook and coho salmon, diet composition was similar between hatchery and unmarked fish.

CONSUMPTION DEMAND

- Weekly consumption demand for each salmon species was higher at SPS than at NPS sites.

- There was a higher consumption demand for insects and fish at NPS sites than at SPS sites.
- Hatchery chinook salmon at NPS sites consumed more prey (by weight in grams) per week than unmarked chinook salmon.
- In a preliminary examination of intrageneric predation by coho and chinook salmon on pink/chum salmon (33-43mm FL), I estimated that an individual juvenile coho salmon (100-130mm FL) consumed 1-2 pink/chum salmon per day, while a chinook salmon (80-90mm FL) consumed one pink/chum salmon every 2.5-5 days.

GROWTH PERFORMANCE

- Overall, growth performance for peak juvenile salmon cohorts was lower but more constant in SPS than in NPS, and higher in 2002 versus 2001, driven primarily by the higher proportions of energy rich adult insects consumed in NPS and in SPS in 2002.
- In NPS, pink and chum salmon experienced the highest growth efficiencies in April, whereas coho salmon had the highest growth efficiencies in mid to late May.
- Modeled chinook salmon cohorts experienced variable feeding conditions with peaks in growth efficiencies both in May and July. Simulated growth efficiencies for chinook salmon were, however, lower than for other salmon, particularly in May when relative abundances of the other salmon species were highest.
- While there were no differences between growth performance of unmarked and hatchery chinook salmon in SPS, unmarked chinook salmon in NPS experienced higher growth rates and efficiency than hatchery counterparts.
- Diet quality for chinok and pink salmon may be more favorable in neritic environments as nearshore foraging conditions decline.
- Increasing spring water temperatures, which approached the upper limits of thermal tolerances for salmon in NPS, may have caused decreased growth efficiencies for salmon nearshore, particularly at peak temperatures in July.

CONCLUSIONS

- Juvenile salmon occupy nearshore Puget Sound waters between at least April-September. Extended species residence times (their seasonal duration in the catches) suggest that nearshore environments may be particularly important to chinook salmon in NPS, and to chum salmon in SPS.
- Juvenile salmon at SPS sites were larger than those at NPS sites, partly due to differences in the magnitude of hatchery inputs.
- The potential for dietary overlap was greatest between juvenile pink and chum salmon, between chinook and coho salmon of a similar size, and between hatchery and unmarked chinook salmon.
- Juvenile and subadult chinook and coho salmon have the potential to be significant predators on smaller juvenile salmon (pink and chum salmon mainly, but also chinook salmon) during peak outmigration pulses.
- Foraging conditions for juvenile salmon were dynamic, varying spatially, annually, and seasonally.
- Insects provide a high quality prey resource at sites in NPS, but fluctuations in diets and water temperatures produced variable growth conditions for juvenile salmon at those sites.
- The greater consistency of foraging conditions and water temperatures at sites in SPS led to more consistent growth conditions at those sites.
- Due to spatial and temporal differences in the forage base and environmental conditions, the timing and location for juvenile salmon entering Puget Sound may influence their early marine growth (e.g. high but variable, or moderate but constant) and ultimately survival.

FUTURE WORK

This study was intended as an initial examination of juvenile salmon trophic dynamics in Puget Sound. Future studies will be needed to target key uncertainties, and increase the understanding of juvenile salmon ecology in Puget Sound. These include:

1) Measuring individual and average residence times and actual growth of juvenile salmon in Puget Sound to obtain more realistic consumption estimates for growing salmon.
2) Increased spatial coverage including offshore sampling will be needed to determine where salmon habitats salmon occupy, in particular elucidating the nearshore-offshore usage patterns. Coordination with similar ongoing projects in Puget Sound will be a very important way to broaden spatial and topical coverage. Diet comparisons are available between historic, literature values, and concurrently from other regions including: nearshore marine areas in central PS (King County), offshore areas in central Puget Sound (DFO, Canada), nearshore and offshore Skagit Bay (NMFS Mukilteo), Shilshole Bay (Army Corps), and Sinclair Inlet (WDFW).
3) Measurements of food supply and availability will be needed to consider questions of food limitation and carrying capacity.
4) Determining abundances of predator populations and conducting a more intensive predation study will help attain a better estimate of potential predation pressure.
5) Expand to the broader food web: Declines have also been observed in at least seven other marine fish in Puget Sound (Pacific herring – *Clupea harengus pallasi*, Pacific cod – *Gadus macrocephalus,* Pacific hake – *Merluccius productus*, walleye pollock – *Theragra chalcogramma*, brown rockfish – *Sebastes auriculatus*, copper rockfish – *S. caurinus*, and quillback rockfish) which include potential competitors, prey, and predators of larval and juvenile salmon.

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APPENDIX A: ADDITIONAL TABLES FOR CHAPTER II

Table A.2.1. Wet weight proportions of major prey items for unmarked and hatchery age-0 chinook salmon in Puget Sound during 2001 and 2002.

YEAR	MONTH	REGION	n	FL (mm)	se	ORIGIN	Barnacle larvae	Copepod	Crab larvae	Euphausiid	Gammarid amphipod	Hyperiid amphipod	Insect	Isopod	Other invertebrate	Polychate	Shrimp	Fish TOTAL
2001	April	NPS	10	65.60	2.64	unmarked	0%	0%	1%	6%	0%	0%	**88%**	4%	0%	0%	0%	0%
2001	May	NPS	46	80.39	2.54	unmarked	8%	0%	19%	5%	**20%**	0%	**31%**	0%	7%	3%	4%	3%
2001	June	NPS	19	85.16	2.86	unmarked	0%	0%	5%	8%	17%	0%	**58%**	4%	4%	0%	4%	0%
2001	July	NPS	48	97.65	1.29	unmarked	12%	0%	10%	1%	9%	2%	**47%**	0%	15%	0%	0%	4%
2001	August	NPS	18	103.39	1.69	unmarked	19%	0%	4%	0%	15%	0%	**49%**	2%	5%	3%	3%	0%
2001	September	NPS	1	126.00		unmarked	0%	0%	0%	0%	**41%**	0%	**33%**	0%	0%	0%	**26%**	0%
2001	April	NPS	1	81.00		hatchery	0%	0%	0%	0%	**100%**	0%	0%	0%	0%	0%	0%	0%
2001	May	NPS	3	64.33	13.69	hatchery	0%	0%	0%	0%	0%	0%	**54%**	0%	**34%**	0%	0%	12%
2001	July	NPS	41	98.29	1.16	hatchery	8%	0%	7%	4%	13%	0%	**34%**	1%	**23%**	5%	0%	5%
2001	August	NPS	4	114.75	3.73	hatchery	12%	0%	13%	0%	**50%**	0%	**25%**	0%	0%	0%	0%	0%
2001	September	NPS	2	126.50	3.50	hatchery	0%	0%	0%	0%	0%	0%	**50%**	0%	0%	0%	**50%**	0%
2001	May	SPS	52	85.88	1.74	unmarked	0%	8%	**26%**	4%	8%	0%	15%	0%	14%	18%	1%	6%
2001	June	SPS	14	86.29	2.00	unmarked	0%	13%	**26%**	3%	9%	0%	15%	3%	16%	11%	3%	1%
2001	July	SPS	28	104.68	1.57	unmarked	3%	0%	7%	**40%**	6%	15%	8%	0%	10%	8%	3%	0%
2001	August	SPS	3	108.33	2.33	unmarked	0%	0%	2%	0%	**26%**	**33%**	5%	**34%**	0%	0%	0%	0%
2001	May	SPS	31	85.97	1.29	hatchery	8%	0%	15%	**24%**	14%	1%	4%	2%	10%	**20%**	2%	0%
2001	June	SPS	18	93.39	4.14	hatchery	1%	0%	**28%**	**29%**	6%	0%	9%	0%	12%	12%	2%	1%
2001	July	SPS	16	109.81	2.78	hatchery	1%	6%	14%	**40%**	7%	**22%**	5%	0%	0%	1%	4%	0%
2001	August	SPS	1	128.00		hatchery	3%	0%	0%	0%	0%	**97%**	0%	0%	0%	0%	0%	0%
2001	September	SPS	3	123.33	2.91	hatchery	0%	0%	16%	**26%**	5%	**36%**	17%	0%	0%	0%	0%	0%

Table A.2.1. (continued)

YEAR	MONTH	REGION	n	FL (mm)	se	ORIGIN	Barnacle larvae	Copepod	Crab larvae	Euphausiid	Gammarid amphipod	Hyperiid amphipod	Insect	Isopod	Other invertebrate	Polychate	Shrimp	Fish TOTAL
2002	May	NPS	18	80.11	2.47	unmarked	4%	2%	17%	7%	13%	4%	**37%**	0%	9%	2%	0%	6%
2002	June	NPS	14	74.36	3.05	unmarked	13%	4%	2%	1%	8%	0%	**47%**	0%	9%	13%	2%	0%
2002	July	NPS	32	84.22	2.03	unmarked	9%	0%	4%	3%	12%	1%	**55%**	0%	7%	0%	3%	6%
2002	August	NPS	11	100.45	3.21	unmarked	5%	0%	4%	0%	17%	0%	**45%**	0%	14%	0%	0%	14%
2002	September	NPS	4	113.50	3.50	unmarked	12%	0%	0%	2%	0%	0%	**65%**	0%	12%	0%	0%	9%
2002	April	NPS	1	44.00		hatchery	0%	4%	0%	0%	0%	0%	0%	0%	0%	**96%**	0%	0%
2002	May	NPS	9	84.44	2.22	hatchery	**29%**	0%	5%	0%	18%	0%	15%	4%	**20%**	8%	1%	0%
2002	July	NPS	30	91.27	1.88	hatchery	11%	0%	2%	3%	18%	0%	**43%**	1%	18%	0%	0%	3%
2002	August	NPS	5	108.40	3.01	hatchery	6%	0%	**26%**	4%	**42%**	0%	17%	0%	4%	0%	0%	0%
2002	April	SPS	5	75.40	3.44	unmarked	0%	9%	0%	11%	**49%**	0%	6%	0%	0%	0%	0%	**25%**
2002	May	SPS	11	81.73	3.44	unmarked	6%	0%	**20%**	**33%**	18%	0%	1%	0%	18%	1%	0%	3%
2002	June	SPS	13	87.00	2.06	unmarked	8%	1%	6%	0%	**23%**	0%	4%	4%	15%	**22%**	0%	17%
2002	July	SPS	11	94.55	3.88	unmarked	6%	0%	6%	1%	3%	4%	**29%**	3%	**29%**	16%	0%	3%
2002	August	SPS	9	108.22	2.90	unmarked	0%	0%	11%	12%	**22%**	7%	**22%**	7%	16%	2%	0%	1%
2002	September	SPS	3	120.67	4.67	unmarked	0%	0%	1%	2%	18%	4%	**51%**	0%	0%	0%	**24%**	0%
2002	May	SPS	36	92.25	1.62	hatchery	3%	9%	**39%**	**25%**	8%	0%	1%	0%	2%	7%	0%	6%
2002	June	SPS	56	95.63	1.45	hatchery	1%	7%	**41%**	11%	3%	0%	19%	0%	7%	9%	0%	2%
2002	July	SPS	14	104.50	2.12	hatchery	8%	1%	**36%**	1%	1%	7%	**20%**	0%	12%	7%	6%	0%
2002	August	SPS	8	113.00	2.52	hatchery	0%	0%	**30%**	**25%**	13%	7%	18%	2%	4%	0%	0%	0%

Table A.2.2. Wet weight proportions of major prey items for unmarked and hatchery juvenile coho salmon in Puget Sound during April-June, 2001 and 2002.

Year	Month	REGION	n	FL(mm)	se	ORIGIN	Barnacle larvae	Copepd	Crab larvae	Euphausiid	Gammarid amphipod	Hyperiid amphipod	Insect	Isopod	Mysid/ shrimp	Ostracod	Other invertebrate	Polychaete	Fish TOTAL
2001	May	NPS	31	104.20	2.07	unmarked	10%	0%	13%	0%	**43%**	0%	9%	4%	0%	0%	**21%**	0%	0%
2001	June	NPS	2	147.00	1.00	unmarked	0%	0%	**95%**	3%	1%	0%	0%	0%	0%	1%	0%	0%	0%
2001	May	NPS	7	132.33	6.48	hatchery	0%	0%	14%	7%	0%	4%	**36%**	**29%**	0%	10%	0%	0%	0%
2001	May	SPS	12	94.01	7.19	unmarked	0%	1%	**25%**	8%	0%	0%	0%	0%	**58%**	0%	8%	0%	0%
2001	June	SPS	3	127.67	6.23	unmarked	3%	0%	11%	0%	**24%**	0%	0%	1%	15%	5%	0%	**40%**	0%
2001	May	SPS	6	109.68	16.10	hatchery	1%	0%	**33%**	0%	4%	1%	0%	0%	**50%**	0%	0%	11%	0%
2001	June	SPS	4	122.50	18.98	hatchery	0%	0%	**67%**	0%	5%	0%	9%	0%	17%	2%	0%	0%	0%
2002	April	NPS	2	33.50	0.50	unmarked	0%	0%	0%	0%	**66%**	0%	**34%**	0%	0%	0%	0%	0%	0%
2002	May	NPS	16	109.56	3.38	unmarked	2%	0%	0%	0%	**48%**	0%	9%	0%	1%	0%	8%	10%	**22%**
2002	June	NPS	14	108.71	5.66	unmarked	4%	1%	1%	0%	**48%**	0%	14%	1%	0%	0%	12%	4%	15%
2002	April	NPS	2	136.50	1.50	hatchery	0%	0%	0%	1%	19%	0%	1%	1%	0%	0%	0%	0%	**77%**
2002	May	NPS	8	143.38	1.90	hatchery	0%	0%	0%	0%	**41%**	0%	0%	0%	0%	0%	12%	**47%**	0%
2002	June	NPS	1	135.00		hatchery	0%	0%	0%	0%	**100%**	0%	0%	0%	0%	0%	0%	0%	0%
2002	April	SPS	8	129.00	5.21	unmarked	0%	0%	7%	12%	**41%**	0%	**25%**	7%	0%	0%	6%	0%	0%
2002	May	SPS	10	126.80	4.13	unmarked	0%	4%	2%	**48%**	3%	0%	1%	0%	**20%**	0%	0%	5%	17%
2002	June	SPS	8	119.13	4.73	unmarked	0%	1%	**45%**	0%	14%	0%	8%	0%	19%	0%	0%	12%	0%
2002	April	SPS	9	118.56	1.31	hatchery	0%	**23%**	10%	0%	**58%**	0%	3%	0%	0%	0%	0%	6%	0%
2002	May	SPS	15	132.53	5.76	hatchery	11%	5%	**23%**	6%	4%	0%	6%	0%	**41%**	0%	0%	0%	5%
2002	June	SPS	4	148.50	8.54	hatchery	0%	2%	**80%**	16%	0%	0%	0%	0%	0%	0%	1%	0%	0%