Early Marine Growth and Consumption Demand of Juvenile Pink Salmon in Prince William Sound and the Northern Coastal Gulf of Alaska

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This is to certify that I have examined this copy of a doctoral dissertation by

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ABSTRACT

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Although early marine growth has repeatedly been correlated with overall survival for Pacific salmon (*Oncorhynchus* spp.), we currently lack a mechanistic understanding of the timing, magnitude, and source of stage-specific mortality periods. Pink salmon (*O. gorbuscha*) are a key plankton consumer in Prince William Sound and the Gulf of Alaska, and hatchery production significantly increases their abundance in this region. This study combined within-season back-calculations of growth and bioenergetics techniques to examine interannual variability in the growth performance and consumption demand of the average hatchery, average wild, and surviving hatchery juvenile pink salmon during the first summer at sea in Prince William Sound and the northern coastal Gulf of Alaska among years corresponding to low marine survival (3% in 2001 and 2003) and high marine survival (9% in 2002, 8% in 2004). Juvenile pink salmon were consistently larger throughout the summer and early fall of 2002 and 2004 than in 2001 and 2003, indicating that larger, faster-growing juvenile pink salmon experienced higher survival. All cohorts ate a larger proportion of their theoretical maximum consumption and consumed more prey during 2002 than during 2001 and 2003 while feeding predominantly on the pteropod *Limacina helicina*. Unmarked "wild" juvenile pink salmon were significantly larger than hatchery fish during low-survival years, but no significant difference was observed during high-survival years. Pink salmon that survived to adulthood were larger at circuli, grew faster, and consumed more prey than the average juvenile. The localized standing stock biomass of key prey exceeded the daily consumption demand of juvenile pink salmon during July–August; however, estimated prey biomass was not enough to sustain the high level of consumption required to satisfy observed growth. The high percentage of prey biomass consumed, low feeding rates during May–July, a mid-summer decrease in circulus spacing and growth efficiency, and the fact that growth and consumption rates were much higher for all cohorts in high-survival years and for surviving cohorts in all years indicate that pink salmon are food limited in Prince William Sound and the coastal Gulf of Alaska during their first summer at sea.

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Chapter 1: Introduction

Background

Cause for Concern

Physical ocean conditions in the Gulf of Alaska can change rapidly and the entire marine ecosystem, including salmon production, responds accordingly (Francis and Hare 1994). The relationship between pink salmon (*Oncorhynchus gorbuscha*) and their environment, however, is poorly understood (Beamish et al. 1995). Appropriate management of pink salmon stocks requires a more detailed awareness of their connection to the ocean environment.

This study examines juvenile pink salmon distribution, growth, and consumption in Prince William Sound and the coastal Gulf of Alaska during their first summer at sea. A better understanding of the relationship between early ocean growth and survival, demand on the prey forage base, and effects on prey supply provides insight on questions of carrying capacity and can ultimately lead to improved management of our ocean resources.

Hatchery Augmentation

Pink salmon are the most abundant Pacific salmon species, and the Gulf of Alaska supports the largest pink salmon population in North America (Heard 1991). Significant hatchery input to Prince William Sound supplements natural production; Armin F. Koernig, Cannery Creek, Wally Noerenberg, and Solomon Gulch hatcheries have released a combined total of over 600 million fry since 2001 (Alaska Department of Fish and Game 2005; Table 1.1, Figure 1.1). These hatchery releases average over three times more fry than the natural production of approximately 190 million wild pink salmon fry migrating into Prince William Sound (S. Moffitt, Alaska Department of Fish and Game, personal communication). Whether sufficient prey are available in this region to absorb the additional consumption demand by hatchery juvenile pink salmon is unknown.

In 2002, the run size of Prince William Sound pink salmon was predicted to be 4.6 million wild and 26.3 million hatchery adults, for a total run of 30.9 million pink salmon (Moffitt 2002). Instead, the combined run totaled only 21.3 million pink salmon. Hatchery fish experienced 3.3% smolt-adult survival, and wild escapement was at its sixth lowest total since 1965, at only 943,000 (Eggers 2003; Table 1.1). The 2002 return provided a commercial harvest of 18.95 million—only the 16th largest single season harvest ever, and the lowest harvest since 1995 (Eggers 2003). The ratio of hatchery to wild fish in the total commercial common property harvest was 33:1 (Eggers 2003).

In 2003, predicted run sizes in Prince William Sound were 5.1 million wild and 25.1 million hatchery adults, for a total run of 30.2 million pink salmon (Merizon 2002). Instead, 56.9 million pink salmon returned during this year, for a record single season harvest of 51.1 million (Plotnick and Eggers 2004). The ratio of hatchery to wild fish in the total commercial common property harvest was 8:1 (Plotnick and Eggers 2004). Hatchery fish experienced 9.0% smolt-adult survival (Table 1.1), and wild escapement was 2.9 million, the second largest escapement since 1965 (Plotnick and Eggers 2004).

In 2004, the run size of pink salmon to Prince William Sound was predicted to be 4.6 million wild (Merizon 2003) and 36.1 million hatchery adults (Eggers 2005), for a return total of 40.7 million pink salmon. Returns to several hatcheries were significantly smaller than projected (Eggers 2005), and totaled 21.8 million pink salmon (White 2005). Hatchery fish experienced 3.3% smolt-adult survival (Table 1.1); estimates of wild escapement are not yet available (Eggers 2005). The 2004 pink salmon run provided a commercial harvest of approximately 23.6 million fish (Eggers 2005).

In 2005, run sizes were predicted to be 6.3 million wild pink salmon (Merizon 2004); no forecast was made for the hatchery return (Merizon 2004). Returns to several hatcheries were larger than average, totaling 30.3 million pink salmon (Prince William Sound Aquaculture Corporation 2005; K. Morgan, Valdez Fisheries Development Association, personal communication). Hatchery fish experienced 7.5% smolt-adult survival (Table 1.1); estimates of wild escapement are not available. The 2005 return provided a commercial harvest of 59 million pink salmon (Lewis and Hollowell 2005).

The run size of pink salmon to Prince William Sound has clearly varied widely in recent years and is difficult to accurately predict based on our current understanding of factors contributing to the survival of pink salmon. For stock enhancement to continue harmlessly, we must understand the physical and biological factors governing marine survival and production, including the spatial, temporal, and ecological overlap among stocks, habitat characteristics, juvenile salmon condition, and the prey forage base. Cooney and Brodeur (1998) contend that severe consequences may arise if we continue to augment salmonid stocks in the North Pacific Ocean before obtaining additional knowledge concerning the distribution of forage resources.

Early Marine Ecology of Pink Salmon

Wild pink salmon fry enter the marine waters of Prince William Sound directly after emergence, between mid-April and early June each year (Cooney 1993; Sharr et al. 1995). Prince William Sound hatcheries time the release of fry to coincide with the spring zooplankton bloom, which typically occurs in May (Cooney et al. 1995). Juvenile pink salmon migrate out of Prince William Sound to the coastal Gulf of Alaska by July or early August (Cooney 1993), move off the continental shelf by their first winter, and return to Prince William Sound the following summer as adults.

Pink salmon fry migrate to sea at a smaller size than any other salmonid (Quinn 2005). Wild fish enter Prince William Sound at approximately 0.26 g (Bailey et al. 1976; Boldt and Haldorson 2002), and the average weight at release for the 2001-2004 hatchery cohorts in Prince William Sound was 0.53 g, 0.56 g, 0.70 g, and 0.59 g, respectively (Alaska Department of Fish and Game 2005; Table 1.1). Throughout the summer and fall of their first year, pink salmon reside over the continental shelf and grow from roughly 7 g in July to larger than 90 g in October. Although juvenile pink salmon are thought to consume 7-8% of their body weight per day (Parker and LeBrasseur 1974), the amount of prey necessary to achieve this high amount of growth is unknown.

Juvenile pink salmon are highly vulnerable to predation during their first months in marine waters (Hunter 1959), and early mortality markedly affects adult year-class strength. The first weeks at sea are often referred to as a "critical period" for growth in the pink salmon's life cycle, since significant mortality occurs during this time (Parker 1968; Beamish and Mahnken 2001). Mortality rates for several Pacific salmon species have been estimated at 2-8% per day after ocean entry (Parker 1968; Fisher and Pearcy 1988), and drop to less than 1% per day later in life (Pearcy 1992).

Rapid growth can reduce size-selective predation mortality (Parker 1971; Hargreaves and LeBrasseur 1985; Heard 1991; Jaenicke and Celewycz 1994; Willette et al. 1999). Larger fish are thought to survive better than smaller individuals (Mortensen et al. 2000), and lower mortality is observed when fry are released at larger sizes or grow faster as juveniles (Willette 2001). A study of juvenile Chinook salmon (*O. tshawytscha*) showed that faster-growing smolts were of higher quality and had higher marine survival than slower-growing smolts, most likely due to their ability to escape size-selective predation (Beckman et al. 1999). Size-selective mortality of chum salmon (*O. keta*) has been observed during the time when the fish laid down circuli 2–4 on their scales (Healey 1982).

However, size and growth soon after ocean entry might not determine year-class strength in all years. Some studies suggest that smolt size relates poorly to early marine growth and survival (Bilton et al. 1982; Pearcy 1992), or that growth does not relate to survival in all years (Holtby et al. 1990; Mortensen et al. 2000). Mortality processes might also vary between species like yearling or older sockeye (*O. nerka*), coho (*O. kisutch*), and Chinook salmon or steelhead (*O. mykiss*) smolts, which are large relative to other salmonids, and pink, chum, or age-0 Chinook salmon smolts, which are small.

Some studies indicate that growth could become more important during the late fall and winter of the first year of marine life, when salmon face a second critical period (Beamish and Mahnken 2001). Salmon might not survive the winter if they do not achieve a threshold size by the end of their first summer at sea (Beamish and Mahnken 2001). Smolt-adult survival in coho (Briscoe et al. 2005) and pink salmon (Moss et al. 2005) is strongly affected by mortality after the first summer at sea.

Pink salmon likely undergo a significant two-stage mortality process, with the first mortality period occurring soon after ocean entry, and the second after the first growing season (Beamish and Mahnken 1999, 2001; Moss et al. 2005). Environmental and trophic factors, namely temperature and zooplankton prey availability, greatly affect pink salmon metabolism, growth and survival (Brett et al. 1969; Weatherly and Gill 1995; Orsi et al. 2000). The relative importance of initial marine mortality versus winter mortality can thus vary among years because of different initial conditions (e.g. juvenile size at entry) and different environmental conditions (e.g. temperature, prey availability) that influence distribution and growth during the first growing season.

Juvenile pink salmon feed primarily on small and large calanoid copepods in April and May (Parker 1997; Cooney et al. 2001b); small, surface zooplankton such as copepods, larvaceans, and pteropods during July and August; and shift to larger prey such as euphausiids, crab megalopae, amphipods, and fish by fall (Sturdevant et al. 1996; Armstrong et al. 2005). Other planktivorous fishes, including walleye pollock (*Theragra chalcogramma*), Pacific herring (*Clupea pallasii*), capelin (*Mallotus villosus*), eulachon (*Thaleichthys pacificus*), sand lance (*Ammodytes hexapterus*), and other salmonids, utilize these resources, as well. On account of such high dietary overlap and the large amount of juvenile pink salmon released each year, both inter- and intraspecific competition for food resources potentially influence the growth and subsequent survival of these species. Recent studies present evidence for the competitive dominance of pink salmon over other salmon species (Ruggerone et al. 2003; Ruggerone and Nielsen 2004). North American pink salmon significantly altered the abundance of prey available to other species of Pacific salmon, resulting in reduced consumption, growth, and survival (Ruggerone and Nielsen 2004). Asian pink salmon also appear to reduce the growth of Bristol Bay sockeye salmon during odd years, when Asian pink salmon are most abundant (Ruggerone et al. 2003).

Although early marine growth has repeatedly been correlated with overall survival in Pacific salmon (Holtby et al. 1990; Henderson and Cass 1991; Murphy et al. 1998; Tovey 1999; Willette et al. 1999; Mortensen et al. 2000; Beamish et al. 2004), we currently lack a mechanistic understanding of the timing, magnitude, and source of stage-specific marine survival. To some extent, prey availability, inter- and intraspecific competition, predation, smolt quality, and ocean conditions all influence growth and survival (Pearcy 1992; Brodeur et al. 2000). The specific role that each factor ultimately plays remains to be identified, and could vary within or among years.

Influences on Marine Growth and Survival

Carrying capacity is related to a species' density, food supply, and tolerance for environmental change, and the density of its competitors and predators (Orsi et al. 2000). Environmental conditions vary significantly on seasonal, interannual, and decadal scales and influence carrying capacity over time. Temporal variation in pink salmon survival rates might be affected by environmental processes that operate at regional rather than ocean-wide spatial scales (Pyper et al. 2001; Mueter et al. 2002).

Coastal oceanographic conditions influence salmon habitat quality, growth, and levels of inter- and intraspecific competition, and thus influence the strength of density-dependence and carrying capacity for juvenile salmonids (Cooney and Brodeur 1998; Mortensen et al. 2000). Ocean conditions can therefore strongly affect, even regulate, salmonid stock productivity (Brodeur et al. 2000). However, we have a limited understanding of how changes in ocean conditions mechanistically relate to the marine ecology of salmon.

Growth rate depends on both the inherent growth potential of a fish and environmental limitations on growth rate imposed by habitat (Brandt et al. 1992). Both biological (prey abundance, species composition, and size structure) and physical (temperature, dissolved oxygen, light intensity, and turbidity) characteristics best indicate habitat quality (Mason et al. 1995). Temperature and zooplankton prey availability in particular can greatly affect pink salmon metabolism, growth and survival (Brett et al. 1969; Weatherly and Gill 1995; Orsi et al. 2000).

A strong positive relationship exists between temperature and early marine growth in salmonids (Weatherly and Gill 1995; Downton and Miller 1998; Mortensen et al. 2000; Orsi et al. 2000). Sea surface temperature has been shown to influence adult size, as well (Rogers and Ruggerone 1993). Prey biomass also appears to affect juvenile pink salmon performance and survival (Perry et al. 1996). Growth has been shown to decrease with decreasing zooplankton biomass (Orsi et al. 2000), and may be limited by prey abundance in early spring (Mortensen et al. 2000). When juveniles enter the marine environment in years of high zooplankton biomass, adult survival is correspondingly higher. In one recent study, however, growth did not consistently correlate with prey biomass (Orsi et al. 2000). Some combination of ideal temperatures and high prey availability encourages growth and allows more juveniles to escape size-selective mortality (Parker 1971; Holtby et al. 1990).

Pink salmon struggle against size-selective predation throughout their juvenile stage. Size at release may influence survival to adulthood more than juvenile growth (Willette et al. 1999; Willette 2001). A larger size at hatchery release decreases risk of predation over the subsequent growth period; hatchery fish are, for this reason, less vulnerable to predators during their first 60 days at sea than are wild salmon (Willette 2001). Both larger and smaller pink salmon fry might be extremely vulnerable to predation, since fry that grow larger initially can be too large for smaller predators, but in the preferred size range for larger predators (Cooney et al. 2001b).

Fish often balance predation risk with foraging rate by feeding at light levels low enough to reduce vulnerability to predators, but not so low that prey detection decreases beyond a reasonable level (Eggers 1978; Clark and Levy 1988). The greatest growth has been found to coincide with a long or increasing photoperiod, perhaps due to a longer feeding period (Brett 1979) or overall high seasonal productivity. Pink salmon in the Gulf of Alaska feed predominantly during daylight hours in the upper water column (Armstrong et al. 2005). Light levels should therefore not limit feeding, but could affect predation risk.

When zooplankton biomass is low, walleye pollock and post-spawning Pacific herring, which are the most abundant fish species in Prince William Sound and overlap spatially and temporally with juvenile pink salmon, switch prey from zooplankton to small fish, including juvenile pink salmon (Willette et al. 2001). Additionally, when zooplankton density is low, juvenile salmon disperse from nearshore to offshore habitats for access to more food and consequently further increase their predation risk (Willette 2001). Size-dependent mortality is rather intense when juvenile salmon migrate to offshore environments (Willette 2001). This increase in piscivorous feeding by other fishes in years with reduced zooplankton thus affects the early marine survival of pink salmon in Prince William Sound and perhaps other regions.

The average body size of pink salmon has been declining for several decades. Reduced average body size has likely decreased overall productivity via a reduction in average fecundity. Wertheimer et al. contend that although ocean conditions primarily drive pink salmon spawner abundance and productivity (2004a), large-scale enhancement in Prince William Sound has contributed to reduced body size due to density dependent growth in the Gulf of Alaska (2004b). They also state that, despite the ecological costs, hatchery releases in Prince William Sound have led to a net benefit in production and have not reduced wild stock productivity (Wertheimer et al. 2001; Wertheimer et al. 2004a). Hilborn and Eggers (2000), on the other hand, argue that hatchery pink salmon have replaced rather than augmented wild stocks. Farley and Carlson (2000) suggest that coastal waters of the Gulf of Alaska could be food limiting, and express concerns about density dependent growth when juvenile pink salmon first emigrate from Prince William Sound.

Although changes in both ocean conditions and the density of juvenile salmon cause changes in carrying capacity (Beamish et al. 1995; Beamish and Mahnken 1999), it is difficult to separate the effects of each on growth and survival (Brandt et al. 1992). Climate change may either mask or add to the effects of density-dependent growth in juvenile salmon (Pyper and Peterman 1999; Ruggerone and Goetz 2004). Increases in abundance and sea surface temperature in the Gulf of Alaska have been significantly related to the reduced body size of adult sockeye salmon (Pyper and Peterman 1999). Abundance had a stronger effect on body size than temperature, and may have offset any benefits gained from an increase in prey supply under a warm thermal regime (Pyper and

Peterman 1999). Similarly, Schindler et al. (2005) saw an overall negative effect of sockeye salmon abundance on juvenile growth, though warmer temperatures appeared to positively affect growth. Density-dependent effects on growth were approximately twice as large as the effects of environmental conditions (Schindler et al. 2005). In contrast, population trends of Japanese pink salmon appear to be more closely explained by climate change than by hatchery production (Morita et al. 2006). Beamish and Mahnken (1999) argue that environmental conditions affect juvenile salmon more strongly than does density-dependence through the fall and winter of their first year, but that competition for prey might affect environmental conditions via reduced prey availability.

Study System

The inland waters of Prince William Sound cover an area of approximately 8800 km^2 (Cooney et al. 2001b), with an average depth of 190 m (Mooers and Wang 1998). The flow from the coastal Gulf of Alaska into the Sound is generally counterclockwise, in through Hinchinbrook Entrance and back out through Montague Strait (Cooney et al. 2001b). The physical environment of Prince William Sound is controlled by such processes as tides, storms, seasonal winds, precipitation and evaporation, freshwater runoff, exchange with oceanic waters, seasonal temperature changes, and climatic events such as the El Niño Southern Oscillation (ENSO) or Pacific Decadal Oscillation (PDO). Seasonal variability in wind regimes influences the level of base production. In summer, a high-pressure system over the Gulf of Alaska causes the dominance of eastward winds in Prince William Sound and, subsequently, offshore Ekman transport and coastal upwelling (Mooers and Wang 1998).

In the coastal Gulf of Alaska, the Alaska Current System (ACS), as part of a subarctic gyre in the Northeast Pacific, regulates oceanographic conditions and nutrient and plankton transport (Stabeno et al. 2001). The Coriolis effect on the counterclockwise-rotating ACS creates divergence and upwelling in the gyre center and convergence and downwelling in coastal areas (Wilson and Overland 1986). Coastal waters of the Gulf of Alaska must acquire their nutrients from freshwater runoff and wind or tidal mixing, all of which vary greatly at small spatial and temporal scales (Wilson and Overland 1986).

A zooplankton bloom occurs in Prince William Sound and the Gulf of Alaska in late spring, following the phytoplankton bloom by one or two months. Zooplankton biomass peaks in May in the northern Gulf of Alaska (Coyle and Pinchuk 2003; Coyle and Pinchuk 2005), and in June in Prince William Sound (Cooney et al. 2001a). Although seasonal cycles of secondary prey production are similar in Prince William Sound and the coastal Gulf of Alaska, zooplankton composition differs between regions. In recent studies, copepods composed the majority of the zooplankton in both regions; however, large calanoid copepods (e.g. *Neocalanus*) were more prominent in the Gulf of Alaska (Coyle and Pinchuk 2003; Coyle and Pinchuk 2005), while smaller copepods (e.g. *Pseudocalanus*) dominated in Prince William Sound (Cooney et al. 2001a). Copepods comprise over 75% of the numbers and 60% of the biomass in Prince William Sound throughout the year (Cooney et al. 2001a). Pteropods and larvaceans compose the majority of the non-copepod biomass in Prince William Sound between May and October (Cooney et al. 2001a). Euphausiids, amphipods, and chaetognaths are also important during this time (Cooney et al. 2001a; Eslinger et al. 2001). In descending order of importance, cnidarians, euphausiids, pteropods, and chaetognaths also contribute to much of the zooplankton biomass in the northern Gulf of Alaska (Coyle and Pinchuk 2003; Coyle and Pinchuk 2005).

Transport between Prince William Sound and the northern Gulf of Alaska carries both deep and surface-layer zooplankton to and from the Sound. Approximately 40% of the volume of Prince William Sound is flushed into the northern Gulf of Alaska during May–September, while closer to 200% is flushed during October–April (Niebauer et al. 1994). In the fall of 1994 and 1995, 50% and 90% of diapausing copepods in Prince William Sound were from the Gulf of Alaska (Kline 1999).

Plankton, by definition, are drifters; plankton inflow into Prince William Sound is therefore passive and dependent on physical oceanographic processes (Kline 1999). Advection of zooplankton is difficult to observe because the flow into Prince William

Sound is spatially and temporally complex (Kline 2001). The composition and abundance of local zooplankton taxa in the Gulf of Alaska shelf region can vary greatly over both time and space (Coyle and Pinchuk 2003), and the macrozooplankton prey base for Prince William Sound fishes can thus fluctuate greatly from year to year (Kline 2001).

Annual variation in marine conditions and nutrient input, and subsequent variation in plankton production, result in annual variation in habitat quality and salmon growth and survival. The strength of advection between Prince William Sound and the coastal Gulf of Alaska affects both bottom-up and top-down biological processes that affect recruitment and nutrition in fish (Kline 1999). Juvenile fish consume zooplankton that originate outside of their forage range (Kline 1999); the flow of inshore waters from the deep Gulf brings with it carbon that is crucial to local populations of juvenile fishes (Eslinger et al. 2001). Oceanographic processes controlling advection therefore influence Prince William Sound fish that depend on Gulf of Alaska carbon (Kline 1999). The increased flow of zooplankton into Prince William Sound in 2002 may have contributed to high survival for this year class of juvenile pink salmon (Kline 2004).

The four hatcheries in Prince William Sound that raise and release pink salmon fry (Figure 1.1) represent one of the largest salmon hatchery programs in the world. The non-profit Prince William Sound Aquaculture Corporation (PWSAC) owns and operates three of these four hatcheries. Together, PWSAC's Armin F. Koernig, Cannery Creek, and Wally Noerenberg hatcheries released 2/3 of all pink salmon reared in Prince William Sound hatcheries during 2001-2003 (Table 1.1). The Solomon Gulch hatchery, owned and operated by the Valdez Fisheries Development Association (VFDA), released the other 1/3 of Prince William Sound hatchery pink salmon during these years (Table 1.1). Prince William Sound hatcheries thermally mark 100% of their pink salmon fry prior to release, providing a unique opportunity to trace each hatchery fish recovered to a specific entry date, location, and size.

Understanding the Ocean-Salmon Connection

An improved understanding of the processes regulating juvenile pink salmon growth and survival requires a thorough investigation of the absolute growth and growth efficiency of juvenile pink salmon, the timing and magnitude of differences in the growth and size of juveniles at-large versus fish from the same year-class that survived to adulthood, the amount of prey fish must consume to accomplish observed growth during the first summer at sea, and possible ecological bottlenecks that limit growth and survival. To achieve these goals, I analyzed scale patterns to estimate past growth and used growth estimates in bioenergetics models to determine requisite consumption. The amount of consumption required by juvenile pink salmon to achieve observed growth was then compared to localized prey availability to gain insight on the effects of local ocean conditions on growth and survival and determine whether sufficient prey are available in the Gulf of Alaska to sustain the pink salmon population.

A heightened understanding of factors controlling pink salmon growth, energetics, and survival at this critical stage in their life history will allow us to address questions regarding the role we can and should play in keeping the ecosystem in balance. This study will directly contribute to achieving the Global Ocean Ecosystem Dynamics (GLOBEC) program goal of understanding how changes in ocean conditions relate to changes in the structure and dynamics of marine ecosystems and fishery production in the Northeast Pacific.

Objectives

The primary intent of this study was to conduct scale analyses and bioenergetics model simulations to compare spatial and temporal patterns of juvenile pink salmon growth and consumption over their first four months in Prince William Sound and the northern coastal Gulf of Alaska. I collaborated with fisheries biologists from the University of Washington School of Aquatic and Fishery Sciences, the University of Alaska Fairbanks School of Fisheries and Ocean Sciences, and the Auke Bay Lab of the National Marine Fisheries Service to achieve the following objectives:

1. Collect juvenile pink salmon, zooplankton, and data on ocean conditions monthly from July–October 2001–2004 at three stations in Prince William Sound and six stations along the GLOBEC-delineated Seward line (Table 1.2, Figure 1.1);
2. Reconstruct the growth histories of collected juvenile salmon and of surviving adults from the same year-class at comparable juvenile life stages through scale pattern analyses and back-calculation techniques;
3. Use back-calculated growth estimates in a bioenergetics model to determine the amount of prey necessary to achieve the amount of growth observed through September of the juvenile pink salmon's first year at sea;
4. Investigate variation in the growth and consumption of juvenile pink salmon over time (seasonal and interannual), by water mass (Prince William Sound and the Alaska Coastal Current, frontal, and mid-shelf transition regions of the coastal Gulf of Alaska), and by origin (hatchery and wild); and
5. Compare interannual and seasonal estimates of available zooplankton density in each water mass to the amount of prey required for observed growth to examine whether prey biomass in Prince William Sound and the coastal Gulf of Alaska could be limiting for juvenile pink salmon.

Specifically, I aimed to answer the following questions:

- Do the early marine growth and consumption demand of pink salmon differ between years of low and high survival? Between hatchery and wild pink salmon? Among Prince William Sound, the Alaska Coastal Current, and the transition zone? Between the population of juveniles at-large and juveniles that survive to adulthood?
- Do juvenile pink salmon need to achieve certain size thresholds at one or more life stages to have the potential to survive to adulthood? When do these critical periods in the growth of pink salmon occur? What is the relative importance of initial marine mortality versus mortality after the first growing season?
- How much prey is necessary to achieve the amount of growth observed through September of the juvenile pink salmon's first year at sea?

- Are juvenile pink salmon food-limited during May–September in Prince William Sound and the coastal Gulf of Alaska?

This dissertation includes three main chapters. Chapter 2 involved analyzing patterns from juvenile pink salmon scales to estimate growth history and look at temporal and spatial variation in early marine growth. In Chapter 3, I examined differential growth between juveniles at-large and fish that survived to adulthood to investigate the timing and magnitude of size-selective mortality for pink salmon. Bioenergetics models were generated in Chapter 4 to determine the level of consumption necessary for both juvenile pink salmon at-large and those that survived to adulthood to achieve observed growth during May–September of their first year at sea. In this chapter, I also estimated the supply of exploitable zooplankton prey and compared spatial and temporal patterns in the consumption demand of juvenile pink salmon to localized prey biomass. A short summary chapter unites the three sections and presents hypotheses regarding the early marine growth and survival of pink salmon in Prince William Sound and the northern coastal Gulf of Alaska.

The Ocean Carrying Capacity (OCC) program of the NMFS Auke Bay Lab conducts a more synoptic survey of cross-shelf patterns in catch, size distribution, diet, environmental conditions, and food supply during a mid-July to mid-August cruise from the eastern to western shelf regions of the Gulf of Alaska (Moss *in prep*). This GLOBEC study therefore examines temporal variability along the Seward Line, while the OCC program provides a broader spatial but more limited temporal picture.

Significance

Poor ocean survival has contributed substantially to salmon declines in recent years (Bradford 1995), and growth rates of juvenile salmon might relate to overall survival (Mortensen et al. 2000). Because pink salmon are sensitive to environmental stress, spend little time in freshwater before ocean entry, do not have multiple age classes, and are a key plankton consumer in the Gulf of Alaska, they are important indicators of the marine environment. Knowing the amount of prey required by juvenile pink salmon to exceed minimum size thresholds for survival during the first summer and fall at sea is critical in determining the health of the species and its habitat. Moreover, by quantifying the consumption demand of both wild and hatchery pink salmon, we can begin to evaluate their role within the larger trophic dynamics of the Prince William Sound and coastal Gulf of Alaska region. Comparing the consumption demand of the population to the biomass of exploitable prey in localized areas allows us to identify and quantify ecological bottlenecks, such as periods of prey depletion. A greater understanding of these issues is particularly significant at present, given the ongoing debate regarding the value of hatcheries (Meffe 1992; Smoker and Linley 1997; Hilborn and Eggers 2000; Wertheimer et al. 2001) and increasing evidence of global warming affecting the world's oceans (Beamish et al. 1995; Hill 1995; Roemmich and McGowan 1995; Welch et al. 1998).

The Northeast Pacific is home to one of the last sustainable large-scale fisheries in the world. Although pink salmon stocks appear abundant, our limited understanding of the system could inhibit our ability to properly manage their populations and be ultimately devastating to the species, the ecosystem, and those who depend on the salmon fishery for their livelihood. Continuing with current enhancement schemes could have significant ecological, economic and social ramifications. Severe consequences, such as declining body size and survival, could result if carrying capacity is exceeded (Cooney and Brodeur 1998). These concerns are especially timely because they stem from a human-initiated challenge to the ecosystem, and we can control the additional demand imposed by hatchery fish by regulating hatchery production. Appropriate environmental and resource management decisions affecting salmonid stocks require an immediate, more detailed understanding of the connections between salmon production and the ocean environment. Future management of Prince William Sound hatchery operations should incorporate an understanding of the spatial and temporal nature of the additional demand on prey resources.

Table 1.1. The average weight of pink salmon fry at release and total number released by Armin F. Koernig (AFK), Cannery Creek (CCH), Solomon Gulch (SGH), and Wally Noerenberg (WNH) hatcheries during 2001–2004, the number of adult pink salmon that returned to each hatchery the following year, and overall smolt-adult survival. Sources: (Eggers 2003; Plotnick and Eggers 2004; Eggers 2005; Prince William Sound Aquaculture Corporation 2005; K. Morgan, Valdez Fisheries Development Association, personal communication).

Year	Hatchery	Avg. wt. (g)	Total Released	Total Returned	Survival (%)
2001	AFK	0.47	150,287,930	7,759,064	5.2
	CCH	0.32	139,226,716	1,588,603	1.1
	SGH	0.60	203,897,201	5,265,239	4.4
	WNH	0.70	127,650,249	5,617,122	2.6
	Total	0.53	621,062,096	20,230,028	3.3
2002	AFK	0.50	155,982,828	7,065,581	4.5
	CCH	0.39	138,626,713	8,288,949	6.0
	SGH	0.68	202,573,328	17,374,811	16.8
	WNH	0.65	106,229,524	17,847,316	8.6
	Total	0.56	603,412,393	50,576,657	9.0
2003	AFK	0.83	146,407,222	5,230,138	3.6
	CCH	0.68	135,584,680	2,761,241	2.0
	SGH	0.54	206,397,607	11,139,932	2.3
	WNH	0.85	119,533,743	2,704,727	5.4
	Total	0.70	607,923,252	21,836,038	3.3
2004	AFK	0.62	174,371,351	10,568,869	6.1
	CCH	0.37	136,288,850	11,743,635	8.6
	SGH	0.69	222,457,568	17,833,491	8.0
	WNH	0.62	109,640,296	8,018,603	7.3
	Total	0.59	642,758,065	30,331,107	7.5

Table 1.2. Locations of sampling stations in Prince William Sound and on the Seward (GAK) line in the Gulf of Alaska.

Station	**Latitude**	**Longitude**	**Approximate Depth (m)**
PWS 1	60 16.3	148 9.0	
PWS 2	60 6.0	147 50.0	
PWS 3	60 3.0	147 40.0	
GAK 1	59 50.7	149 28.0	265
GAK 2	59 41.5	149 19.6	220
GAK 3	59 33.2	149 11.3	220
GAK 4	59 24.5	149 2.9	200
GAK 5	59 15.7	148 54.5	175
GAK 6	59 7.0	148 46.2	445

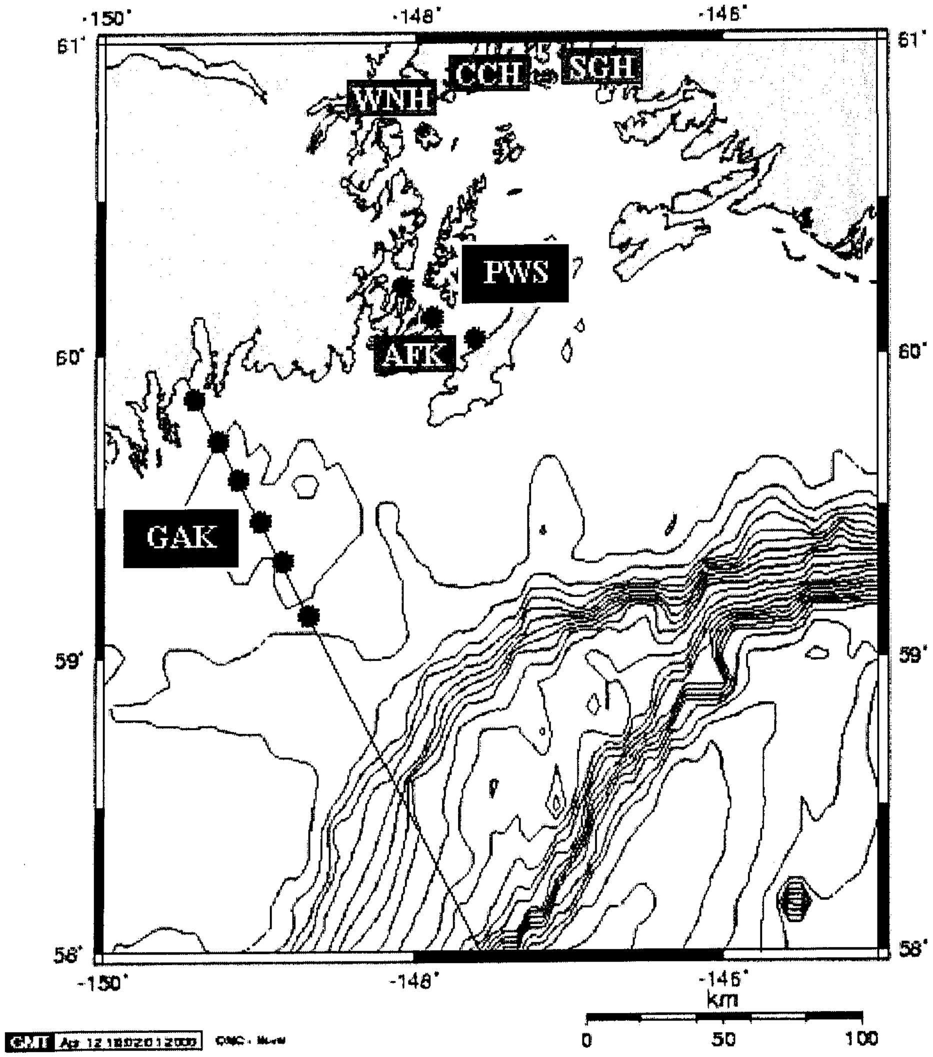

Figure 1.1. Locations of three sampling stations in Prince William Sound (PWS) and stations 1-6 on the Seward Line (GAK) in the coastal Gulf of Alaska. Station one is the station closest to shore on all lines. Also shown (in gray) are the approximate locations of the four hatcheries in PWS that release pink salmon: Armin F. Koernig (AFK), Cannery Creek (CCH), Solomon Gulch (SGH), and Wally Noerenberg (WNH).

NOTES TO CHAPTER 1

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Chapter 2. Early Marine Growth of Pink Salmon in Prince William Sound and the Northern Coastal Gulf of Alaska During Years of Low and High Survival

INTRODUCTION

The four hatcheries in Prince William Sound that release pink salmon (*Oncorhynchus gorbuscha*) fry (Figure 2.1) represent one of the largest salmon hatchery programs in the world, with a combined annual release of over 600 million fry since 2001 (Alaska Department of Fish and Game 2005; Table 2.1). These hatchery releases average over three times more fry than the natural production of approximately 190 million wild pink salmon fry migrating into Prince William Sound (S. Moffitt, Alaska Department of Fish and Game, personal communication).

Although early marine growth has repeatedly been correlated with overall survival in Pacific salmon (Holtby et al. 1990; Henderson and Cass 1991; Murphy et al. 1998; Tovey 1999; Willette et al. 1999; Mortensen et al. 2000; Beamish et al. 2004), we currently lack a mechanistic understanding of the timing, magnitude, and source of stage-specific marine survival. Early growth and mortality of pink salmon are likely governed by some combination of prey availability, smolt quality, inter- and intra-specific competition, predation, and ocean conditions. This study examines interannual variability in the growth performance of juvenile pink salmon among years corresponding to low marine survival (3% for adult pink salmon returning to Prince William Sound in both 2002 and 2004) and high marine survival (9% in 2003 and 8% in 2005; Alaska Department of Fish and Game 2005; Prince William Sound Aquaculture Corporation 2005; K. Morgan, Valdez Fisheries Development Association, personal communication). On account of their two-year life cycle, juvenile pink salmon that entered the ocean during 2001-2004 returned as adults in the following summers of 2002-2005.

Pink salmon fry migrate to sea at a smaller size than any other salmonid (Quinn 2005). Wild fish enter Prince William Sound at approximately 0.26 g (Bailey et al. 1976; Boldt and Haldorson 2002), and the average weight at release for the 2001-2004 hatchery cohorts was 0.53 g, 0.56 g, 0.70 g, and 0.59 g, respectively (Alaska Department of Fish and Game 2005). Juvenile pink salmon are highly vulnerable to predation during their first months in marine waters (Hunter 1959), and rapid growth can reduce size-selective predation mortality (Parker 1971; Hargreaves and LeBrasseur 1985; Heard 1991; Jaenicke and Celewycz 1994; Willette et al. 1999). Throughout the summer and fall, juvenile pink salmon reside over the continental shelf and grow from roughly 7 g in July to larger than 90 g in October.

Mortality during the first weeks/months in marine waters and again after the first growing season significantly influences overall marine survival. The first weeks at sea are often referred to as a "critical period" for growth in the pink salmon's life cycle, since significant mortality occurs during this time (Parker 1968; Beamish and Mahnken 2001). Some studies indicate that growth might become more important during the late fall and winter of the first year of marine life, when salmon face a second critical period (Beamish and Mahnken 2001). Salmon may not survive the winter if they do not reach a critical size by this time (Beamish and Mahnken 2001). Smolt-adult survival in coho salmon (*O. kisutch;* Briscoe et al. 2005) and pink salmon (Moss et al. 2005) is strongly affected by mortality after the first summer at sea. The relative importance of initial marine mortality versus winter mortality might vary among years because of different initial conditions (e.g. juvenile size at entry) and different environmental conditions (e.g. temperature, prey availability) that influence distribution and growth during the first growing season. Mortality processes might also vary between species like yearling or older sockeye (*O. nerka*), coho, and Chinook (*O. tshawytscha*) salmon or steelhead (*O. mykiss*) smolts, which are large relative to other salmonids, and pink, chum (*O. keta*), or age-0 Chinook salmon smolts, which are small.

Calcified structures in fish, such as scales, can be used to estimate growth history. Fish produce circuli on their scales at regular intervals of approximately 4-8 d (Courtney et al. 2000); the rate of circulus formation and the growth of the scale determine the spacing between rings (Fukuwaka and Kaeriyama 1997). Scale radius is proportional to fish length (Lee 1920; Ricker 1992), thus the radius of the scale at previous circuli reflects size at a younger age, and the width of circulus increment spacing reflects growth during specific intervals (Fukuwaka and Kaeriyama 1997; Courtney et al. 2000; Beamish et al. 2004). Scales can therefore be used to reconstruct the growth histories of individual fish. Using scales to study growth, rather than tracking mean sizes of fish captured at sea, eliminates ambiguity in estimates of average size at a given time (caused by variability in the timing of ocean entry or size-selective mortality) and allows more accurate comparisons of growth among different cohorts.

Growth studies rely on random, unbiased samples that are representative of all sizes and ages in the population (Bagenal and Tesch 1978; Francis 1990; Pierce et al. 1996). Also, two assumptions must hold when using the width of circulus increments as a proxy for growth rate: 1) the frequency of formation is constant, and 2) the distance between increments is proportional to fish growth (Campana and Jones 1992). Most published studies assume that a linear relationship exists between scale radius and fish length, and between circulus spacing and growth rate (Fraser 1916; Lee 1920; Francis 1990; Ricker 1992).

Growth rates provide an integrative history of foraging success and metabolic response to environmental conditions (Mason et al. 1995). Species-specific growth rates can reflect habitat quality and indicate oceanographic change, with higher growth rates signifying better growth conditions (Mason et al. 1995; Brodeur et al. 2004). Both biological (prey availability and quality) and physical (temperature, salinity, light intensity, and turbidity) characteristics determine habitat quality (Mason et al. 1995).

Environmental factors can affect spacing between circuli by changing somatic growth rates (Fukuwaka and Kaeriyama 1997). Changes in temperature, zooplankton availability, and competitor abundance result in periods of slower or faster growth, which are apparent in the growth of scales and otoliths. During periods of faster growth, rings on scales and otoliths will form at wider intervals; slower growth results in narrower spacing. Thus, salmon can record general ocean conditions in their scales (Welch 1997).

The primary intent of this study was to use scale circulus spacing to compare spatial and temporal patterns of juvenile pink salmon growth over their first five months in Prince William Sound and the coastal Gulf of Alaska. My objectives were to determine how early marine growth during years of low and high survival differed seasonally during May–October, spatially among Prince William Sound, Alaska Coastal Current, front, and mid-shelf transition regions, and between hatchery and wild fish. I expected to observe faster growth during high-survival years, better growth opportunities as fish migrated out of Prince William Sound, and no large differences in growth between hatchery and wild fish among years.

METHODS

Field Sampling

Juvenile pink salmon and data on physical oceanographic conditions were collected in 2001, 2002, 2003, and 2004 at three stations in southwest Prince William Sound and stations 1-6 on the GLOBEC-delineated Seward (GAK) Line (Figure 2.1). Stations were sampled during 6-10 d cruises monthly from July to October (Table 2.1) with the following exceptions: An early October 2002 cruise was scheduled in place of the two cruises held in mid-September and mid-October 2001. Because October catches were very low in 2001 and 2002, no October cruise was scheduled during 2003 or 2004. We sampled out to station 10 on the Seward Line in August 2002, and to station 7 in September 2003. In 2003 and 2004, we also sampled a transect extending south from Cape Fairfield, east of the Seward Line, during all months (Table 2.1, Figure 2.1). Two stations west of the Seward Line were also sampled in August 2003. This sampling scheme encompassed the migration period from Prince William Sound to the coastal Gulf of Alaska for juvenile pink salmon and allowed reasonably high spatial and temporal data resolution during the first growing season.

Juvenile Pink Salmon Collection

At each station, two or more trawls were performed during daylight hours using a Nordic 264 surface rope trawl with 3 m doors and a 1.2 cm mesh liner in the cod end. The net fished a depth of approximately 11.4 m and a width of approximately 14.3 m (S.

Patterson, Net Systems, personal communication) for 30 min at 3.5–5 knots (6.5–9.3 km·h^{-1}). If juvenile pink salmon were present, but fewer than 10 were caught in a single haul, the tow was repeated to increase sample size. Catches were sorted to species and counted; large catches were subsampled. The fork lengths of up to 200 fish of each species were measured. Up to 50 juvenile pink salmon from each tow were frozen in seawater for subsequent analysis.

Ocean Conditions

At each station, vertical profiles of conductivity and temperature were recorded with a Seabird Seacat SBE-19 CTD. The CTD, equipped with a fluorometer, recorded depth, temperature, salinity, and fluorescence at 1 m intervals over 0—100 m depths or to 5 m above the sea floor in shallower waters. Sea surface temperature was measured with a thermometer placed in a bucket of water collected from the sea surface (at approximately 1 m) because the CTD did not function well at this depth.

Laboratory Analyses

Personnel at the University of Alaska Fairbanks – Juneau recorded lengths and weights of all juvenile pink salmon collected and read otoliths for thermal markings (L. Haldorson, J. Boldt, J. Piccolo, personal communication). Prince William Sound hatcheries thermally mark 100% of their pink salmon fry prior to release, providing a unique opportunity to trace each hatchery fish recovered to a specific entry date, location, and size.

Salinity measurements were obtained from the CTD cast at each station. Because salinity gradients can affect the distribution of forage fishes (Abookire and Piatt 2005), and because sea-surface salinity prior to migration can affect the survival of pink salmon fry (Mueter et al. 2005), we assigned a water mass category to each station on the Seward Line according to the salinity at 2 m depth: salinity < 30 psu in the Alaska Coastal Current (ACC); 30 psu ≤ salinity < 31.5 psu in the frontal zone, and salinity ≥ 31.5 psu in the mid-shelf transition zone. All stations in Prince William Sound were classified as the

Prince William Sound water mass (range 19.4-30.1 psu). In July 2003, July 2004, and August 2004, the range of salinity values declined between ACC and transition waters, with consistently low salinity in the transition zone. Consequently, we distinguished ACC and front regions by reviewing the salinity profiles for a number of stations that were sampled contiguously, and defined the transition zone as being ≥ 31.0 psu for these cruises.

Growth Rates

Scales were collected from the preferred area of the juvenile pink salmon collected at sea. Preferred scales were located in a rectangular area located one to four scale rows above the lateral line between two vertical lines drawn from the posterior edge of the dorsal fin and halfway between the posterior edge of the dorsal fin and the anterior edge of the adipose fin. Scales from up to 15 individuals from each station were collected during each year. The scales from each fish were placed on gummed cards, sculptured surface up, and impressed in transparent acetate at a pressure of 5000 psi for 3 min.

Acetate impressions were read using a computerized video digitizing system (Optical Pattern Recognition System, Model OPR-512). The first scale from each fish showing clear, unbroken circulus bands, an unbroken scale edge, and no signs of regeneration was measured. Scale circuli were measured along the anterior-posterior axis, from the back of the focus to the scale edge—the most commonly used measurement (Martinson et al. 2000). Each circulus that crossed the measurement axis was automatically marked by the digitizing system and errors were manually edited.

Total scale radius equaled the distance from the mid-point of the focus (focus/2) to the scale edge. To remove outliers, measurements from fish with a fork length to scale radius ratio of > 0.45 or a focus > 250 μm were deleted (K. Myers, University of Washington High Seas Salmon Research Program, personal communication). Between 3–15% of juvenile scales were removed as outliers. Frequency histograms of total scale size from fish caught during each month tracked size modes during May–October. Fork lengths were regressed against total scale radius to determine the relationship between fish length and scale size (Figure 2.2).

The number of complete circuli on each scale, if not noted during the scale measurement process, was determined by examining patterns in circulus increments. If the final increment was larger than the second-to-last increment, I assumed that the scale margin was at a complete circulus; if the last increment was < 20 μm, I assumed that the increment to the scale margin was not at a full circulus. In some cases, it was difficult to determine when the last complete circulus formed, and scale growth patterns were used to obtain the best estimate of the final circulus.

Circulus formation rate was determined by regressing the Julian sampling day on the number of complete circuli at capture. The regression equation from each relationship was used to estimate the average date on which each circulus formed, and the average number of days between circuli during each year approximated the rate of circulus formation. The one hatchery fish caught in October was excluded from this analysis.

Growth trajectories were reconstructed using estimates of the scale radius at each complete circulus. I used ANCOVA or repeated-measures ANOVA and multiple comparison tests to determine differences in growth among months (May-October), years (2001-2004), origins (hatchery and unmarked "wild" fish), and hatchery cohorts (Armin F. Koernig (AFK), Cannery Creek (CCH), Wally Noerenberg (WNH), and Solomon Gulch (SGH)). Because the model violated the assumption of homogeneity of regression slopes for nearly all comparisons, ANOVA was most often used to determine differences between groups.

Variation in growth with respect to water mass (Prince William Sound, Alaska Coastal Current, front, and mid-shelf transition regions) was determined from measurements of the last full circulus increment, as the mobility of the fish precludes the assumption that growth occurred in a particular water mass any earlier in their life. Growth with respect to water mass was estimated by first back-calculating fish length at the last full circulus using the Fraser-Lee equation:

$$L_i = \frac{L_c - a}{S_c} \cdot S_i + a \,,$$

where $(L_c-a)/S_c$ is the slope of the linear regression of scale radius on fish length, a is the intercept of the regression, L_i the fish length at which the i^{th} increment formed, L_c the fish length at capture, S_c the scale radius at capture, and S_i the scale radius at the i^{th} increment (Fraser 1916; Lee 1920). Since growth rate or size at scale formation can vary among populations of the same species (Lee 1920), only cohorts of fish with similar growth trajectories were used in the regression for each year (Figure 2.2). Incremental growth between the final two circuli was calculated for individual fish, although the intercept parameter a was estimated from the regression for each cohort. Back-calculated lengths at each circulus were then converted to weights using the regression for wet weight (without stomach contents) on fork length for each cohort (Figure 2.3).

To report overall growth between the last two complete circuli ($g \cdot d^{-1}$), I divided the amount of weight gained over the last complete circulus increment by the number of days between circuli. Specific growth rate ($g \cdot g^{-1} \cdot d^{-1}$) was estimated by dividing growth over the last full circulus increment by the total wet weight without stomach contents (g) of each fish at capture. I assumed that individual fish did not move between water masses during the formation of the final two circuli that formed just prior to capture. It is also important to note that the removal of incomplete circulus measurements at the scale margin potentially imposes a time lag of 1-6 d between the size of the fish at capture and the size of the fish when the last complete circulus formed.

Catch per unit effort (CPUE; $catch \cdot h^{-1}$) was determined by dividing the number of juvenile pink salmon caught during each haul by the duration of the haul (in hours) and averaging the results for each combination of water mass, month, and year. Because juvenile salmon were misidentified in the field during September 2001 and August 2002, no CPUE data is available for these months. I also examined patterns in temperature over the top 10 m of the water column to gain insight on the effect of ocean conditions on early ocean growth. The average temperature in each water mass was weighted in terms of the average CPUE in each water mass to determine the thermal experience of the majority of the fish during each month within each year. Because CPUE was unavailable for September 2001 and August 2002, the average temperature over all water masses substituted for the average thermal experience during these months.

RESULTS

A total of 676 scales were analyzed from hatchery and unmarked juvenile pink salmon during 2001-2004 (Table 2.2). A linear scale-fork length relationship most closely characterized the early marine growth of juvenile pink salmon in Prince William Sound and the coastal Gulf of Alaska during all years ($r^2 = 0.77$-0.80, $P < 0.001$ for all years; Figure 2.2). Standardized residuals were homoscedastic and normally distributed, and Durbin-Watson tests indicated that variances were independent of predicted values (value < 2). Because of the linear relationship between scale size and fish length, fish length can be back-calculated directly from scale radius and growth rate can be inferred from scale circulus spacing. The effect of origin (hatchery versus wild) and scale size on fork length was significant in 2001 (ANCOVA, $P < 0.05$) but not in 2002-2004 ($P < 0.42$). Therefore, the fork length-scale size relationship for 2001 was determined using only hatchery fish, but the pooled group of hatchery and wild fish was used in the regressions for 2002, 2003, and 2004. Scales began to form when pink salmon were approximately 44-48 mm in length (Figure 2.2), approximately at the time of hatchery release. The relationship between fork length and wet weight during all years was best described by a power curve ($r^2 = 0.98$-0.99, $P < 0.001$ for all years; Figure 2.3).

In 2001, the estimated date of initial circulus formation was 14-Jun, and circuli formed at an average rate of one every 6.1 d ($r^2 = 0.79$, $P < 0.001$):

$$\text{Julian Date} = 160.8 + 6.1 \cdot X;$$

in 2002, the initial circulus formed on 15-Jun, with new circuli averaging one every 5.8 d ($r^2 = 0.54$; $P < 0.001$):

$$\text{Julian Date} = 161.4 + 5.8 \cdot X;$$

in 2003, the initial circulus formed on 18-Jun, with new circuli averaging one every 5.5 d ($r^2 = 0.51$; $P < 0.001$):

$$\text{Julian Date} = 164.9 + 5.5X;$$

and in 2004, the initial circulus formed on 17-Jun, with new circuli averaging one every 4.4 d ($r^2 = 0.56$; $P < 0.001$):

$$\text{Julian Date} = 165.0 + 4.4 \cdot X$$

(Figure 2.4). Only hatchery fish were used to estimate circulus formation rate in 2001, and fish caught in October 2001 were not included in this analysis. The average number of complete circuli in all months was greater during the high survival years (2002 and 2004) than during the low-survival years (2001 and 2003). In July, juvenile pink salmon had an average of 9.2 circuli in 2002 and 10.4 in 2004 versus 6.1 in 2001 and 7.5 in 2003. Pink salmon also had more complete circuli on average in August 2002 (12.0) and 2004 (13.4) than in August 2001 and 2003 (10.9 in both years), and in September 2004 (17.7) than in September 2001 (15.0) and 2003 (17.0, although only one fish was used in this analysis).

The frequency distributions of scale radii at most circuli for juvenile pink salmon did not deviate significantly from normality during any month from 2001-2004 (Kolmogorov-Smirnov, $P > 0.05$; Figure 2.5). Within each year, the mean scale size at each circulus was similar for juvenile pink salmon caught in July, August, September, or October (ANOVA, $P > 0.05$; Figure 2.5), with the exception of significant differences at circulus 3 between fish caught in July and October 2001 (Tukey, $P = 0.047$), at circuli 8-10 between fish caught in July and August 2002 (Tukey, $P < 0.004$), and at circuli 4-5 between fish caught in August and September 2003 (Tukey, $P < 0.029$). Juvenile pink salmon caught in July 2004 were significantly larger at circuli 5-17 than were fish caught in August and September 2004 (ANOVA, $P < 0.05$; Tukey, $P < 0.025$). Although juvenile pink salmon that survived until September or October 2001-2003 were not significantly larger or smaller during earlier months than the average juvenile, the general trend was that juveniles captured in September and October 2001 and 2003 were larger than the average juvenile during earlier months, while juveniles captured in 2002 and 2004 appeared smaller than average during earlier months (Figure 2.5).

Growth by Month

The mean scale sizes at each circulus for juveniles caught in July and August were generally larger in 2002 and 2004 (high-survival years) and smallest in 2001 (a low-survival year). Juveniles caught in July 2001 were significantly smaller than in July 2002 at circuli 5-9 (ANOVA, $P < 0.005$; Tukey, $P < 0.031$) and significantly smaller than in July 2004 at circuli 2-9 (Tukey, $P < 0.014$; no fish in July 2001 had > 9 circuli). Juveniles caught in July 2003 were significantly smaller than in July 2002 at circulus 9 (Tukey, $P = 0.025$) and significantly smaller than in July 2004 at circuli 5-9 (Tukey, $P < 0.01$). In August, juvenile pink salmon caught in 2001, 2002, and 2003 were smaller at several circuli than in 2004 (ANOVA, $P < 0.05$). Juveniles caught in 2001 were significantly smaller than in 2004 at circuli 1-10 (Tukey, $P < 0.01$) and smaller than in 2002 at circulus 14 (Tukey, < 0.05). Juveniles caught in 2002 were smaller than in 2004 at circuli 1-6 (Tukey, $P < 0.05$) but larger than in 2004 at circuli 14 and 15 (Tukey, $P < 0.001$). Juveniles caught in 2003 were smaller than in 2004 at circuli 1-5 (Tukey, $P < 0.05$). Juvenile pink salmon caught in September 2001 were smaller than fish caught in September 2003 at circuli 3-8 (ANOVA, $P < 0.05$; Tukey, $P < 0.05$), and were smaller than fish caught in September 2004 at circuli 17-18 (Tukey, $P < 0.005$). There were no significant differences in mean scale size at specific circuli between fish caught in late October 2001 and early October 2002 (ANOVA, $P > 0.27$).

Growth by Origin

Unmarked "wild" juveniles were significantly larger than hatchery fish at several circuli in 2001 and 2003, but few differences were evident between unmarked and hatchery fish caught in 2002 and 2004 (Figure 2.6). Unmarked fish were significantly larger than hatchery fish in 2001 at circuli 2-16 (t-test, $P < 0.05$). No significant differences were evident at circuli 17-21 (t-test, $P > 0.05$), but sample sizes were small for these circuli. In 2002, unmarked fish were significantly smaller than hatchery fish at circulus 16 (t-test, $P = 0.042$); however, only one hatchery fish was sampled. Unmarked fish were significantly larger than hatchery fish in 2003 at circuli 3-10 and 12-13 (t-test, P

< 0.05; only 1 hatchery fish had > 13 circuli) and in 2004 only at circuli 2-4 (t-test, $P < 0.05$). Few significant differences among years were observed in wild juveniles in 2001, 2002, and 2003, but wild fish were larger in 2004 than in other years (ANOVA, $P < 0.05$; Figure 2.7). Wild juvenile pink salmon in 2003 were significantly larger than wild juveniles in 2001 at circuli 3-5 (Tukey, $P < 0.032$), but not significantly different at larger sizes. In 2004, wild juveniles were larger than in 2001 at circuli 1-19 (Tukey, $P < 0.013$), larger than in 2002 at circuli 2-7 (Tukey, $P < 0.044$), and larger than in 2003 at circuli 6 and 8 (Tukey, $P < 0.047$).

Hatchery juveniles were larger in 2002 and 2004 than in 2001 and 2003 (ANOVA, $P < 0.05$; Figure 2.7). The 2002 hatchery cohort was significantly larger than hatchery juveniles in 2001 at circuli 5-13 (Tukey, $P < 0.05$) and in 2003 at circuli 9-10 (Tukey, $P < 0.05$). The 2004 hatchery cohort was significantly larger than the 2001 cohort at circuli 2-13 (Tukey, $P < 0.02$), larger than the 2002 cohort at circuli 6-7 (Tukey, $P < 0.05$), and larger than the 2003 cohort at circuli 5-12 (Tukey, $P < 0.005$).

Growth of Hatchery Cohorts

Thermal otolith markings enabled each hatchery individual to be associated with a specific hatchery of origin, release date, and size at release. The AFK and WNH hatcheries released groups of hatchery fry on more than one date during each year (Table 2.3). To determine whether differences existed among hatchery fish based on hatchery of origin, I first confirmed that separate release groups within each hatchery were not significantly different from one another and could be pooled for analysis. For each year, release groups within AFK and WNH hatcheries came from the same population and could be pooled into one group for each hatchery (ANCOVA, $P > 0.05$; Kolmogorov-Smirnov, $P > 0.08$ for circuli 3, 6, 9, 12, and 15).

No significant differences in mean size during the first growing season existed among AFK, CCH, SGH, and WNH hatchery cohorts during each year (ANOVA, $P > 0.075$) or between each hatchery cohort and wild fish in 2002 and 2004 (ANOVA, $P > 0.05$; Figure 2.8). However, some significant differences were found between hatchery cohorts and wild fish in 2001 and 2003 (ANOVA, $P < 0.05$; Figure 2.8). In 2001, wild juveniles were significantly larger than AFK fish at circuli 5-14 (Tukey, $P < 0.05$), larger than CCH fish at circuli 6-12 (Tukey, $P < 0.05$), and larger than SGH fish at circuli 5-6 and 8-10 (Tukey, $P < 0.05$; Figure 2.8). No post-hoc tests were conducted for circulus 16 and greater. No significant differences were observed among juveniles from different hatcheries and wild fish in 2002 (ANOVA, $P > 0.17$), although fish from SGH were larger than fish from all other cohorts (Figure 2.8). In 2003, wild juveniles were significantly larger than WNH juveniles at circuli 3 and 5 (Tukey, $P < 0.05$), but no differences were seen between other groups (Figure 2.8). No post-hoc tests were conducted for circulus 12 and greater. Some difference existed between hatchery cohorts and wild fish at circulus 3 in 2004 (ANOVA, $P = 0.04$), but a multiple comparison test at this circulus showed no significant differences (Tukey, $P > 0.16$).

Comparing the growth of each cohort among years showed that for each, juvenile pink salmon were larger in 2002 and 2004 than in 2001 and 2003 (ANOVA, $P < 0.05$), and juveniles in 2003 were more similar in size to juveniles in 2002 than to juveniles in 2001 (Figure 2.9). AFK juveniles were significantly larger in 2002 than in 2001 at circuli 11-12 (Tukey, $P < 0.01$; no post-hoc tests were conducted for circulus 13 and greater). CCH fish were larger in 2004 than in 2001 at circuli 4-10 (Tukey, $P < 0.004$), than in 2002 at circuli 4-9 (Tukey, $P < 0.026$), and than in 2003 at circuli 5-10 (Tukey, $P < 0.017$). Juveniles from SGH were larger in 2002 than in 2001 at circuli 5-11 (Tukey, $P < 0.028$) and 2003 at circulus 9 (Tukey, $P = 0.036$), larger in 2003 than in 2001 at circulus 4 (Tukey, $P =0.041$), and larger in 2004 than in 2001 at circuli 4-12 (Tukey, $P < 0.004$) and 2003 at circuli 7-12 (Tukey, $P < 0.016$; no post-hoc tests conducted at circulus 12 and greater; Figure 2.9). No significant differences among years were observed in WNH juveniles (ANOVA, $P > 0.06$).

Growth by Water Mass

Because mean scale sizes and measurement distributions were similar within each year for AFK, CCH, SGH, and WNH hatchery cohorts, hatchery groups were pooled for the water mass analysis. Similarly, because no differences in growth were observed between hatchery and unmarked fish in 2002 and 2004, these groups were combined within each of these years. Growth in Prince William Sound, the Alaska Coastal Current, the front, and the mid-shelf transition zone was thus determined for hatchery fish in 2001 and 2003 and for the pooled group of hatchery and wild fish in 2002 and 2004. Because sample sizes were smaller in 2002, the intercept of the regression of fork length on scale size and the equation from the regression of wet weight on fork length were used for the pooled group of wild and hatchery fish when back-calculating size at circuli for this year. The average back-calculated weight at each circulus was very similar to the average wet weight (without stomach contents) of juvenile pink salmon that had that number of full circuli when captured at sea (Table 2.5).

Pink salmon grew more per day on average over the last full circulus increment in July 2002 and 2004 (0.64 and 0.81 $g \cdot d^{-1}$, respectively), the high-survival years, than in July 2001 and 2003 (0.26 and 0.34 $g \cdot d^{-1}$, respectively), the low survival years. Juveniles also grew more per day on average in August 2002 and 2004 (0.91 and 0.64 $g \cdot d^{-1}$) than in August 2001 and 2003 (0.53 and 0.48 $g \cdot d^{-1}$). During July-October in all years, total growth generally increased and specific growth generally decreased (Figure 2.10). Specific growth decreased the most during July-October in 2004, from an average of 0.031 $g \cdot g^{-1} \cdot d^{-1}$ to an average of 0.018 $g \cdot g^{-1} \cdot d^{-1}$.

During July in Prince William Sound, juvenile pink salmon grew more over the last full circulus increment in 2002 than in 2001 (ANOVA, $P < 0.001$) and 2003 ($P = 0.026$), and more in 2004 than in 2001 ($P < 0.001$) and 2003 ($P = 0.003$). Fish also grew more overall in 2004 than in 2003 in the Alaska Coastal Current during July ($P = 0.03$). No significant differences in overall growth among years were found in the front and transition zones in July (Front: $P = 0.14$, Trans: $P = 0.83$). Differences in overall growth among years were also not significant in Prince William Sound and the Alaska Coastal Current in August (PWS: $P = 0.43$, ACC: $P = 0.18$). Growth was greater in the front in August 2002 than August 2003 and 2004 ($P < 0.05$ for both), and greater in the transition zone in August 2002 than August 2001, 2003, and 2004 ($P < 0.001$ for all). No significant differences in overall growth were observed during September in Prince William Sound or the Alaska Coastal Current ($P > 0.65$).

Specific growth in different water masses was not significantly different among years during July, August, and September (ANOVA, $P > 0.05$ for all combinations) except in the front in August, when fish grew more in 2004 than in 2002 ($P = 0.034$). Due to small sample sizes, no comparison could be made for the month of October.

Few differences in the growth of juvenile pink salmon in different water masses were found among months during each year (Figure 2.10). Neither total growth ($g \cdot d^{-1}$) nor specific growth ($g \cdot g^{-1} \cdot d^{-1}$) over the last full circulus increment differed significantly among water masses in August and September 2001 (ANOVA, total growth: $P > 0.56$, specific growth: $P > 0.57$). Because only one hatchery fish was captured in July 2001, weights could not be compared for this month. During July and August 2002, total growth was lower for juvenile pink salmon in Prince William Sound than in the transition zone (ANOVA, $P < 0.005$ for both months). However, specific growth did not differ significantly among water masses in July or August during this year (July: $P = 0.95$, August: $P = 0.05$). All fish caught in October 2002 were in the Alaska Coastal Current. In July and August 2003, total growth and specific growth were not significantly different among water masses (total growth: $P > 0.15$, specific growth: $P > 0.31$). Only one hatchery fish was captured in September 2003. During July 2004, total growth was less in Prince William Sound and the Alaska Coastal Current than in the front ($P < 0.005$) and less in Prince William Sound than in the transition zone ($P < 0.05$). Specific growth, however, was greater in the Alaska Coastal Current than in the front ($P < 0.05$). No significant differences in total or specific growth were observed in August and September 2004 ($P > 0.05$).

Growth in Relation to Movement Patterns and Ocean Conditions

Catch Per Unit Effort

The average catch per unit effort (CPUE; $catch \cdot h^{-1}$) in each salinity zone provided further insight into the growth and migration patterns of juvenile pink salmon during

2001, 2002, 2003, and 2004. Average CPUE reached a maximum of 2498.0 fish·h^{-1} in July (Prince William Sound, 2002), 80.0 fish·h^{-1} in August (Prince William Sound, 2003), 26.4 fish·h^{-1} in September (Alaska Coastal Current, 2003), and 4.7 fish·h^{-1} in October (transition zone, 2001; Figure 2.11). Average CPUE was much lower in August than July due to both mortality and dispersal, and lower in September and October than August, as most juvenile pink salmon had by this time migrated out of the study area.

In July, CPUE was, as expected, much higher in Prince William Sound than in the Alaska Coastal Current, front, and transition zone during all years (Figure 2.11). The majority of pink salmon caught in August 2001 and 2003 were in Prince William Sound, but most fish in August 2004 were found in the transition zone (Figure 2.11). The majority of fish in September 2003 were found in the Alaska Coastal Current. The catch in September 2004 was low but distributed approximately evenly between Prince William Sound and the Alaska Coastal Current. Pink salmon were found in Prince William Sound, the Alaska Coastal Current, and the transition zone during October 2001, but only in the Alaska Coastal Current during October 2002.

In Prince William Sound in July, CPUE was much higher in 2002, a high-survival year, than in the low-survival years of 2001 (735 fish·h^{-1}) and 2003 (465 fish·h^{-1}), and also higher than in 2004, the other high-survival year (689 fish·h^{-1}). Juvenile pink salmon were more evenly dispersed among water masses in July during 2004. Pink salmon were found in the transition zone during July only in 2002 and 2004. CPUE in Prince William Sound, the Alaska Coastal Current, and the front was much lower in August 2004 than in 2001 and 2003, and lower in September 2004 than in September 2001 and 2003. Although hatchery-raised pink salmon were released at a larger average size in 2003 than in other years, and released earlier than in 2001 (Table 2.3), the population of juvenile pink salmon appeared to linger in Prince William Sound and the coastal Gulf of Alaska longer in 2003 and 2001 than in 2004 (Figure 2.11).

Temperature

The average juvenile pink salmon experienced cooler temperatures during July than during August each year, and cooler temperatures in September than during July except in 2004, when the average temperature was warmer in September (Figure 2.12). Average temperatures ranged from 12.0–13.9°C in July, 13.2–15.4°C in August, 11.7–13.4°C in September, and 8.9–10.9°C in October (Figure 2.12). Thermal experience during July-August was not consistently warmer or cooler during any one year. The average temperature was much cooler in July 2001 (12.0°C) than July 2003 (13.9°C), but similar during August 2001 and 2003 (14.1°C). Temperature was cooler in July 2001 than July 2002, 2003, and 2004, but cooler in August 2002 than August 2001, 2003, and 2004 (Figure 2.12). In September and October, temperatures were again cooler in 2001 than in other years. Temperatures were warmer in August and September 2004 than during these months in all other years.

DISCUSSION

This study used scale patterns to show that juvenile pink salmon were consistently larger throughout the summer and early fall of 2002 and 2004 than in 2001 and 2003, indicating that larger, faster-growing juvenile pink salmon experienced higher survival. Although no significant difference in size was observed between unmarked "wild" and hatchery juvenile pink salmon during high-survival years, wild juvenile pink salmon were significantly larger than hatchery fish during low-survival years. No differences in size were found among hatchery groups during each year, but, in some cases, smolt-adult survival varied widely among these cohorts. Juvenile pink salmon did not gain any immediate growth advantage in the northern coastal Gulf of Alaska after leaving Prince William Sound, but appeared to migrate onto the continental shelf and out of the sampling area more quickly during 2004, when they were of a larger average size. Differences in size among years were determined by some combination of growing conditions and early mortality, the strength of which could vary significantly among years.

If surviving fish were larger at a particular circulus than the average juvenile in our samples, either size-selective mortality occurred between sampling periods or larger fish emigrated from the area during the summer and were not sampled later in the season. Juvenile pink salmon that survived until September or October during 2001–2003 were not significantly larger or smaller than the average juvenile during previous months. Under the assumption that juvenile pink salmon captured at sea were representative of the juvenile population at-large, size-selective mortality was not a significant force throughout the summer during these years. During 2004, however, juvenile pink salmon that survived until August or September were significantly smaller in July than the average fish, indicating that larger fish experienced size-selective mortality or emigrated from the study area during the summer of this year. In general, surviving fish were larger than the average juvenile caught during previous months in 2001 and 2003, while fish caught in September or October 2002 and 2004 were smaller than the average juvenile caught earlier in the summer. Catch per unit effort was much lower in August 2004 than in August 2001 and 2003 in Prince William Sound, the Alaska Coastal Current, and the front, and lower in September 2004 than in September 2003 in all regions, suggesting that juvenile pink salmon did migrate onto the continental shelf and out of the sampling area more quickly during 2004, when they were of a larger average size. Due to misidentification in the field, I was unable to examine trends in CPUE during August 2002. However, the Ocean Carrying Capacity (OCC) Program of the National Marine Fisheries Service (NMFS) found that juvenile pink salmon moved offshore more quickly during 2002 than during 2001 (J. Moss, NMFS, unpublished data). It thus appears that size-selective mortality removed smaller pink salmon throughout the summers of 2001 and 2003, while larger fish emigrated out of the sampling area more quickly during 2002 and 2004.

The larger size of juvenile pink salmon during 2002 and 2004 (high-survival years) compared to 2001 and 2003 (low-survival years) suggests that growth during the first five months at sea is directly related to smolt-adult survival. Pink salmon also grew faster (in total $g \cdot d^{-1}$) over the last full circulus increment just prior to capture during July and August of high-survival years than during low-survival years. However, pink salmon fry released in May 2002 and 2004 were smaller (0.56 and 0.59 g) than fry released in 2003 (0.7 g). Some combination of early environmental conditions and mortality processes during May–July severely affects growth and survival and must vary significantly among years; unfortunately, because no sampling was conducted during this period, it is difficult to pinpoint the causes of contrasting patterns of growth and mortality.

Pink salmon fry released into the peak of the zooplankton bloom survive better than later-released fry, which may encounter poor forage conditions and subsequently exhibit lower marine survival (Cooney et al. 1995). Pink salmon might have experienced good conditions (e.g. fewer predators, greater prey availability) soon after ocean entry in 2002 and 2004, leading to faster growth, larger body size, and subsequently higher survival. Juveniles in 2001 and 2003 might have encountered conditions leading to poor growth and decreased survival, such as suboptimal thermal experience, decreased prey availability, and/or density-dependent growth. The release of hatchery pink salmon at an earlier average date in 2003 could have caused them to miss optimal forage conditions and consequently exhibit poor growth and survival, preventing this cohort from taking advantage of their larger size at release.

Alternatively, high early size-selective mortality during high-survival years could have culled smaller individuals and left the larger survivors, which then performed well throughout the summer and on to adulthood. However, high relative CPUE in Prince William Sound in July 2002 suggests that early mortality was lower during May–July 2002 than during May–July 2001, 2003, and 2004. A combination of spatial and temporal differences in growing conditions, prey availability and accessibility, and predation likely influenced the early experience of juvenile pink salmon in Prince William Sound and the coastal Gulf of Alaska during each year. Additional sampling conducted frequently throughout the May–July period would help ascertain processes influencing growth and mortality shortly after ocean entry.

Ocean conditions and salmon survival appear to vary on regional scales of up to 1000 km, as opposed to basin-wide scales (Mueter et al. 2002). A strong relationship exists between temperature and early marine growth in salmonids (Weatherly and Gill 1995; Downton and Miller 1998; Mortensen et al. 2000; Orsi et al. 2000; Mueter et al. 2002; Mueter et al. 2005), and cool temperatures shortly after ocean entry may limit growth (Weatherly and Gill 1995; Mortensen et al. 2000; Schindler et al. 2005). Because no consistent pattern existed between thermal experience and growth for pink salmon during July–October, it is difficult to determine the effect of temperature on growth during 2001–2004. Cool temperatures in 2001 in July, when most fish were in Prince William Sound, perhaps resulted in reduced growth rates and smaller sizes throughout the summer and fall. Conversely, warm temperatures in July 2003 might have led to low over-winter survival by reducing fitness either directly or indirectly. The metabolism of fish increases with temperature, and a higher metabolism requires an increased ration of prey. If prey availability declined due to large numbers of hatchery releases or if warmer temperatures were associated with reduced zooplankton production in the spring, juvenile pink salmon might not have encountered sufficient amounts of key prey and subsequently experienced poor growth and survival during this year (Barber and Walker 1988).

However, density-dependent effects on growth may be stronger than the effects of environmental conditions (Schindler et al. 2005). Increases in abundance have been significantly related to reduced body size in sockeye salmon (Rogers and Ruggerone 1993; Pyper and Peterman 1999; Ruggerone and Rogers 2003). Ruggerone et al. (2003) found that the growth of sockeye salmon scales was below average in years of high pink salmon abundance, and above average during years where pink salmon were less abundant. Beamish and Mahnken (1999) argue that environmental conditions affect juvenile salmon more strongly than does density-dependence through the fall and winter of their first year, but that competition for prey might exacerbate environmental effects. Growth and survival are likely influenced by the interaction of surface temperature with factors such as prey availability, competition, and predation.

Interestingly, most of the disparity in growth between 2001/2003 and 2002/2004 was due to annual differences in the growth of hatchery, as opposed to wild, fish. Wild fish were larger than hatchery fish in 2001 and 2003 and not significantly different from hatchery fish in 2002 and 2004. This suggests that wild pink salmon were more resilient in the face of some stress or avoided some force that negatively affected the growth of hatchery fish during the low-survival years. Although releases of hatchery pink salmon in Prince William Sound may not affect wild stock productivity (Wertheimer et al. 2004), large hatchery releases may be resulting in density-dependent growth in pink salmon. Wild fish might perform better than hatchery fish in the face of this pressure. Alternatively, wild fish, which enter marine waters at much smaller sizes than hatchery fish, might have undergone severe early size-selective mortality, such that by July, size-selective mortality had culled the smaller individuals and the remaining larger fish enjoyed higher survival thereafter. If size-selective mortality operates on wild fish during fall-winter, it might be considerably lower than for the smaller hatchery fish.

The larger size of wild juvenile pink salmon compared to hatchery fish in 2001 and 2003 might also simply reflect the immigration of large unmarked hatchery fish from other regions into the sampling area during these years. We can be fairly confident that the unmarked fish caught in Prince William Sound through August originated in Prince William Sound, where 100% of hatchery-released fry are thermally marked. Studies on the incidence of thermally marked juvenile pink salmon in the coastal Gulf of Alaska found that only 0–2% of marked pink salmon caught west of Prince William Sound in July and August originated in Southeast Alaska (Farley and Munk 1997; Farley and Carlson 2000). However, hatcheries in Southeast Alaska do not mark all of their pink salmon fry. By September or October, unmarked fish from Southeast Alaska could have moved into Prince William Sound and across the Seward Line. Consequently, the unknown origin of unmarked fish caught during these months adds uncertainty to comparisons between hatchery and wild fish at larger sizes.

No differences in size at each circulus were observed among hatchery groups during each year. However, in some cases, smolt-adult survival varied widely among hatchery cohorts (Table 2.4). For example, although no differences in size were apparent as juveniles, pink salmon released from AFK hatchery in 2002 exhibited 4.5% smolt-adult survival while WNH fish experienced 16.8% survival (Prince William Sound Aquaculture Corporation 2005). WNH released approximately 68% of the number of pink salmon released by AFK hatchery during this year (WNH: 106,229,524; AFK: 156,325,094). If AFK juveniles did not suffer much higher early mortality than fish from WNH, and if growth directly related to smolt-adult survival, conditions experienced after the first growing season might strongly impact overall survival for pink salmon. Unfortunately, the data collected for this study were not sufficient to determine the CPUE of individual cohorts during July-October.

Specific growth over the last complete circulus increment did not differ among water masses each year, suggesting that pink salmon did not gain any immediate growth advantage after leaving Prince William Sound and that no particular water mass supported higher growth. Any differences in size among water masses likely resulted from the migration of larger fish further from Prince William Sound. However, hatchery pink salmon caught in Prince William Sound were larger than hatchery fish caught in the coastal Gulf of Alaska during some months. The largest fish during each month were therefore not necessarily furthest from Prince William Sound, although the greater trend was for pink salmon to increase in size as they migrated westward into the coastal Gulf of Alaska (Farley and Carlson 2000).

During each month, juvenile pink salmon had more complete circuli in high survival years than in low-survival years. Circuli formed at the fastest rate in 2004, when juvenile pink salmon were large, and slowest rate in 2001, when pink salmon were smaller than in other years. Circulus formation rate was slightly faster in 2003 than in 2002, however, suggesting that no consistent relationship exists between fish size and circulus formation rate. Potential misidentification of the last complete circulus could have affected estimates of the rate of circulus formation.

The fact that high-survival years were both even years raises questions of odd-even year variability in Prince William Sound pink salmon. Because their fixed two-year life span prevents stocks from overlapping, broods of pink salmon from odd and even years are genetically distinct. However, no evidence of inherent differences in mean size or growth rate between odd and even year cohorts exists for pink salmon in Prince William Sound.

Although r^2 was consistently around 0.80 and significant, the linear relationship between fork length and scale radius in juvenile pink salmon was not as strong as expected. This may have affected my interpretation of growth patterns from scales. Because residuals were evenly distributed around the regression line across all scale radii and variances were independent of predicted values, growth estimates are probably reasonably accurate, though less precise than anticipated. For this reason, I am confident that I captured the average relationship between scale radius and fish fork length.

Conclusions

Juvenile pink salmon were consistently larger throughout the summer and early fall of 2002 and 2004 than in 2001 and 2003, indicating that larger, faster-growing juveniles experienced higher survival. Size-selective mortality removed smaller pink salmon during July–October 2001 and 2003, but was not severe. Wild juvenile pink salmon were larger than hatchery fish during low-survival years, but not different in size from hatchery fish during high-survival years. During low-survival years, wild pink salmon perhaps were more resilient in the face of some stress, experienced severe early size-selective mortality, or avoided some force that negatively affected the growth of hatchery fish. No differences in size were found among hatchery groups during each year, although, in some cases, smolt-adult survival varied widely among these cohorts. Conditions experienced after the first growing season thus might also affect overall survival. Juvenile pink salmon did not gain any immediate growth advantage in the northern coastal Gulf of Alaska after leaving Prince William Sound, but appeared to migrate onto the continental shelf and out of the sampling area more quickly during 2002 and 2004, when they were of a larger average size. No consistent pattern existed between thermal experience and growth for pink salmon during July–October. The interaction of surface temperatures, prey availability and accessibility, competition, and predation likely influences juvenile growth and survival, and varies from year to year.

Related research will compare early marine growth in the juvenile population at large to the early marine growth of pink salmon that survived to adulthood to gain further insight on the timing and importance of early ocean growth. Bioenergetics modeling will further investigate the possibility of density-dependent growth as well as the effects of habitat quality (prey availability and thermal experience) on growth performance. In light of global warming, additional research on the effects of temperature on prey availability, density-dependent growth, and survival is urgent and essential.

Table 2.1. Sampling dates and locations in Prince William Sound (PWS), the coastal Gulf of Alaska (GAK), Cape Fairfield (CF), and West Fairfield (WF) during July–October 2001–2004, and the total number of juvenile pink salmon caught during each month.

Start date	End date	Stations sampled	Total juvenile pink salmon
7/8/01	7/14/01	PWS 1-3; GAK 1-6	2794
8/11/01	8/19/01	PWS 1-3; GAK 1, 1i-6	308
9/18/01	9/22/01	PWS 1-3; GAK 1-6	*
10/21/01	10/24/01	PWS 1-3; GAK 1-5	13
7/20/02	7/26/02	PWS 1-3; GAK 1i-6	2704
8/20/02	8/24/02	PWS 1-3; GAK 1i-10	*
10/3/02	10/4/02	GAK 1i-6	12
7/13/03	7/19/03	PWS 1-3; GAK 1i-6; CF 1, 5, 10	677
8/1/03	8/7/03	PWS 1, 3; GAK 1i-6; CF 0, 9, 12, 13; WF 1, 2	417
9/9/03	9/15/03	PWS 1-3; GAK 1i-6; CF 5, 6, 12, 13	147
7/18/04	7/24/04	PWS 1-3; GAK 1i-5; CF 3, 6, 10, 11	1655
8/17/04	8/23/04	PWS 1-3; GAK 1i-6; CF 3, 4, 5, 10, 11	190
9/12/04	9/17/04	PWS 1-3; GAK 1i, 2, 6, 7; CF 1, 2, 4, 6, 8	30

* Due to misidentification in the field, the total number of juvenile pink salmon caught this month is unknown.

Table 2.2. The number of juvenile pink salmon represented in scale samples (total n = 676). Pink salmon were caught during July–October 2001–2004 in Prince William Sound (PWS), the Alaska Coastal Current (ACC), the front, and the mid-shelf transition zone (Trans), and belonged to the Armin F. Koernig (AFK), Cannery Creek (CCH), Solomon Gulch (SGH), or Wally Noerenberg (WNH) hatcheries, or the unmarked "wild" cohort (N).

Year	**Month**	**Water Mass**	**AFK**	**CCH**	**SGH**	**WNH**	**N**	**?**	**Grand Total**
2001	July	PWS	5	4	13	13	8		**43**
	July Total		**5**	**4**	**13**	**13**	**8**		**43**
	August	ACC	2		3	2	45	1	**53**
		PWS	16	12	18	15	24		**85**
		Trans	2	1	4	1	15		**23**
	August Total		**20**	**13**	**25**	**18**	**84**	**1**	**161**
	September	ACC	1		1		8		**10**
		PWS	1	2			12		**15**
		Trans	10	6	1	2	50		**69**
	September Total		**12**	**8**	**2**	**2**	**70**		**94**
	October	ACC					2		**2**
		PWS					2		**2**
		Trans		1			6		**7**
	October Total			**1**			**10**		**11**
	Grand Total		**37**	**26**	**40**	**33**	**172**	**1**	**309**
2002	July	PWS		2	11	1	1	1	**16**
		Trans			3	3	1		**7**
	July Total			**2**	**14**	**4**	**2**	**1**	**23**
	August	ACC		2			2		**4**
		Front					2		**2**
		PWS		3		3	9		**15**
		Trans		4	5		11		**20**
	August Total			**9**	**5**	**3**	**24**		**41**
	October	ACC					4		**4**
		?					3		**3**
	October Total						**7**		**7**
	Grand Total			**11**	**19**	**7**	**33**	**1**	**71**

Table 2.2 (continued)

Year	Month	Water Mass	AFK	CCH	SGH	WNH	N	?	Grand Total
2003	July	ACC	1	1	1				**3**
		Front			1	1			**2**
		PWS		2	4	1	6		**13**
	July Total		**1**	**3**	**6**	**2**	**6**		**18**
	August	ACC	1	3	3	1	17		**25**
		Front			1	1	3		**5**
		PWS	2	3	2		3		**10**
		Trans	1	4	3	2	8		**18**
	August Total		**4**	**10**	**9**	**4**	**31**		**58**
	September	ACC	1				25		**26**
		Front					2		**2**
		Trans					7		**7**
	September Total		**1**				**34**		**35**
	Grand Total		**6**	**13**	**15**	**6**	**71**		**111**
2004	July	ACC	1	7	2	2	3		**15**
		Front			5	2	13		**20**
		PWS	2	8	3	6	7		**26**
		Trans	2	3	4	5	24		**38**
	July Total		**5**	**18**	**14**	**15**	**47**		**99**
	August	ACC	2				20		**22**
		Front	1				10		**11**
		Trans					34		**34**
	August Total		**3**				**64**		**67**
	September	ACC					5		**5**
		PWS	1			2	2		**5**
		?					9		**9**
	September Total		**1**			**2**	**16**		**19**
	Grand Total		**9**	**18**	**14**	**17**	**127**		**185**

Table 2.3. The number of pink salmon released by Armin F. Koernig (AFK), Cannery Creek (CCH), Solomon Gulch (SGH), and Wally Noerenberg (WNH) hatcheries during 2001–2004. The date of last release and average weight at release are also given for each release group. Source: Alaska Department of Fish and Game 2005

Year	Hatchery	Total released	Last release	Avg. wt (g)
2001	AFK	77,941,373	5/7	0.46
	WNH	58,767,800	5/7	0.71
	WNH	68,882,449	5/17	0.69
	SGH	203,897,201	5/18	0.60
	AFK	72,346,557	5/23	0.48
	CCH	139,226,716	5/31	0.32
	Total	621,062,096	5/18	0.53
2002	AFK	78,402,575	5/10	0.43
	WNH	51,859,376	5/10	0.60
	WNH	54,370,148	5/19	0.69
	SGH	202,573,328	5/23	0.68
	AFK	77,922,519	5/25	0.58
	CCH	138,626,713	5/31	0.39
	Total	603,754,659	5/21	0.56
2003	AFK	73,090,583	5/1	0.68
	WNH	60,032,016	5/1	0.74
	SGH	130,977,332	5/2	0.41
	WNH	29,866,690	5/7	0.85
	AFK	35,145,651	5/12	0.97
	SGH	75,420,275	5/14	0.77
	WNH	29,655,037	5/14	1.09
	AFK	38,170,988	5/19	1.00
	CCH	135,584,680	5/31	0.68
	Total	607,943,252	5/12	0.70
2004	SGH	71,935,299	5/3	0.62
	SGH	72,359,988	5/4	0.57
	AFK	84,490,553	5/6	0.54
	WNH	55,968,308	5/7	0.58
	SGH	78,162,281	5/14	0.86
	AFK	37,899,397	5/20	0.66
	AFK	48,070,195	5/20	0.72
	CCH	136,288,850	5/20	0.37
	WNH	28,137,181	5/20	0.59
	WNH	25,534,807	5/20	0.73
	Total	638,846,859	5/12	0.59

Table 2.4. The average weight of pink salmon fry at release and total number released by Armin F. Koernig (AFK), Cannery Creek (CCH), Solomon Gulch (SGH), and Wally Noerenberg (WNH) hatcheries during 2001–2004, the number of adult pink salmon that returned to each hatchery the following year, and overall smolt-adult survival. Sources: (Eggers 2003; Plotnick and Eggers 2004; Eggers 2005; Prince William Sound Aquaculture Corporation 2005; K. Morgan, Valdez Fisheries Development Association, personal communication).

Year	Hatchery	Avg. wt. (g)	Total Released	Total Returned	Survival (%)
2001	AFK	0.47	150,287,930	7,759,064	5.2
	CCH	0.32	139,226,716	1,588,603	1.1
	SGH	0.60	203,897,201	5,265,239	4.4
	WNH	0.70	127,650,249	5,617,122	2.6
	Total	0.53	621,062,096	20,230,028	3.3
2002	AFK	0.50	155,982,828	7,065,581	4.5
	CCH	0.39	138,626,713	8,288,949	6.0
	SGH	0.68	202,573,328	17,374,811	16.8
	WNH	0.65	106,229,524	17,847,316	8.6
	Total	0.56	603,412,393	50,576,657	9.0
2003	AFK	0.83	146,407,222	5,230,138	3.6
	CCH	0.68	135,584,680	2,761,241	2.0
	SGH	0.54	206,397,607	11,139,932	2.3
	WNH	0.85	119,533,743	2,704,727	5.4
	Total	0.70	607,923,252	21,836,038	3.3
2004	AFK	0.62	174,371,351	10,568,869	6.1
	CCH	0.37	136,288,850	11,743,635	8.6
	SGH	0.69	222,457,568	17,833,491	8.0
	WNH	0.62	109,640,296	8,018,603	7.3
	Total	0.59	642,758,065	30,331,107	7.5

Table 2.5. The total number of circuli at capture, estimated date of circulus formation, and average back-calculated weight (BCW) and observed weight at each circulus for juvenile pink salmon during July–October 2001–2004. Estimated weights for 2001 were determined from hatchery fish, while the pooled group of hatchery and wild fish was used to estimate average weight at circuli during 2002, 2003, and 2004.

2001

Total	Date of circ.	BCW		Obs. weight	
circuli	formation	Avg. (g)	2SE (g)	Avg. (g)	2SE (g)
3	27-Jun	4.2		3.7	
4	3-Jul	5.0		4.8	
5	9-Jul	7.0	1.0	6.8	1.5
6	15-Jul	7.7	0.8	7.9	0.8
7	21-Jul	9.4	1.0	9.5	0.9
8	27-Jul	11.8	1.7	11.7	1.7
9	2-Aug	15.8	3.9	15.6	3.6
10	8-Aug	24.7	4.2	24.7	3.9
11	15-Aug	24.7	1.7	24.4	1.6
12	21-Aug	28.5	2.7	28.6	2.6
13	27-Aug	32.9	2.5	33.2	2.6
14	2-Sep	41.9	5.8	42.4	5.5
15	8-Sep	49.1	6.3	49.9	6.4
16	14-Sep	54.2	4.5	55.3	4.9
17	20-Sep	61.4	5.7	62.0	6.5
18	26-Sep	60.7	5.6	61.0	6.0
19	3-Oct	72.7	15.4	70.3	11.0
20	9-Oct	97.6	23.1	99.9	25.3
21	15-Oct	105.1	33.1	108.6	27.1
22	21-Oct				

2002

Total	Date of circ.	BCW		Obs. weight	
circuli	formation	Avg. (g)	2SE (g)	Avg. (g)	2SE (g)
3	26-Jun				
4	2-Jul				
5	8-Jul				
6	14-Jul	7.7		8.4	
7	19-Jul	7.9		8.3	
8	25-Jul	12.7	6.1	11.7	4.4
9	31-Jul	19.1	4.5	18.5	4.9
10	6-Aug	23.7	3.0	24.1	2.9
11	12-Aug	27.1	5.1	26.9	5.3
12	17-Aug	29.1	5.2	29.0	5.4
13	23-Aug	35.3	6.2	35.2	6.2
14	29-Aug	43.0	5.5	43.0	3.9
15	4-Sep	69.6	13.3	75.2	15.7
16	10-Sep	52.9		46.3	
17	15-Sep				
18	21-Sep	79.0	15.4	76.3	19.8
19	27-Sep	66.9	15.4	66.1	14.1
20	3-Oct				
21	9-Oct				
22	14-Oct				

Table 2.5 (continued)

2003

Total circuli	Date of circ. formation	BCW Avg. (g)	BCW 2SE (g)	Obs. weight Avg. (g)	Obs. weight 2SE (g)
3	29-Jun				
4	4-Jul	8.3		7.5	
5	10-Jul				
6	15-Jul	6.4		6.4	
7	20-Jul	9.5	3.5	9.7	4.0
8	26-Jul	13.7	1.8	13.4	1.6
9	31-Jul	16.5	2.1	16.7	2.2
10	6-Aug	19.0	3.2	18.7	2.9
11	11-Aug	22.4	3.2	22.3	2.8
12	17-Aug	23.7	1.9	23.8	1.9
13	22-Aug	30.9	4.4	30.4	4.7
14	27-Aug	37.0	2.1	38.1	2.4
15	2-Sep	37.3	7.8	38.7	8.0
16	7-Sep	51.4	11.3	51.5	11.0
17	13-Sep	51.1	16.4	50.8	14.4
18	18-Sep	50.6	13.9	49.1	13.2
19	24-Sep	70.0		73.7	
20	29-Sep				
21	4-Oct				
22	10-Oct	64.5		63.0	

2004

Total circuli	Date of circ. formation	BCW Avg. (g)	BCW 2SE (g)	Obs. weight Avg. (g)	Obs. weight 2SE (g)
3	26-Jun				
4	30-Jun				
5	5-Jul	9.2		8.9	
6	9-Jul				
7	14-Jul	6.4		6.1	
8	18-Jul	12.1	2.2	12.7	2.0
9	22-Jul	15.5	2.0	15.7	2.0
10	27-Jul	20.7	1.5	20.5	1.6
11	31-Jul	23.5	2.4	24.1	2.6
12	5-Aug	25.7	3.0	26.0	3.5
13	9-Aug	29.4	2.7	29.3	3.2
14	14-Aug	32.5	5.6	33.3	5.9
15	18-Aug	35.2	4.9	35.2	5.1
16	22-Aug	52.0	11.7	53.0	12.8
17	27-Aug	46.5	16.3	46.7	19.1
18	31-Aug	41.7	16.5	40.8	15.9
19	5-Sep	36.5	12.8	38.1	12.5
20	9-Sep	56.3	14.3	54.1	16.0
21	14-Sep	66.2	12.7	66.7	18.1
22	18-Sep	69.6	10.5	73.1	11.4

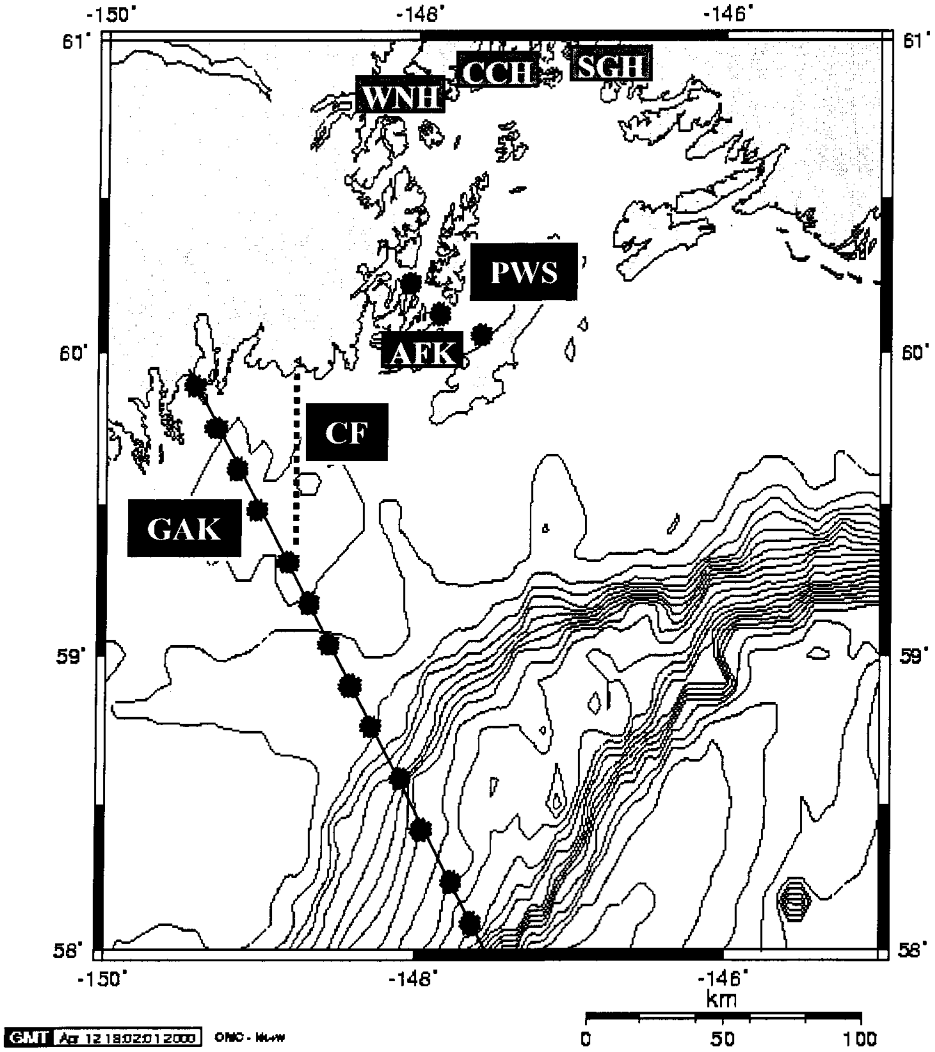

Figure 2.1. Locations of Prince William Sound (PWS), Gulf of Alaska (GAK), and Cape Fairfield (CF) stations (in black). Station one is the station closest to shore on all lines. Also shown (in gray) are the approximate locations of the four hatcheries in PWS that release pink salmon: Armin F. Koernig (AFK), Cannery Creek (CCH), Solomon Gulch (SGH), and Wally Noerenberg (WNH).

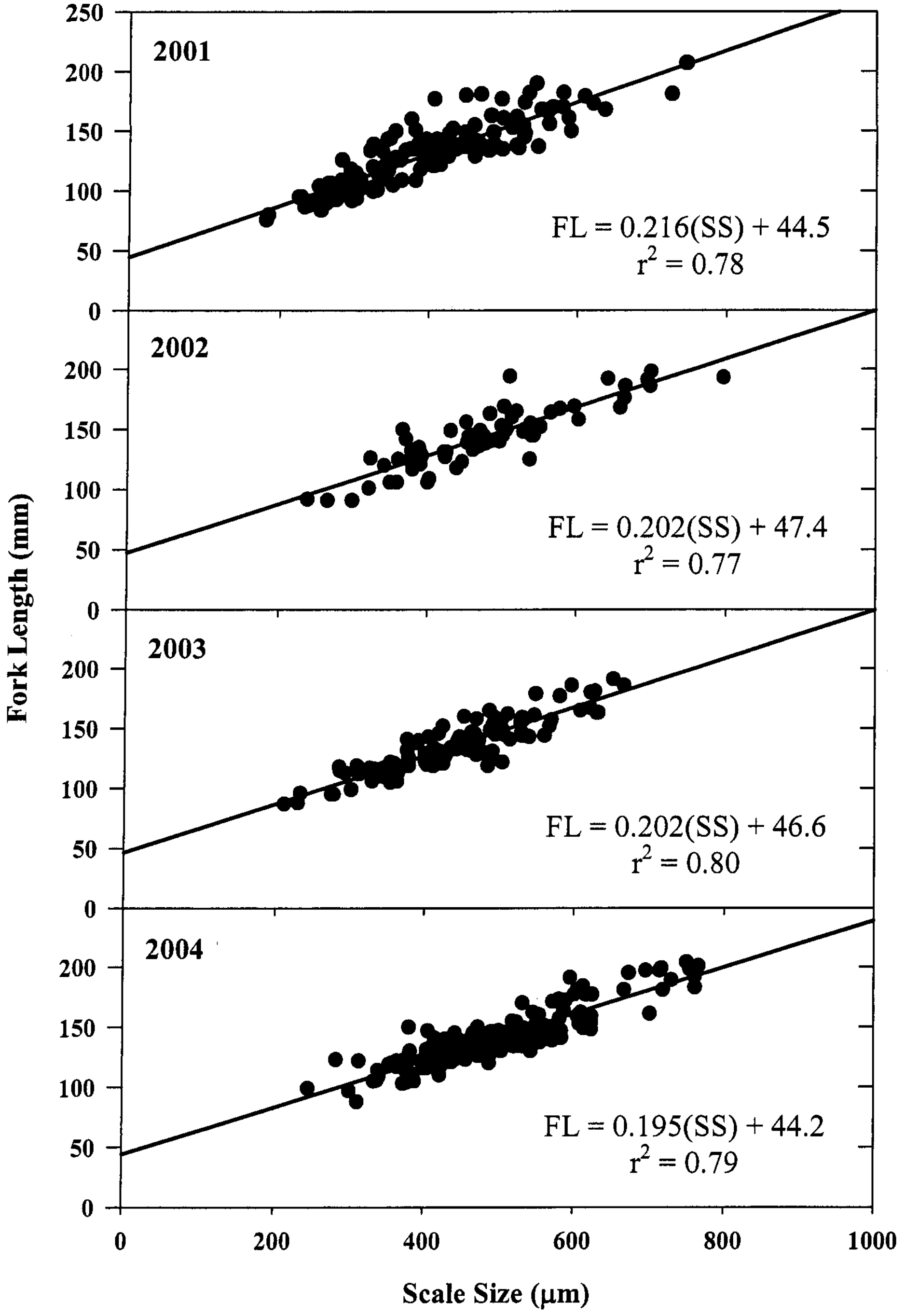

Figure 2.2. A linear relationship between fork length (FL; mm) and scale radius (SS; μm) exists for juvenile pink salmon. The relationship for 2001 was determined using only hatchery fish, but the pooled group of hatchery and wild fish was used in the regressions for 2002, 2003, and 2004.

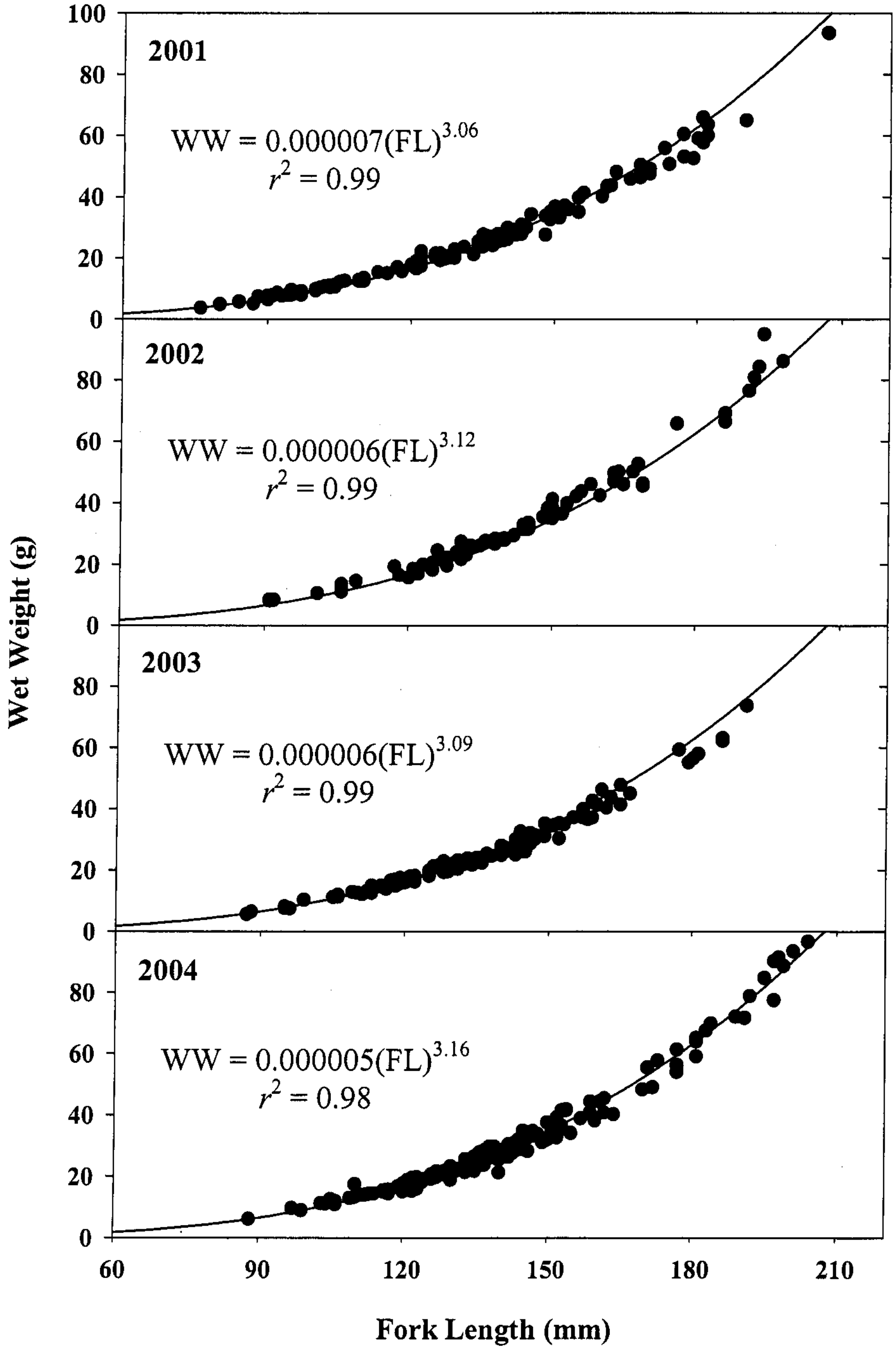

Figure 2.3. Fork length (FL; mm) is significantly related to wet weight without stomach contents (WW; g) in juvenile pink salmon. The relationship for 2001 was determined using only hatchery fish, but the pooled group of hatchery and wild fish was used in the regressions for 2002, 2003, and 2004.

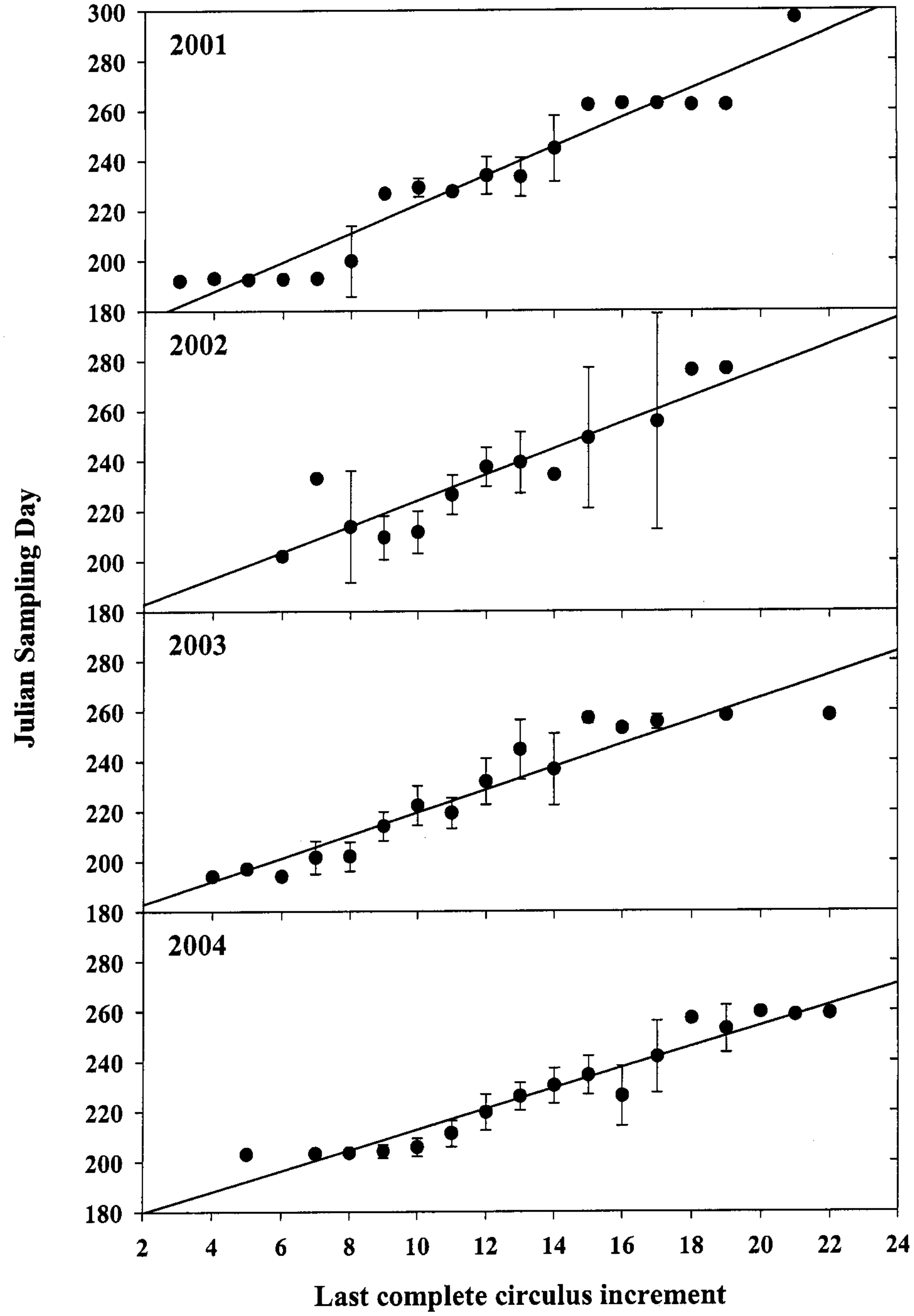

Figure 2.4. The rate of circulus formation for juvenile pink salmon during 2001-2004, estimated by regressing the day of the year on which each fish was caught (day 200 = July 19) on the number of complete circuli the fish had at capture. Shown above at each circulus is the mean Julian sampling day ± 2SE. The relationship for 2001 was determined using only hatchery fish, but the pooled group of hatchery and wild fish was used in the regressions for 2002, 2003, and 2004.

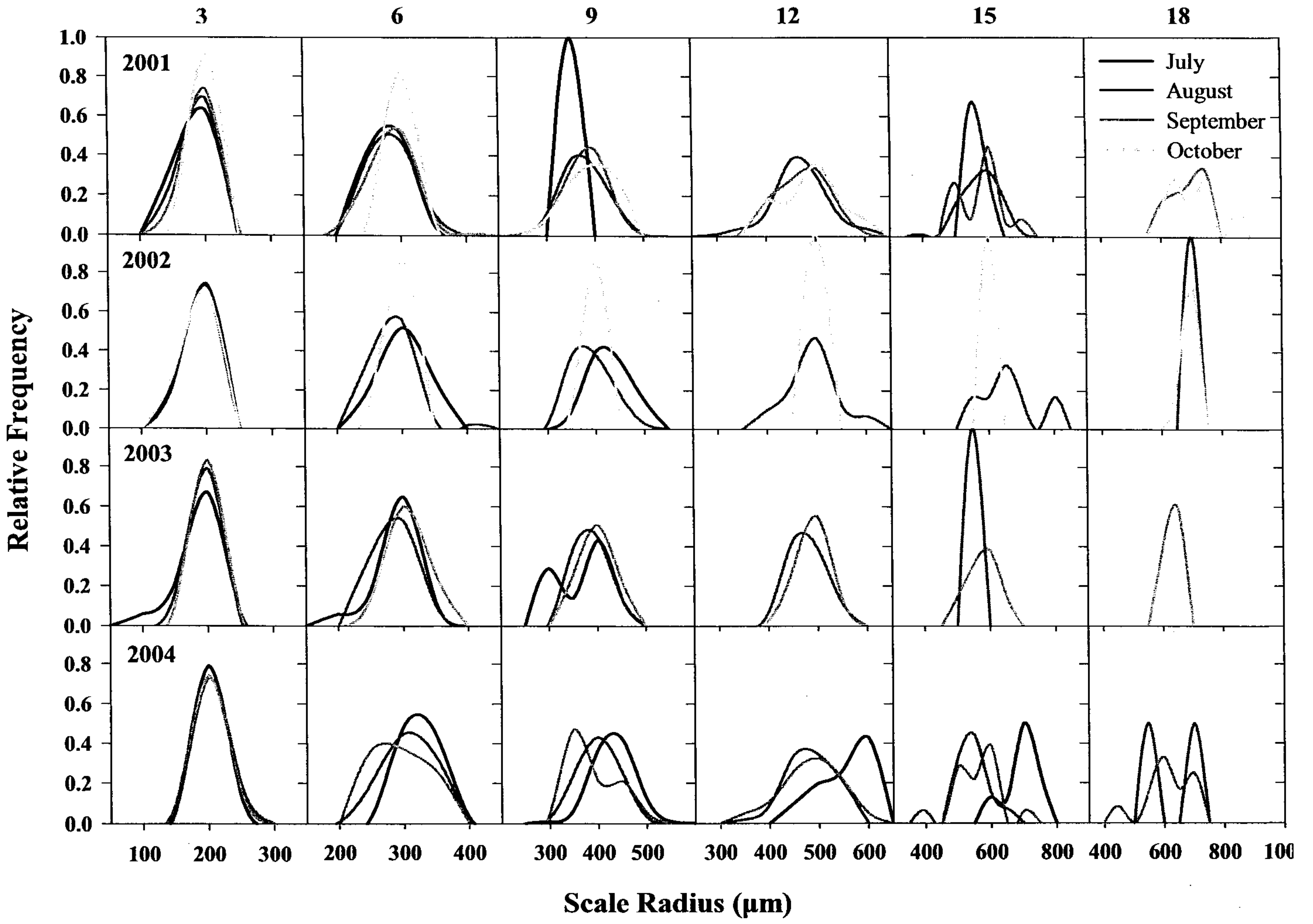

Figure 2.5. The relative distribution of scale measurements (μm) at every third circulus from juvenile pink salmon collected during July–October 2001–2004, in bins of 50 μm.

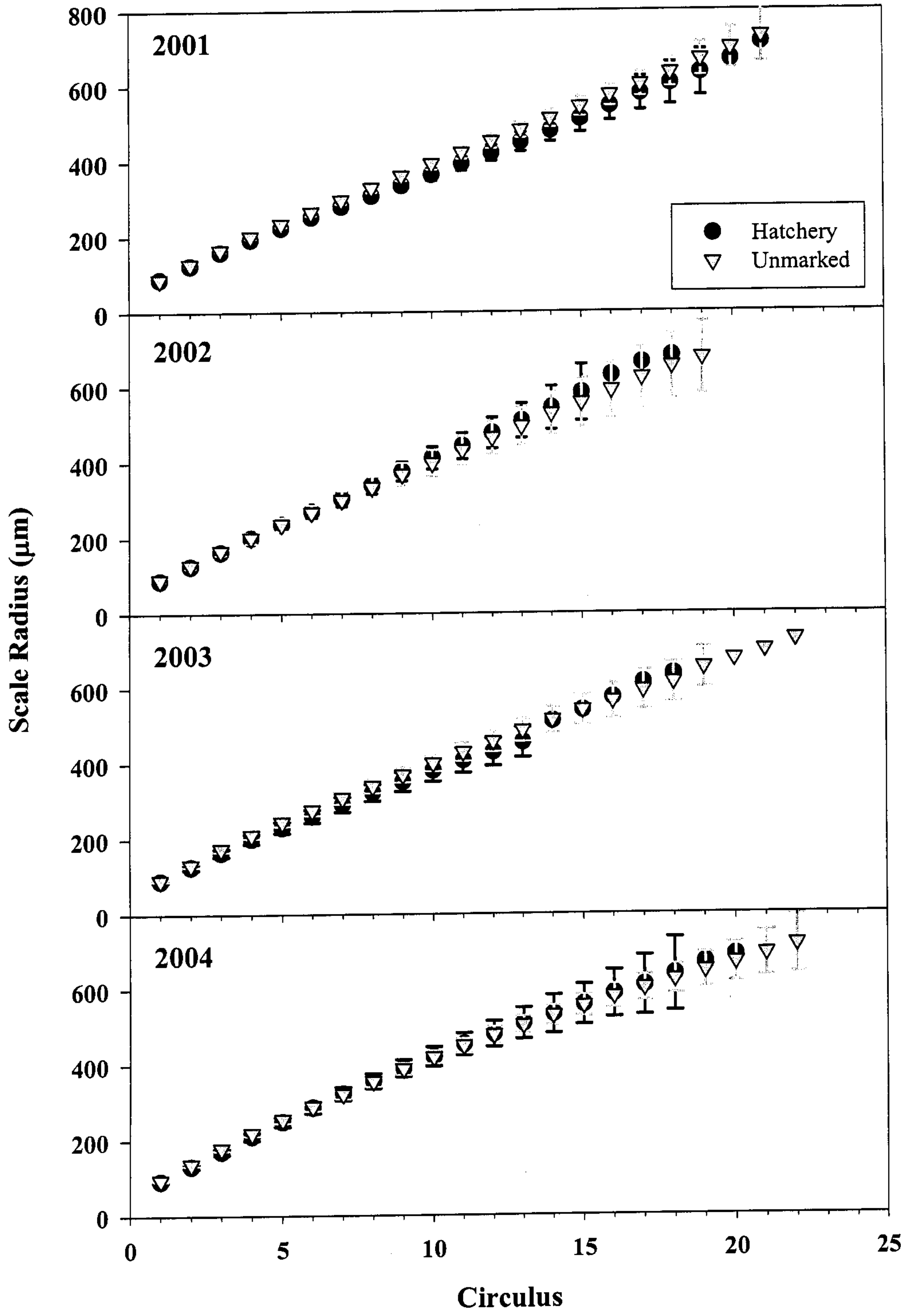

Figure 2.6. Average scale size (µm) at each circulus for hatchery and unmarked "wild" juvenile pink salmon caught during July–October 2001–2004. Error bars are ± 2SE.

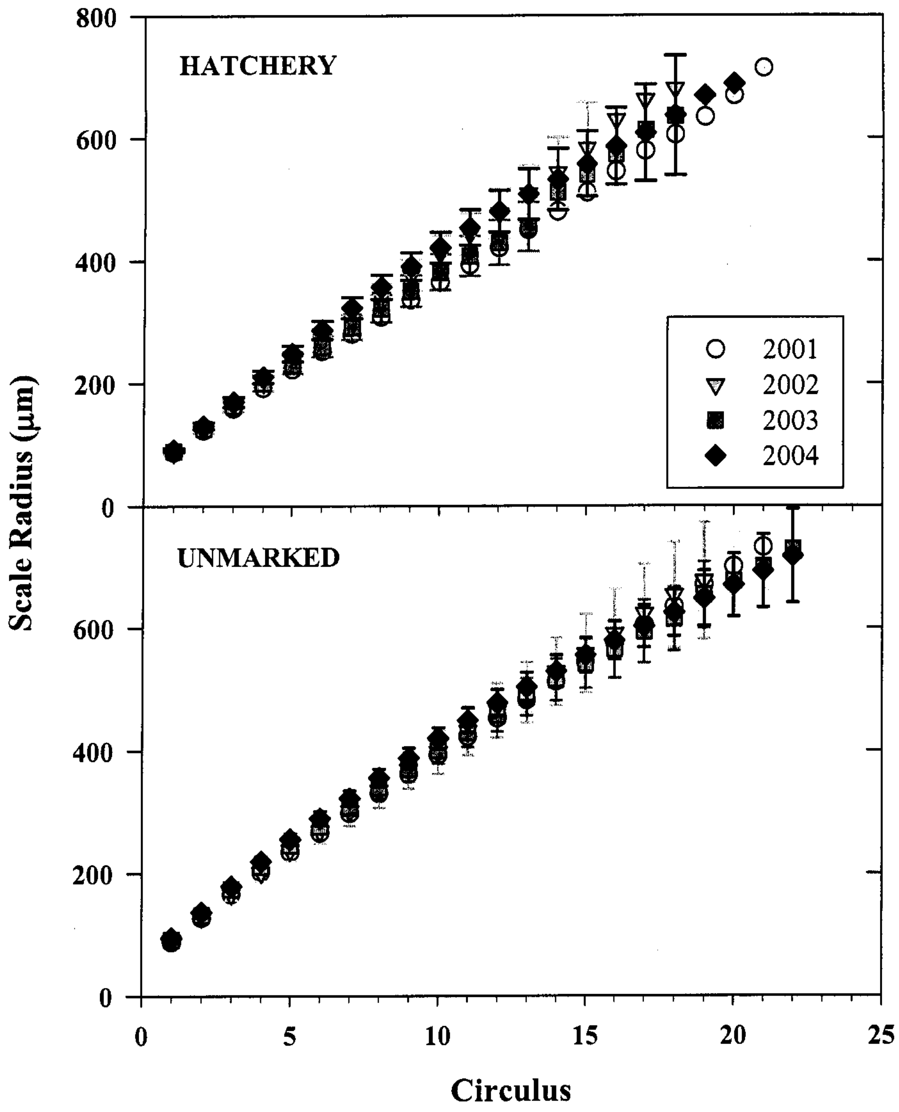

Figure 2.7. Interannual differences in average scale size (µm) at each circulus for hatchery and unmarked "wild" juvenile pink salmon caught during July–October 2001–2004. Error bars are ± 2SE.

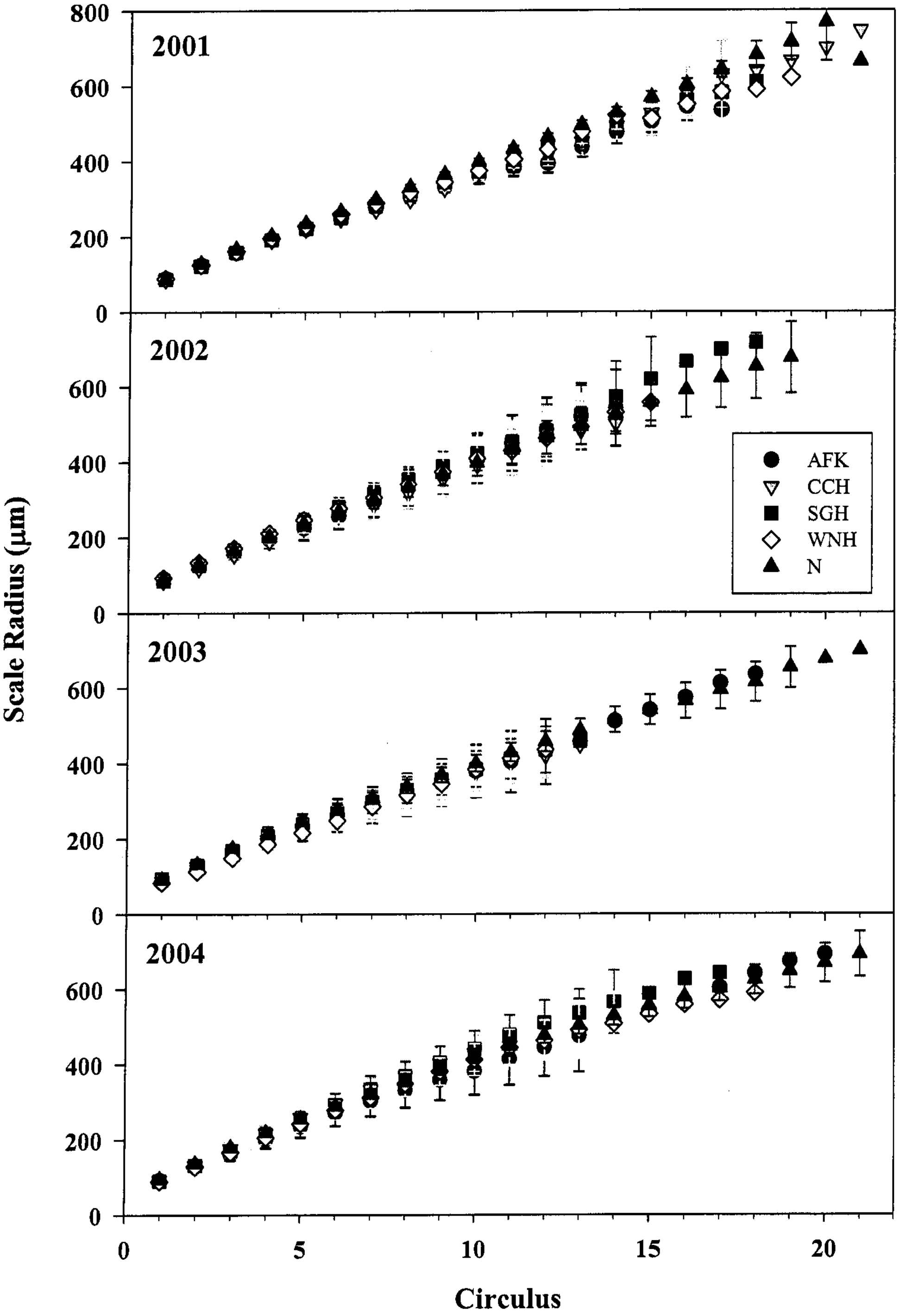

Figure 2.8. Average scale size (µm) at each circulus for cohorts of juvenile pink salmon from individual hatcheries and unmarked "wild" fish during July–October 2001–2004. AFK = Armin F. Koernig, CCH = Cannery Creek, SGH = Solomon Gulch, WNH = Wally Noerenberg, N = unmarked. Error bars are ± 2SE.

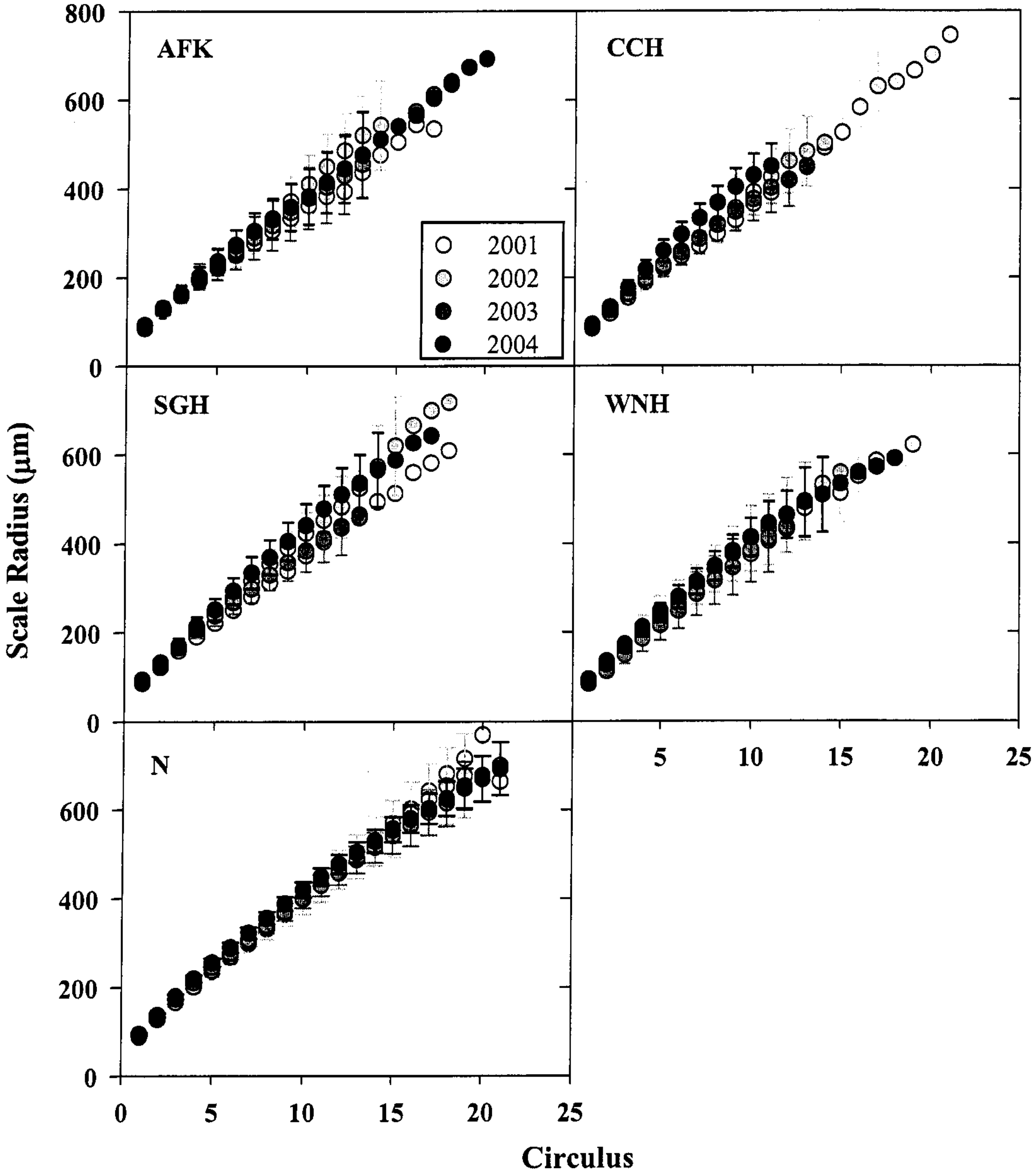

Figure 2.9. Interannual differences in average scale size (µm) at each circulus for individual hatchery cohorts and unmarked "wild" juvenile pink salmon caught during July–October 2001–2004. AFK = Armin F. Koernig, CCH = Cannery Creek, SGH = Solomon Gulch, WNH = Wally Noerenberg, N = unmarked. Error bars are ± 2SE.

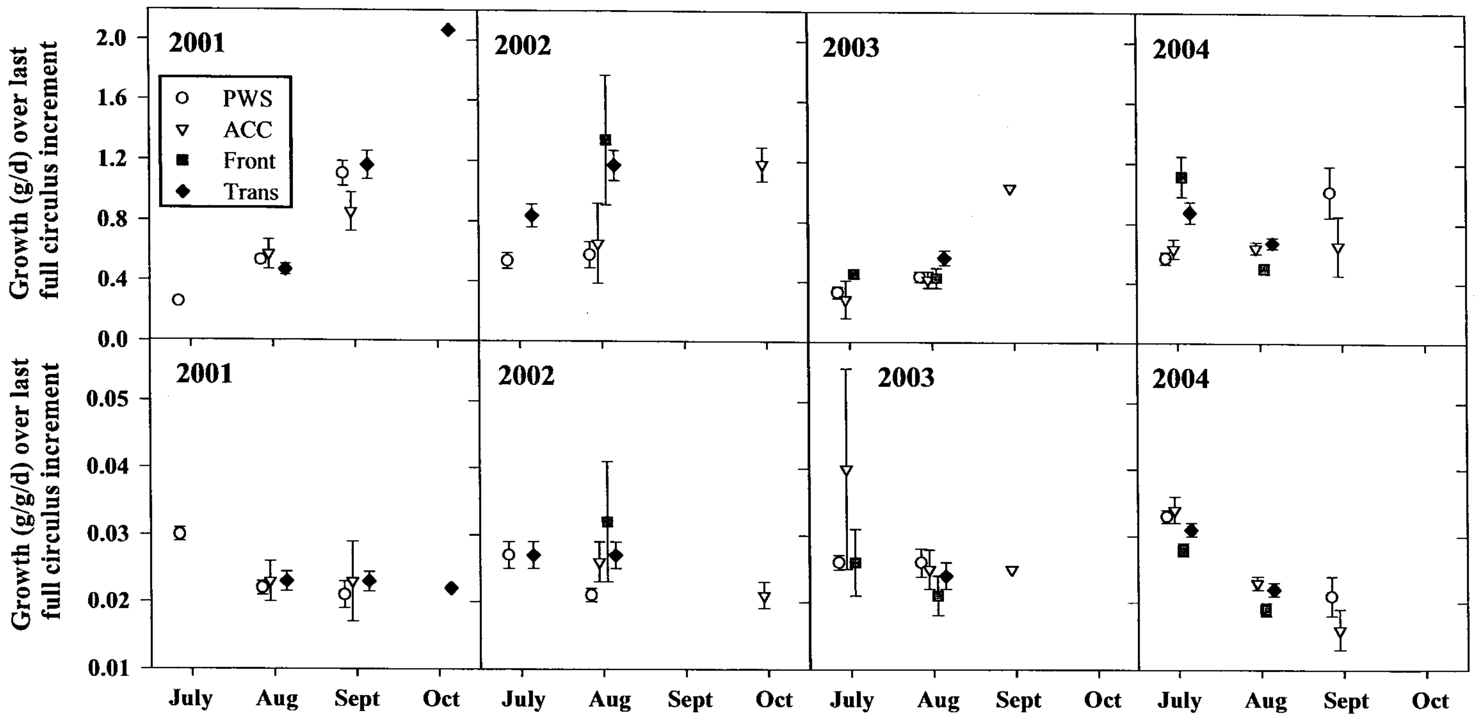

Figure 2.10. Growth (g·d^{-1} and g·g^{-1}·d^{-1}) over the last full circulus increment for juvenile pink salmon caught in different water masses during July–October 2001–2004. PWS = Prince William Sound, ACC = Alaska Coastal Current, Trans = mid-shelf transition region. Error bars are ± SE.

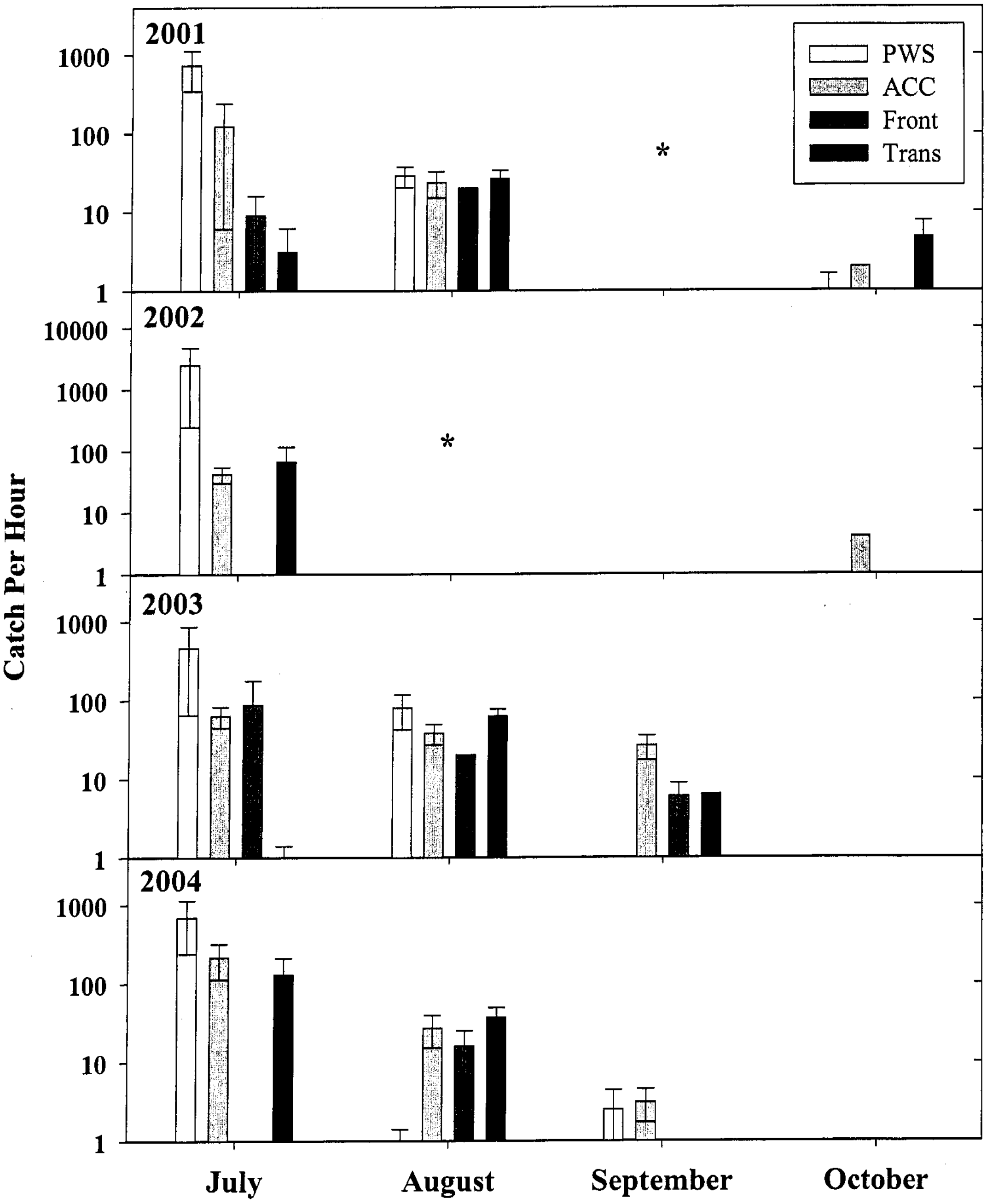

Figure 2.11. Average catch per unit effort (CPUE; fish·h^{-1}) during July–October 2001–2004 in Prince William Sound (PWS) and the Alaska Coastal Current (ACC), front, and mid-shelf transition (Trans) regions of the coastal Gulf of Alaska. Error bars are ± SE. Note that the y-axis is on a log scale. * Due to misidentification in the field, no CPUE data is available for September 2001 or August 2002.

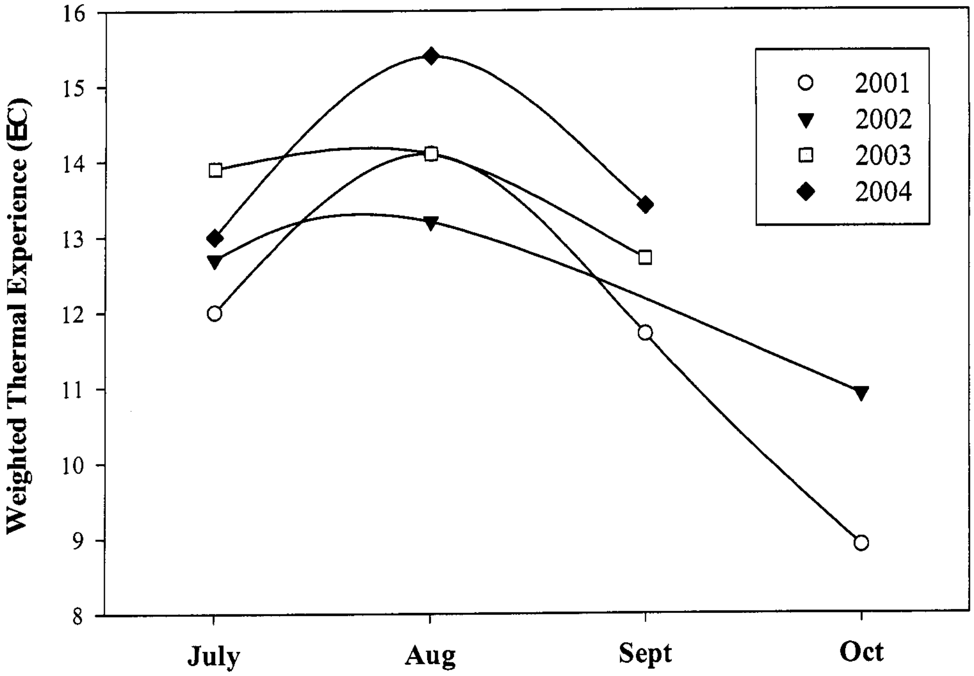

Figure 2.12. The average thermal experience over the top 10 m for juvenile pink salmon during July–October 2001–2004, weighted by the catch per unit effort in Prince William Sound, the Alaska Coastal Current, the front, and the mid-shelf transition region of the coastal Gulf of Alaska. Because CPUE was unavailable for September 2001 and August 2002, the average temperature over all water masses substituted for the average thermal experience during these months.

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Chapter 3. The Relationship Between Early Marine Growth and Smolt-to-Adult Survival of Prince William Sound Pink Salmon

INTRODUCTION

Although early marine growth has repeatedly been correlated with overall survival in Pacific salmon (*Oncorhynchus* spp.; Holtby et al. 1990; Henderson and Cass 1991; Murphy et al. 1998; Tovey 1999; Willette et al. 1999; Mortensen et al. 2000; Beamish et al. 2004), we currently lack a mechanistic understanding of the timing, magnitude, and source of stage-specific marine survival. The run size of adult pink salmon (*O. gorbuscha*) returning to Prince William Sound has varied widely in recent years and is difficult to accurately predict based on our current understanding of factors contributing to the survival of pink salmon. Smolt-to-adult survival of pink salmon was lower than average for hatchery juveniles released in 2001 and 2003 (3% for each year), and high for pink salmon released in 2002 (9%) and 2004 (8%; (Alaska Department of Fish and Game 2005; Prince William Sound Aquaculture Corporation 2005); K. Morgan, Valdez Fisheries Development Association, personal communication). This study compares the early marine growth of juvenile pink salmon captured during the first summer at sea with the early marine growth of fish from the same year-class that survived to adulthood.

Prince William Sound hatcheries time their release of fry to coincide with the spring zooplankton bloom, which typically occurs in May (Cooney et al. 1995). Juvenile pink salmon migrate westward out of Prince William Sound to the coastal Gulf of Alaska by July or early August (Cooney 1993, Farley and Carlson 2000), move off the continental shelf by their first winter, and return to Prince William Sound the following summer as adults (Heard 1991). Although some juvenile pink salmon remain in Prince William Sound through October, the most common pattern is to migrate to the coastal Gulf of Alaska around July. On account of their two-year life cycle, juvenile pink salmon that entered the ocean during 2001-2004 returned as adults during the following summers of 2002-2005.

Pink salmon fry migrate to sea at a smaller size than any other salmonid (Quinn 2005). Wild fish enter the marine environment at approximately 0.26 g (Bailey et al. 1976; Boldt and Haldorson 2002), and the average weight at release for the 2001-2004 hatchery cohorts in Prince William Sound was 0.53 g, 0.56 g, 0.70 g, and 0.59 g, respectively (Alaska Department of Fish and Game 2005). Due to their small size at ocean entry, juvenile pink salmon are highly vulnerable to predation during their first months in marine waters (Hunter 1959), and consequent high juvenile mortality markedly affects adult year-class strength. Mortality rates for several Pacific salmon species have been estimated at 2-8% per day after ocean entry (Parker 1968; Fisher and Pearcy 1988), but as high as 46% per day (Bax 1983). Mortality decreases during the first 40 d after ocean entry (Bax 1983), and drops to less than 1% per day later in life (Pearcy 1992). Predators consume approximately 75% of pink salmon fry during their first 45-60 days in Prince William Sound (Cooney et al. 2001b). The first weeks at sea are often referred to as a "critical period" for growth in salmon, since significant mortality occurs during this time (Parker 1968; Beamish and Mahnken 2001).

Rapid growth can minimize predation mortality (Parker 1971; Hargreaves and LeBrasseur 1985; Heard 1991; Jaenicke and Celewycz 1994). Larger fish are thought to survive better than smaller individuals (Mortensen et al. 2000), and reduced mortality has been associated with larger size or faster growth of juveniles (Willette 2001). A study of juvenile Chinook salmon (*O. tshawytscha*) showed that faster-growing smolts were of higher quality and had higher marine survival than slower-growing smolts, most likely due to their ability to escape size-selective predation (Beckman et al. 1999). Size-selective mortality of chum salmon (*O. keta*) has been observed during the time when the fish laid down circuli 2–4 on their scales (Healey 1982).

However, size and growth soon after ocean entry might not determine year-class strength in all years, and the factors that affect survival could vary among years. Some studies suggest that smolt size relates poorly to early marine growth and survival (Bilton et al. 1982; Pearcy 1992), or that growth during the juvenile stage does not relate to survival in all years (Holtby et al. 1990; Mortensen et al. 2000). Size at marine entry could influence survival to adulthood more than juvenile growth (Willette et al. 1999; Willette 2001). Age-2 sockeye salmon smolts from four lake systems in Bristol Bay, Alaska, achieve higher survival on average than smaller age-1 smolts (Quinn 2005). Other studies indicate that growth might become more important during the late fall and winter of the first year of marine life, when salmon may face a second critical period (Beamish and Mahnken 2001; Beamish et al. 2004; Moss et al. 2005). Under this hypothesis, juvenile salmon that do not achieve a threshold size by the end of their first summer at sea will not survive the following winter (Beamish and Mahnken 2001).

Pink salmon are hypothesized to undergo a two-stage mortality process, with the first mortality period occurring soon after ocean entry, and the second after the first growing season, presumably during the winter (Beamish and Mahnken 1999, 2001; Moss et al. 2005). Temperature and prey availability greatly affect pink salmon metabolism, growth and survival (Brett et al. 1969; Weatherly and Gill 1995; Orsi et al. 2000; Mueter et al. 2005). The relative importance of initial marine mortality versus winter mortality can thus vary among years because of different initial conditions (e.g. juvenile size at entry) and different environmental conditions (e.g. temperature, prey availability) that influence distribution and growth during the first growing season. Mortality processes might also vary between species with large smolts such as sockeye, coho, steelhead and yearling Chinook salmon, and species with smaller smolts: pink, chum, and age-0 Chinook salmon.

Calcified structures in fish, such as scales, can be used to estimate growth history. Juvenile salmon produce circuli on their scales at regular intervals of approximately 4-8 d (Courtney et al. 2000); the rate of circulus formation and the growth of the scale determine the spacing between rings (Fukuwaka and Kaeriyama 1997). Scale radius is proportional to fish length (Lee 1920; Ricker 1992), thus the radius of the scale at previous circuli reflects size at a younger age, and the width of circulus increment spacing reflects growth during specific intervals (Fukuwaka and Kaeriyama 1997; Courtney et al. 2000; Beamish et al. 2004). During periods of faster growth, rings on scales and otoliths will form at wider intervals; slower growth results in narrower spacing. Scales can therefore be used to reconstruct the growth histories of individual fish.

Growth studies rely on random, unbiased samples that are representative of all sizes and ages in the population (Bagenal and Tesch 1978; Francis 1990; Pierce et al. 1996). Also, two assumptions must hold when using the width of circulus increments as a proxy for growth rate: 1) the frequency of formation is constant, and 2) the distance between increments is proportional to fish growth (Campana and Jones 1992). Most published studies assume that a linear relationship exists between scale radius and fish length, and between circulus spacing and growth rate (Fraser 1916; Lee 1920; Francis 1990; Ricker 1992).

Prince William Sound hatcheries thermally mark the otoliths of 100% of their pink salmon fry prior to release, providing a unique opportunity to trace each hatchery fish recovered to a specific entry date, location, and size. Because of variability in the timing of ocean entry, using scales to study growth allows more accurate comparisons between different cohorts at certain points in their life history than by tracking mean sizes of fish captured at sea. Moss et al. (2005) recently used this technique to compare the early marine growth of pink salmon entering Prince William Sound as juveniles in 2001 and returning in 2002 as adults. Pink salmon that survived to adulthood grew faster than the average juvenile during the first summer at sea, and significant size-selective mortality occurred after the first growing season. This chapter extends this analysis to an interannual comparison of the timing and magnitude of differences in the growth and size of juveniles versus surviving adults. By comparing observed patterns over four years, we can determine whether the processes regulating survival are similar among years.

The main objective of this study was to use scale patterns to compare the early marine growth histories of juvenile pink salmon collected during July–September 2001–2004 and of surviving adults from the same year-class. Specifically, I aimed to address the following questions:

1) Must juvenile pink salmon achieve a certain threshold size or growth rate at one or more life stages to increase survival to adulthood?

2) If so, when might critical periods in the growth of pink salmon occur?

3) What is the relative importance of initial marine mortality versus mortality after the first growing season?

If surviving adult pink salmon were larger at comparable circuli and showed wider spacing between circuli than the average juvenile at the same life stage, then I would conclude that larger, faster-growing fish experienced higher survival. If growth trajectories for juvenile and adult pink salmon were not identical before juvenile fish were last sampled in September, significant size-selective mortality must have occurred after the first growing season (Moss et al. 2005).

METHODS

Pink salmon collection

Juvenile pink salmon were collected in 2001, 2002, 2003, and 2004 at three stations in southwest Prince William Sound and stations 1-6 on the GLOBEC-delineated Seward Line (GAK; Table 2.1, Figure 2.1). Stations were sampled during 6-10 d cruises monthly from July to September (Table 2.1) with the following exceptions: No cruise occurred during September 2002. We sampled out to station 10 on the Seward Line in August 2002, and to station 7 in September 2003. In 2003 and 2004, we also sampled a transect extending south from Cape Fairfield, east of the Seward Line, during all months (Table 2.1, Figure 2.1). Two stations west of the Seward Line were sampled in August 2003, as well. This sampling scheme encompassed the migration period from Prince William Sound to the coastal Gulf of Alaska for juvenile pink salmon and allowed reasonably high spatial and temporal data resolution during the first growing season.

At each station, two or more trawls were performed during daylight hours using a Nordic 264 surface rope trawl with 3 m doors and a 1.2 cm mesh liner in the cod end. The net fished a depth of approximately 11.4 m and a width of approximately 14.3 m (S. Patterson, Net Systems, personal communication) for 30 min at 3.5–5 knots (6.5–9.3 $km \cdot h^{-1}$). If juvenile pink salmon were present but fewer than 10 were caught in a single haul, the tow was repeated to increase sample size. Catches were sorted to species and counted; large catches were subsampled. The fork length of up to 200 fish of each species was measured. Up to 50 juvenile pink salmon from each tow were frozen in seawater for subsequent analysis by personnel at the University of Alaska Fairbanks – Juneau, who recorded lengths and weights of all juvenile pink salmon collected at sea and read otoliths for thermal markings (L. Haldorson, J. Boldt, J. Piccolo, personal communication).

Adult pink salmon were collected in terminal cost-recovery fisheries during the summers of 2002-2005 upon return to Armin F. Koernig (AFK), Cannery Creek (CCH), Wally Noerenberg (WNH), and Solomon Gulch (SGH) hatcheries in Prince William Sound (Table 3.1). Adult fish were captured by purse seine at hatchery-specific terminal fishery sites, located directly in front of each hatchery (Figure 2.1).

Scale Growth Analysis

Several scales were collected from the preferred area of both the juvenile and adult pink salmon. Preferred scales were located in a rectangular area located one to four scale rows above the lateral line between two vertical lines drawn from the posterior edge of the dorsal fin and halfway between the posterior edge of the dorsal fin and the anterior edge of the adipose fin. Scales from up to 15 juvenile pink salmon captured at each station during each year were analyzed. Scales were collected from 50 adult pink salmon at each hatchery (AFK, CCH, SGH, and WNH) in 2002, from 50 pink salmon at AFK and CCH hatcheries in 2004, and from 250 pink salmon at each hatchery in 2005. Because no adult scales were collected by Prince William Sound hatcheries in 2003, scales from adult pink salmon collected during the summer of 2003 by the Ocean Carrying Capacity (OCC) and Observer (OBS) programs of the National Marine Fisheries Service were used as surrogate scales for adults returning to Prince William Sound during this year (Table 3.1). While the Observer program collected scales from a broader geographic area in the Gulf of Alaska, scales collected by the OCC program and used in this analysis were obtained from pink salmon captured just west of Prince William Sound during late July and early August (Figure 3.1). Thermal otolith markings were not read to determine the origin of these adult pink salmon. However, due to the location of these fish on the capture date and the large number of pink salmon released by Prince William Sound hatcheries, many of these fish were presumably returning to Prince William Sound. Recent studies show that environmental processes during the early marine period are related to juvenile salmon survival and affect survival at regional (up to 1000 km) rather than ocean basin-wide scales (Pyper et al. 2001; Mueter et al. 2002; Pyper et al. 2005). This suggests that even if fish from the OCC program were not bound for Prince William Sound, they likely experienced similar early marine conditions.

The scales from each pink salmon were placed on gummed cards, sculptured surface up, and impressed in transparent acetate at a pressure of 5000 psi for 3 min. I read acetate impressions using a computerized video digitizing system (Optical Pattern Recognition System, Model OPR-512). The first scale from each fish showing clear, unbroken circulus bands, an unbroken scale edge, and no signs of regeneration was measured. Scale circuli were measured along the anterior-posterior axis, from the back of the focus to the scale edge—the most commonly used measurement (Martinson et al. 2000). Each circulus that crossed the measurement axis was automatically marked by the digitizing system and errors were manually edited.

Total scale radius equaled the distance from the mid-point of the focus (focus/2) to the scale edge. To remove outliers, I deleted measurements from fish with a fork length to scale radius ratio of > 0.45 or a focus > 250 μm (K. Myers, University of Washington High Seas Salmon Research Program, personal communication). Between 3–15% of juvenile scales were removed as outliers, while 3–43% of adult scales were removed. Scales were analyzed from a total of 135 hatchery pink salmon juveniles caught during July–September 2001, from 37 hatchery juveniles caught during July and August 2002, from 40 hatchery juveniles caught during July–September 2003, and from 58 hatchery juveniles caught during July–September 2004 (Appendix A). Scales were analyzed from 94, 102, 81, and 348 adult pink salmon captured during 2002, 2003, 2004, and 2005, respectively (Appendix A).

For these fish, I estimated the frequency distribution of scale radius measurements at circuli 3, 6, 9, 12, and 15 from pink salmon from the same year-class caught as juveniles and as adults to track size modes during May–September (see Chapter 2 for details on the timing of circulus formation). Differences in distributions of scale size at circuli for juveniles and adults were compared with Kolmogorov-Smirnov statistical tests. I also determined the amount of growth between circulus increments during May–September and used analysis of variance (ANOVA) and Tukey multiple comparison tests to determine differences in mean scale size at circuli and circulus spacing among adult cohorts (AFK, CCH, SGH, WNH, OCC, and OBS) within each year, between juvenile and adult fish from the same year-class, and among adult cohorts caught during different years. The mean daily growth rate of juvenile and adult scales was determined by dividing the mean scale growth increment over groups of three circuli by the number of days between circuli: 6.1 d in 2001, 5.8 d in 2001, 5.5 d in 2001, and 4.4 d in 2001 (Chapter 2).

RESULTS

A linear scale radius-body length relationship most closely characterized the early marine growth of juvenile pink salmon in Prince William Sound and the coastal Gulf of Alaska during all years ($r^2 = 0.77\text{-}0.80$, $P < 0.001$ for all years; Figure 2.2; Chapter 2). Because of the linear relationship between scale size and fish length, and between circulus spacing and fish growth rate, fish length could be inferred directly from scale radius and growth rate from scale circulus spacing. Scales began to form when pink salmon were approximately 44-48 mm in length, and the first circulus appeared during mid-June, approximately one month after marine entry (Chapter 2). After initial formation, circuli continued to develop at a rate of one every 4.4-6.1 d (Chapter 2). Because growth trajectories did not differ significantly among juvenile pink salmon from different hatcheries during May–October 2001–2004 (ANOVA, $P > 0.075$; Chapter 2), I pooled all hatchery juveniles within each year for growth analyses.

Few significant differences in the distribution of scale measurements were apparent among adult pink salmon from AFK, CCH, SGH, and WNH hatcheries returning in 2002 (Kolmogorov-Smirnov, $P > 0.05$ for circuli 1-41, with few exceptions between cohorts), or from AFK and CCH hatcheries returning in 2004 (Kolmogorov-Smirnov, $P > 0.05$ for circuli 1-30; Figure 3.2). There were also few significant differences in mean size at circuli among adult pink salmon from different hatcheries returning in 2002 (ANOVA, $P = 0.770$-0.998 for circuli 1-42, except adults from AFK were smaller at circuli 4 and 5 than adults from CCH; Tukey, $P = 0.015$-0.032, Figure 3.3), or 2004 (ANOVA, $P = 0.128$-0.792 for circuli 1-30, Figure 3.3).

During 2003, adult pink salmon from the Observer program were larger than OCC adults (Kolmogorov-Smirnov, $P < 0.032$ at circuli 4-38, Figure 3.4; t-test, $P < 0.047$ at circuli 2-3 and 5-38, Figure 3.5). For fish returning to AFK, CCH, SGH, and WNH hatcheries during 2005, differences in mean size existed at circuli 1-41 (ANOVA, $P < 0.001$ for all except circulus 42, $P = 0.042$; Figure 3.5).

Adult pink salmon captured at all hatcheries in 2002 and 2004 were therefore also pooled within each year, while OBS and OCC adults in 2003 and adults returning to different hatcheries in 2005 were analyzed as discrete cohorts.

Average Size at Circuli

The average juvenile pink salmon was smaller than the average surviving adult throughout the first growing season during all years, indicating that larger, faster-growing juveniles were more likely to survive than smaller ones (Figure 3.5, Appendix A). During 2001, the juvenile cohort at-large was significantly smaller than surviving adults at circuli 1-18 (Table 3.2). During 2002, juveniles at-large were significantly smaller than surviving fish captured by the OCC program at circuli 1-12 and the Observer program at circuli 1-14 (Table 3.2). Juveniles captured during 2003 were significantly smaller than surviving adults from the same year-class only at circuli 1-3, 5, and 12 (Figure 3.5), and the distribution of scale radius measurements at each circulus was significantly different only at circuli 1-2 (Table 3.2). During 2004, juveniles were consistently and significantly smaller than survivors from the SGH cohort at circuli 1-18, but rarely differed significantly from the sizes of survivors from AFK, CCH, or WNH hatcheries (Table 3.2, Figure 3.5).

The same trends were seen when comparing juveniles and adults from specific hatcheries during each year. During May–September 2001, juvenile pink salmon from AFK were significantly smaller than those that survived to adulthood at circuli 1-16, juveniles from CCH were significantly smaller than adult survivors from CCH at circuli 1-15, juveniles from SGH were significantly smaller than adult survivors at circuli 1-14, and juveniles from WNH were significantly smaller than adult survivors at circuli 1-13 (Table 3.3). During 2003, juveniles from AFK were not significantly different in size from those that survived to adulthood at circuli 1-12, nor were juveniles from CCH at circuli 1-12 (Table 3.3). During 2004, the average juvenile from AFK was not significantly different in size from the average adult survivor from AFK at circuli 1-13, the average juvenile from CCH was not significantly different from CCH survivors at circuli 1-11, and the average juvenile from WNH was not significantly different from WNH survivors at circuli 1-9 and 11-14 (Table 3.3). The average juvenile from SGH was significantly smaller in size during 2004 than fish that survived to adulthood at circuli 1-11; however, the distribution of scale measurements differed only at circuli 1, 3, and 5 (Table 3.3).

There were, in fact, more differences in scale size during 2004 among surviving adults from different hatcheries than between the survivors and juveniles at-large from the same hatchery (Appendix A). Pink salmon from AFK that survived to adulthood were significantly smaller than CCH adults between circuli 3-18 (Tukey, $P < 0.01$), smaller than SGH adults between circuli 1-18 (Tukey, $P = 0.000\text{-}0.033$), and smaller than WNH adults between circuli 7-16 and 18 (Tukey, $P < 0.05$). Survivors from CCH were significantly smaller than SGH adults between circuli 4-18 (Tukey $P < 0.05$), and smaller than WNH adults at circuli 1, 3, and 4 (Tukey, $P = 0.004\text{-}0.031$). Interestingly, CCH fry were also released at a much smaller average size than fry from AFK, SGH, and WNH (0.37 g compared to 0.62–0.69 g; Table 2.4), but had higher survival than AFK and WNH fish (Table 2.4) and were larger at return than WNH adults, and similar in size to AFK adults (Table 3.1).

Adult pink salmon from specific hatchery cohorts were not consistently larger during 2004, a high-survival year, than during 2001 and 2003, low-survival years (Table 3.4, Figure 3.6). Few differences were apparent among adult survivors from the AFK hatchery among years. Pink salmon from AFK captured as adults were significantly larger as juveniles in 2001 than in 2003 at circuli 27-30 and in 2004 at circuli 1-2 and 29-32 (Table 3.4). Pink salmon from AFK captured as adults were also significantly larger as juveniles in 2004 than in 2003 at circuli 13-15. Pink salmon from CCH captured as adults were significantly larger in 2001 than in 2003 at circuli 4-6 and 19-30, and larger than in 2004 at circuli 1-2 (Table 3.4, Figure 3.6). Pink salmon from CCH caught as adults were significantly larger as juveniles in 2004 than in 2003 at circuli 4-39. Juvenile pink salmon from SGH were significantly larger in 2004 than in 2001 at circuli 4-40 (Table 3.4, Figure 3.6). For pink salmon from WNH, fish that survived to adulthood were significantly larger in 2001 than in 2004 at circuli 1-2, but larger in 2004 than in 2001 at circuli 9-17 and 23-26 (Table 3.4, Figure 3.6). The pooled group of hatchery pink salmon that survived to adulthood was significantly larger during 2001 than during 2003, both low-survival years, at circuli 1 and 7-34 (Table 3.4).

Frequency distributions of scale measurements at every third circulus indicated that surviving fish were larger than the average juvenile. Scale size distributions were not aligned by circulus 15 (Figures 3.4 and 3.7), suggesting that significant size-selective mortality occurred after the juveniles were sampled in September.

Total scale size at return was largest during high-survival years, 2003 and 2005, and smallest during low-survival years, 2002 and 2004 (Table 3.1). However, no consistent relationship was observed between final fork length and survival (Figure 3.8). Adult pink salmon returning to Prince William Sound hatcheries were on average largest during 2004, a low-survival year, and smallest during 2005, a high-survival year. Adults returning to Prince William Sound in 2003, a high-survival year, were larger than adults returning in 2002, a low-survival year. However, pink salmon returning to SGH in 2005 were larger at capture than all other cohorts in all other years (Figure 3.8).

Trends in mean size at each circulus were consistent with trends in smolt-to-adult survival for pink salmon that survived to return to Prince William Sound hatcheries in 2005. Surviving fish from SGH were larger than survivors from AFK, WNH, and CCH from circuli 1-45 and had the highest survival, 10.3% (Table 2.4; Figure 3.5). Surviving fish from CCH were larger than survivors from AFK and WNH between circuli 1-41 and experienced 8.6% survival. Surviving fish from WNH were larger than survivors from AFK between circuli 4-42 and experienced 7.3% survival, while the AFK cohort experienced 6.1% survival. Adults returning to AFK during 2004 were larger at circuli than the CCH cohort, though not significantly, and experienced higher survival (3.6% compared to 2.0%; Figure 3.3). However, pink salmon returning to CCH in 2002 were larger than survivors from AFK, SGH, and WNH between circuli 1-29 and 35-38, though not significantly, and experienced lower survival (1.1%) than all other cohorts (5.2%, 4.4%, and 2.6%, respectively; Table 2.4; Figure 3.3; (McNair 2002). During this year, the high-surviving AFK cohort was larger than other hatchery cohorts only between circuli 30-35.

Growth Rate

The comparison of incremental scale growth between specific circuli reveals the timing and magnitude of differential growth between juveniles that survived to adulthood and the general population of juveniles at large. Because of the linear relationship between fork length and scale size for juvenile pink salmon, a decrease in average scale growth rate over time indicates a decrease in growth rate of the fish. During 2001-2004, growth rate for juveniles at-large and the population that survived to adulthood was similar at circuli 2-4 and 5-7 (Figure 3.9). At circuli 5-7, a period corresponding to early-mid July, growth rate for both juveniles and adults declined during all years, and began to diverge thereafter (Figure 3.9).

Surviving fish began growing at a faster rate than the average juvenile by circuli 8-10 during all years, which corresponded to the period between late July and early August (Table 3.5, Figure 3.9). The 2002 pooled adult cohort (juveniles during 2001), 2003 Observer adults (juveniles during 2002), and the 2005 SGH cohort (juveniles during 2004) began growing significantly faster than the average juvenile at circuli 5-7 (Table 3.5). Survivors from the AFK cohort grew significantly faster during 2004 than the average juvenile at circuli 2-4, or late June (Table 3.5).

Juvenile growth rate continued to decline through circuli 8-10, but then increased during 2001 and 2003, the low-survival years. During 2002 and 2004, the high-survival years for juvenile rearing, growth rate for the average juvenile decreased steadily from circuli 2-19, or from approximately mid-late June to late September. The growth rate of adult survivors increased from circuli 8-19 during all years, corresponding to the period from late July to late September, although this trend was not as pronounced during high-survival years (Figure 3.9). Both the juvenile pink salmon population at-large and all cohorts that survived to adulthood grew faster during high-survival years (2002 and 2004) than during low-survival years (2001 and 2003) at circuli 2-13, or from mid-late June to mid-late August (Table 3.6, Figure 3.9).

DISCUSSION

Pink salmon that survived to adulthood were larger at a given date (inferred from circuli measurements) and grew faster than the average juvenile pink salmon at the same life stages throughout the first growing season, indicating that larger, faster-growing juveniles experienced higher survival. Juvenile pink salmon at-large were not significantly smaller than the surviving cohorts in 2003 and 2004, though the general pattern resembled that in the other years. Early growth and mortality of pink salmon are likely governed by some combination of prey availability, smolt quality, inter- and intra-specific competition, predation, and ocean conditions. Periods of differential growth between the average juvenile and adult survivors might be linked to heterogeneous feeding opportunities, size-dependent foraging ability, or limiting physiological conditions. A decrease in prey availability, patchiness, or quality, or an increase in predation, could severely impact growth and survival.

The increased abundance of juveniles from hatchery production has elicited concerns that we are reaching or exceeding the carrying capacity for juvenile pink salmon; juvenile pink salmon could be potentially food-limited at one or more stages in their life cycle and in one or more regions. Recent studies present evidence for the competitive dominance of pink salmon over other salmon species (Ruggerone et al. 2003; Ruggerone and Nielsen 2004), and it is not unreasonable to think that intraspecific competition exists, as well. Wertheimer et al. (2004a, 2004b) contended that although density-independent ocean conditions primarily drive pink salmon spawner abundance and productivity, large-scale enhancement in Prince William Sound has contributed to reduced body size due to density dependent growth in the Gulf of Alaska. Farley and Carlson (2000) suggested that coastal waters of the Gulf of Alaska could be food limiting, thus eliciting concerns about density dependent growth when juvenile pink salmon first emigrate from Prince William Sound. Consumption demand by juvenile pink salmon exceeded the average standing stock biomass of key prey in Prince William Sound and the coastal Gulf of Alaska during July–September 2001, indicating the potential for food limitation in this region (Cross et al. 2005).

Growth rates declined for both the average juvenile and for adult survivors in early-mid July during all years. Growth decreases with zooplankton biomass (Orsi et al. 2000), and might be limited by prey abundance in early spring (Mortensen et al. 2000). Zooplankton biomass peaks in May in the northern Gulf of Alaska (Coyle and Pinchuk 2003; Coyle and Pinchuk 2005), and in June in Prince William Sound (Cooney et al. 2001a). As zooplankton production in Prince William Sound and the coastal Gulf of Alaska declines beginning in early June and large copepods migrate to diapause depths (Cooney et al. 2001a), the overall amount of zooplankton in the surface layer is usually reduced (Eslinger et al. 2001). Juvenile pink salmon might have experienced a bottleneck in growth at this time. Surviving fish began growing faster than the average juvenile between late June and late July each year. Pink salmon that survived this growth bottleneck were the larger individuals of each year-class and grew at a faster rate than the average juvenile throughout the rest of the summer.

Ocean conditions and abundance likely regulate the strength of density-dependence and carrying capacity for juvenile salmon, although it is difficult to separate the effects of each on growth and survival. The large influx of larger-bodied juveniles (with greater consumption demand) into the Gulf of Alaska, in conjunction with the seasonal dynamics of zooplankton prey, likely creates localized prey depletions and density dependent growth. Localized depletions during early to mid summer could disproportionately affect the smallest fish in each cohort, which are probably less effective foragers and encounter a reduced suite of available prey due to their smaller size and gape width. However, smaller fish also impose a lower per-capita consumption demand on prey resources during early summer, so the growth of smaller fish might not be affected as much as growth for larger juveniles, which consume more per individual and therefore require a greater density of prey. This might explain why the growth rate of the average juvenile continued to decline from July through late September during high-survival years, when the average pink salmon was larger, but increased slightly after July during low-survival years, when the average pink salmon was smaller.

As pink salmon disperse or more prey becomes available, the surviving fraction of the juvenile population may experience higher growth rates than the average juvenile. Both the juvenile pink salmon population at-large and all cohorts that survived to adulthood grew at a faster rate during 2002 and 2004 than during 2001 and 2003 from approximately mid-late June to mid-late August. If density-dependent growth occurred, it might have been less intense during the summers of high-survival years for juvenile rearing than during low-survival years. In addition, more differences in size at all circuli existed among adult hatchery cohorts during high-survival years than during low-survival years. More variation in size might indicate more growth scenarios, which led to higher survival, while growth was more limited during low-survival years. Diversified feeding or distribution strategies could produce greater variability in the growth trajectories of surviving adults during high-survival years.

Annual variation in marine conditions and nutrient input, and subsequent variation in plankton production, result in interannual variation in habitat quality and salmon growth and marine survival. The strength of advection between Prince William Sound and the coastal Gulf of Alaska affects both bottom-up and top-down biological processes that affect recruitment and nutrition in fish (Kline 1999). Juvenile fish in Prince William Sound consume zooplankton that originate outside of their forage range (Kline 1999); deep Gulf waters subsidize inshore waters with carbon that is crucial to local populations of juvenile fishes (Eslinger et al. 2001). Oceanographic processes controlling advection therefore influence Prince William Sound fish that depend on Gulf of Alaska carbon (Kline 1999). Increased flow of zooplankton into Prince William Sound in 2002 might have led to extremely high survival for this year class of juvenile pink salmon (Kline 2004).

The dynamics behind high initial mortality are largely unknown (Brodeur et al. 2000), but early marine growth and mortality are undoubtedly affected by size-selective predation. The abundance and size of predators that feed on juvenile pink salmon, such as walleye pollock (*Theragra chalcogramma*), Pacific herring (*Clupea pallasii*), and other salmonids, and the abundance of alternative prey for these fish, will influence the extent of early mortality during each year (Willette et al. 2001). The availability of small copepods, which compose the majority of the diet of pink salmon fry (Cooney et al. 1981; Parker 1997), will affect consumption rates of pink salmon and, subsequently, growth. If zooplankton prey availability is such that fry can consume enough to reach a critical size, predation pressure will be lessened (Willette 2001). The 2001 CCH cohort, which experienced only 1.1% survival yet grew well throughout the summer relative to other hatchery cohorts during this year, may have encountered better initial growing conditions but a greater abundance of predators. Competitor abundance will also impact prey availability. The high apparent growth of the CCH cohort during 2001 could also be a result of reduced school sizes, if higher initial mortality rates reduced their numbers and thus increased the availability of prey for the remaining survivors.

In some years, enough early size-selective mortality during May-July might cull the smallest fish from some hatcheries, such that the survivors are few, but experience good growth and are successful throughout the summer. The high realized growth of the CCH hatchery stock during 2001 compared to other hatchery cohorts during this year suggests that there might be a critical size for surviving the early mortality phase, and that the CCH cohort that performed well throughout the summer were the fish that achieved this early critical size. A similar pattern occurs in the early marine growth of juveniles during 2003, when growth throughout the summer was relatively strong even though this year-class experienced low survival (Chapter 2).

Beamish and Mahnken (2001) hypothesize that while growth-based mortalities are continuous throughout the summer months, mortality predominantly occurs in two major stages: immediately after ocean entry and during the late fall and winter of the first year. This study supports the findings of Beamish and Mahnken (2001) and Moss et al. (2005) that additional size-selective mortality occurs after the first growing season and determines smolt-to-adult survival for pink salmon. The discrepancy in body size between the juvenile population at-large and those that survived to adulthood through circulus 15 suggests that significant mortality had not occurred by late summer. In addition, the smallest survivors were smaller than the average juvenile through circulus 18 during 2001-2004, indicating that if a critical size is required to survive the winter, the critical period must come after late September. The probability of reaching a critical size in order to survive winter could be exacerbated by bottlenecks in prey supply. The relative importance and magnitude of early and late size-selective mortality might differ among years, and the results of the earlier phase might alter the severity of the later phase. Mortality may also be more of a continuous process rather than in distinct stages, but this study was not set up to gain insight on overall mortality of the population throughout the summer. However, the results of Chapter 2 suggest that size-selective mortality was not severe throughout the summers of 2001–2003.

Aydin et al. (2005) recently hypothesized that mixed-layer depth influences final body weight for pink salmon. As the mixed-layer depth decreases in the spring, zooplankton become more concentrated in the surface layer, where pink salmon feed. Foraging costs rise when the mixed layer depth increases and zooplankton are less concentrated. Under such conditions, pink salmon that survived the winter at larger sizes will have an advantage over smaller individuals due to their ability to shift their diet from zooplankton to energy-rich squid in the spring (Aydin et al. 2005). The size threshold for pink salmon success could therefore vary among years in response to conditions experienced during later life stages. Size achieved by the end of the first growing season could potentially determine the ability to exploit the high-energy squid and impact overall survival.

Low sample sizes in September hindered further analysis, and likely contributed to the absence of juveniles with sizes extending up to the size of the largest adults. Theoretically, the largest juvenile should have scales no smaller than those of the largest adult at any point in their growth history. Measurements of scale radii for juveniles should always encompass the largest adult radii, but could show much smaller radii than observed for adults. However, when sample sizes become too small at higher circuli counts, the larger (and less abundant) radii might not be detected either by random chance, or perhaps because the large, successful fish had moved out of the sampling area.

To allay concerns that the trawls could be catching a disproportionate number of smaller or larger fish, we examined the potential for size-selective sampling by our trawl gear. We collected many yearling sockeye salmon that were larger than juvenile pink salmon captured concurrently in the same net haul (Moss et al. 2005). Our trawls also consistently caught larval rockfish (*Sebastes* spp.), squid, prowfish (*Zaprora silenus*), and young-of-the-year walleye pollock measuring between 40-50 mm, the approximate size of juvenile pink salmon when released from hatcheries. This suggests that the trawls did not impose a size-selective sampling bias over the range of juvenile sizes pertinent to our analysis. Although juvenile pink salmon are thought to reside in the top approximately 10 m and the net sampled to a depth of 11.4 m, larger fish residing below the depth of the net may have not been sampled, imposing a subtle bias on these results.

Pink salmon stray from their natal breeding grounds more than other species of Pacific salmon (Quinn 2005). Some of the adult pink salmon caught in terminal fisheries could have been released from a hatchery other than the one to which they returned, or might have been a stray member of the wild cohort. Thedinga et al. (2000) estimated an overall straying rate of 5.1% for pink salmon in Prince William Sound, averaging up to 9.2% for the intertidal stock. Hatchery pink salmon might have fewer opportunities for imprinting than wild stocks, thereby increasing the relative rate of straying for hatchery fish (Dittman and Quinn 1996). The possibility of straying adds uncertainty to the origin of returning adults and could affect estimates of stock-specific survival, as well as comparisons of the growth performance of adults from different hatcheries.

As mentioned earlier, there is also a possibility that adult pink salmon captured by the OCC and Observer programs were not returning to Prince William Sound. However, because environmental processes have been shown to affect salmon at regional spatial scales of up to 1000 km (Pyper et al. 2001; Mueter et al. 2002; Pyper et al. 2005), OCC and OBS pink salmon likely experienced similar conditions, even if they were not returning to Prince William Sound.

A major assumption of this scale back-calculation method is that the relationship between scale radius and fish growth is perfectly linear and does not change with the growth rate of the fish. Some studies indicate that linear models might not represent growth in juvenile fishes as accurately as nonlinear models (Chen et al. 1992). However, linear models of fish growth are preferred over other methods by many scientists (Ricker 1992; Klumb et al. 2001), and continue to be the most widely used. A linear model best captured the relationship between fork length and scale size for juvenile pink salmon in Prince William Sound and the Gulf of Alaska during 2001-2004.

The radius of each scale from juvenile pink salmon was measured to the scale edge, which was not necessarily at the edge of a complete circulus increment. Not accounting for the portion of the circulus increment that would develop after the moment of measurement could have affected estimates of size at circuli for the juvenile cohort.

However, the inclusion of incomplete circulus increments likely had a negligible effect on the comparison of scale growth between juvenile and adult pink salmon.

Conclusions

Larger, faster-growing juveniles experienced higher survival and possibly escaped a mid-summer bottleneck in growth. Both the average juvenile pink salmon and those that survived to adulthood grew at a faster rate during high-survival years than during low-survival years, suggesting that if density-dependent growth occurred, it might have been less intense during high-survival years. Diversified feeding or distribution strategies could produce higher variability in the growth trajectories of surviving adults during high-survival years. This study also provides additional evidence that significant mortality occurs after the first growing season and influences survival for pink salmon. The relative importance and magnitude of early and late mortality might differ among years.

Investigating the importance of early marine growth to smolt-to-adult survival, as well as the timing and magnitude of mortality periods, is an initial step toward understanding the processes that regulate growth and survival for juvenile pink salmon. Related research will compare the consumption demand of juvenile pink salmon to the biomass of exploitable prey in localized areas in an attempt to identify and quantify ecological bottlenecks, such as periods of prey depletion. Scale-based growth estimates from juvenile pink salmon collected during or shortly after the first winter could also help fill in part of the temporal gap between ocean entry and return and give insight on the rate and importance of ocean growth after the first growing season. The integration of scale data from juvenile, mature, and returning pink salmon would provide insight into the timing of one or more "critical periods" in their life history, the magnitude of size-selective mortality, and the importance of early juvenile growth to adult survival and run strength. Understanding the timing and causes of mortality will lead to more effective management practices and provide insight into mechanisms regulating growth and survival for pink salmon.

Table 3.1. Total fork length, total scale size, average number of circuli, and date of collection for adult pink salmon caught during 2002-2005 at four hatcheries in Prince William Sound (AFK = Armin F. Koernig, CCH = Cannery Creek, SGH = Solomon Gulch, WNH = Wally Noerenberg) and by the Ocean Carrying Capacity (OCC) and Observer (OBS) programs of the National Marine Fisheries Service. Rows in bold indicate cohorts used for scale analyses.

Year	Source	Avg FL (mm)	2SE FL (mm)	Avg SS (μm)	2SE SS (μm)	Avg # Circuli	Collection Date
2002	AFK	495.4	11.5	1489.9	56.0	37.7	
	CCH	514.6	13.8	1396.1	114.1	34.9	
	SGH	485.1	8.9	1498.9	77.1	38.0	
	WNH			1495.0	77.3	37.6	
	Total	**495.6**	**6.1**	**1479.5**	**37.9**	**37.3**	
2003	**OCC**	**502.7**	**5.5**	**1645.0**	**39.3**	**39.2**	**7/24-8/1**
	OBS	**507.3**	**44.3**	**1568.7**	**141.0**	**34.9**	**2/23-7/23**
	Total	503.4	7.9	1633.8	39.4	38.6	
2004	AFK	510.9	10.6	1519.4	68.7	38.2	8/10
	CCH	521.7	12.3	1521.0	55.6	39.0	8/1-8/15
	Total	**516.0**	**8.1**	**1520.2**	**44.6**	**38.6**	
2005	**AFK**	**492.9**	**4.5**	**1577.2**	**26.8**	**39.1**	**8/3-8/9**
	CCH	**491.6**	**6.0**	**1658.8**	**27.2**	**40.1**	**8/6**
	SGH	**522.2**	**10.1**	**1614.2**	**44.6**	**38.0**	**7/5-7/13**
	WNH	**467.1**	**5.1**	**1663.3**	**24.2**	**40.4**	**7/26**
	Total	490.0	3.5	1630.0	15.0	39.6	

Table 3.2. The average juvenile pink salmon was smaller at circuli throughout the first growing season than fish that survived to adulthood during all years, but differences were consistently significant only during 2001 and 2002. During 2002, 2004, and 2005, adult pink salmon were collected at terminal fisheries in front of four hatcheries in Prince William Sound: AFK = Armin F. Koernig; CCH = Cannery Creek; SGH = Solomon Gulch; WNH = Wally Noerenberg. In 2003, adult pink salmon were captured in the Gulf of Alaska by the Ocean Carrying Capacity (OCC) and Observer (OBS) programs of the National Marine Fisheries Service. * indicates that the difference is significant at the $\alpha = 0.05$ level.

Comparison	**Test**	**Circuli**	**Significance (P)**	
2001 juveniles vs. 2002 pooled adults	ANOVA	1-16	< 0.001	*
		17-18	0.004-0.037	*
	Kolmogorov-Smirnov	1-16	< 0.001	*
		17	0.021	*
2002 juveniles vs. 2003 adult cohorts	ANOVA	1-20	< 0.05	*
vs. 2003 OCC adults	Tukey	1-4, 6-12	0.000-0.048	*
	Kolmogorov-Smirnov	1-13	< 0.009	*
vs. 2003 OBS adults	Tukey	1-14	< 0.002	*
	Kolmogorov-Smirnov	1-14	< 0.004	*
2003 juveniles vs. 2004 pooled adults	ANOVA	1-3, 5, 12	0.000-0.047	*
	Kolmogorov-Smirnov	1-2	0.001-0.030	*
2004 juveniles vs. 2005 adult cohorts	ANOVA	1-20	< 0.001	*
vs. 2005 AFK adults	Tukey	1-4, 6-18	> 0.05	
	Kolmogorov-Smirnov	2-4, 8-14, 18	> 0.05	
vs. 2005 CCH adults	Tukey	2-15, 17-18	> 0.05	
	Kolmogorov-Smirnov	2, 6-8, 11-14, 18	> 0.05	
vs. 2005 SGH adults	Tukey	1-18	< 0.001	*
	Kolmogorov-Smirnov	1-18	< 0.001	*
vs. 2005 WNH adults	Tukey	1-18	> 0.05	
	Kolmogorov-Smirnov	1-14, 18	> 0.05	

Table 3.3. The average juvenile pink salmon was smaller at circuli throughout the first growing season than fish from the same hatchery that survived to adulthood during all years, but differences were consistently significant throughout the first growing season only during 2001 and for the Solomon Gulch cohort during 2004. Adult pink salmon were collected at terminal fisheries in front of four hatcheries in Prince William Sound: AFK = Armin F. Koernig; CCH = Cannery Creek; SGH = Solomon Gulch; WNH = Wally Noerenberg. * indicates that the difference is significant at the $\alpha = 0.05$ level.

Comparison	Test	Circuli	Significance (P)	
2001 AFK juveniles vs. 2002 AFK adults	ANOVA	1-16	< 0.042	*
	Kolmogorov-Smirnov	1-16	< 0.016	*
2001 CCH juveniles vs. 2002 CCH adults	ANOVA	1-15	< 0.012	*
	Kolmogorov-Smirnov	1-15	< 0.042	*
2001 SGH juveniles vs. 2002 SGH adults	ANOVA	1-14	< 0.015	*
	Kolmogorov-Smirnov	1-12, 14	< 0.019	*
2001 WNH juveniles vs. 2002 WNH adults	ANOVA	1-13	< 0.030	*
	Kolmogorov-Smirnov	1-4, 9-11	< 0.016	*
2003 AFK juveniles vs. 2004 AFK adults	ANOVA	1-12	0.084-0.416	
	Kolmogorov-Smirnov	1-12	0.088-0.558	
2003 CCH juveniles vs. 2004 CCH adults	ANOVA	1-12	0.055-0.932	
	Kolmogorov-Smirnov	1-12	0.326-0.989	
2004 AFK juveniles vs. 2005 AFK adults	ANOVA	1-13	0.086-0.989	
	Kolmogorov-Smirnov	1-13	0.167-0.973	
2004 CCH juveniles vs. 2005 CCH adults	ANOVA	1-11	0.276-0.952	
	Kolmogorov-Smirnov	1-11	0.191-0.926	
2004 SGH juveniles vs. 2005 SGH adults	ANOVA	1-11	< 0.045	*
	Kolmogorov-Smirnov	1, 3, 5	< 0.018	*
2004 WNH juveniles vs. 2005 WNH adults	ANOVA	1-9, 11-14	0.066-0.688	
	Kolmogorov-Smirnov	1-9, 11-14	0.068-0.855	

Table 3.4. Adult pink salmon from specific hatchery cohorts were not consistently larger during 2004 (adults returning in 2005), when survival was high, than during 2001 and 2003 (returning in 2002 and 2004, respectively), when survival was low. Adults were collected at terminal fisheries in front of four hatcheries in Prince William Sound: AFK = Armin F. Koernig; CCH = Cannery Creek; SGH = Solomon Gulch; WNH = Wally Noerenberg. * indicates that the difference is significant at the $\alpha = 0.05$ level.

Comparison	**Test**	**Circuli**	**Significance (P)**	
2002 vs. 2004 vs. 2005 AFK adults	ANOVA	1-2, 14-15, 27-32	< 0.05	*
2002 vs. 2004 AFK adults	Tukey	27-30	0.021-0.028	*
2002 vs. 2005 AFK adults	Tukey	1-2, 29-32	< 0.047	*
2004 vs. 2005 AFK adults	Tukey	13-15	0.014-0.036	*
2002 vs. 2004 vs. 2005 CCH adults	ANOVA	1-2, 4-39	< 0.038	*
2002 vs. 2004 CCH adults	Tukey	4-6, 19-30	< 0.028	*
2002 vs. 2005 CCH adults	Tukey	1-2	< 0.027	*
2004 vs. 2005 CCH adults	Tukey	4-39	< 0.020	*
2002 vs. 2005 SGH adults	t-test	4-40	< 0.043	*
2002 vs. 2005 WNH adults	t-test	1-2, 9-17, 23-26	< 0.048	*
2002 vs. 2004 pooled adults	t-test	1, 7-34	< 0.047	*

Table 3.5. Surviving fish grew significantly faster than the average juvenile by circuli 8-10 during all years. Incremental circulus spacing was averaged over groups of three circuli to circulus 16. During 2002, 2004, and 2005, adult pink salmon were collected at terminal fisheries in front of four hatcheries in Prince William Sound: AFK = Armin F. Koernig; CCH = Cannery Creek; SGH = Solomon Gulch; WNH = Wally Noerenberg. In 2003, adult pink salmon were captured in the Gulf of Alaska by the Ocean Carrying Capacity (OCC) and Observer (OBS) programs of the National Marine Fisheries Service. * indicates that the difference is significant at the $\alpha = 0.05$ level.

Comparison	**Test**	**Circuli**	**Significance (P)**	
2001 juveniles vs. 2002 pooled adults	t-test	5-7 to 14-16	< 0.004	*
2002 juveniles vs. 2003 adult cohorts	ANOVA	5-7 to 14-16	< 0.009	*
vs. 2003 OCC adults	Tukey	8-10	< 0.05	*
vs. 2003 OBS adults	Tukey	5-7	< 0.006	*
2003 juveniles vs. 2004 pooled adults	t-test	8-10 to 11-13	< 0.013	*
2004 juveniles vs. 2005 adult cohorts	ANOVA	2-4 to 14-16	< 0.001	*
vs. 2005 AFK adults	Tukey	2-4 to 14-16	< 0.030	*
vs. 2005 CCH adults	Tukey	8-10 to 14-16	< 0.001	*
vs. 2005 SGH adults	Tukey	5-7 to 14-16	< 0.001	*
vs. 2005 WNH adults	Tukey	8-10 to 14-16	< 0.001	*

Table 3.6. Juvenile pink salmon at-large and fish that survived to adulthood grew at a significantly faster rate during high-survival years (2002 and 2004 juveniles, 2003 and 2005 adults) than during low-survival years (2001 and 2003 juveniles, 2002 and 2004 adults). Incremental circulus spacing was averaged over groups of three circuli to circulus 16. During 2002, 2004, and 2005, adult pink salmon were collected at terminal fisheries in front of four hatcheries in Prince William Sound: AFK = Armin F. Koernig; CCH = Cannery Creek; SGH = Solomon Gulch; WNH = Wally Noerenberg. In 2003, adult pink salmon were captured in the Gulf of Alaska by the Ocean Carrying Capacity (OCC) and Observer (OBS) programs of the National Marine Fisheries Service. * indicates that the difference is significant at the $\alpha = 0.05$ level.

Comparison	**Test**	**Circuli**	**Significance (P)**	
2001-2004 juveniles	ANOVA	2-4 to 8-10	< 0.05	*
2002 vs. 2001 juveniles	Tukey	2-4, 8-10	< 0.041	*
vs. 2003 juveniles	Tukey	5-7, 8-10	< 0.010	*
2004 vs. 2001 juveniles	Tukey	2-4 to 8-10	< 0.001	*
vs. 2003 juveniles	Tukey	5-7	< 0.001	*
2002-2005 adults	ANOVA	2-4 to 14-16	< 0.010	*
2003 OCC adults vs. 2002 pooled adults	Tukey	2-4 to 11-13	< 0.008	*
vs. 2004 pooled adults	Tukey	5-7 to 14-16	< 0.001	*
2003 OBS adults vs. 2002 pooled adults	Tukey	2-4 to 14-16	< 0.009	*
vs. 2004 pooled adults	Tukey	5-7 to 14-16	< 0.001	*
2005 AFK adults vs. 2002 pooled adults	Tukey	5-7	0.045	*
vs. 2004 pooled adults	Tukey	5-7	< 0.001	*
2005 CCH adults vs. 2002 pooled adults	Tukey	2-4 to 8-10	< 0.002	*
vs. 2004 pooled adults	Tukey	2-4 to 8-10	< 0.001	*
2005 SGH adults vs. 2002 pooled adults	Tukey	2-4 to 11-13	< 0.038	*
vs. 2004 pooled adults	Tukey	2-4 to 14-16	< 0.002	*
2005 WNH adults vs. 2002 pooled adults	Tukey	2-4 to 14-16	< 0.023	*
vs. 2004 pooled adults	Tukey	5-7 to 11-13	< 0.001	*

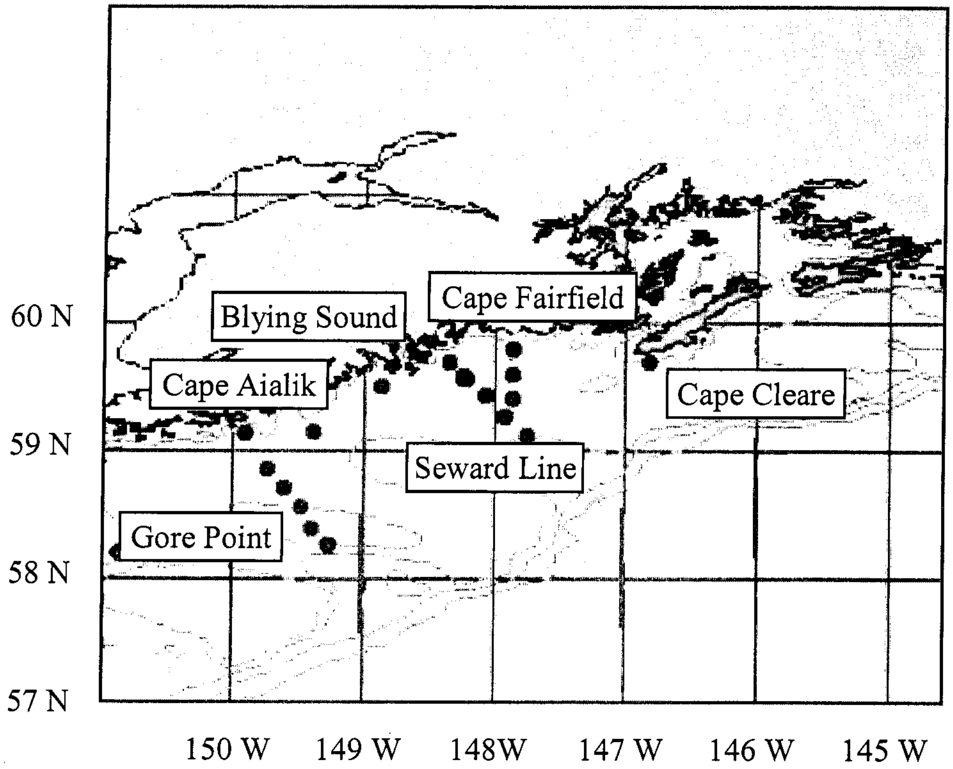

Figure 3.1. Stations where adult pink salmon scales were collected by the Ocean Carrying Capacity (OCC) Program of the National Marine Fisheries Service during 7/24/03–8/1/03.

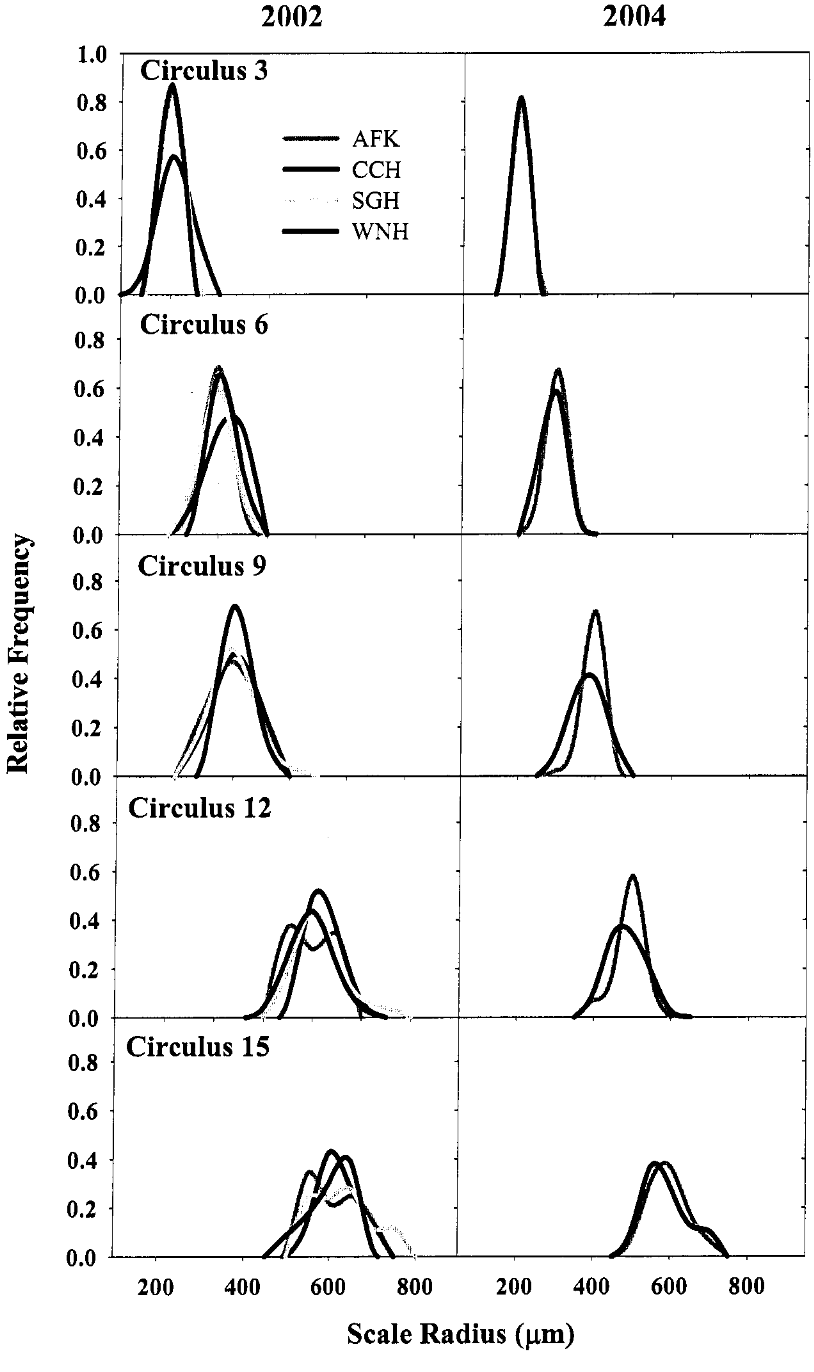

Figure 3.2. The distribution of scale measurements at every third circulus during the first growing season for adult pink salmon collected in 2002 and 2004 at terminal fisheries in front of four hatcheries in Prince William Sound. AFK = Armin F. Koernig; CCH = Cannery Creek; SGH = Solomon Gulch; WNH = Wally Noerenberg. No significant differences were found between cohorts; therefore, adults from each year were pooled for scale analyses.

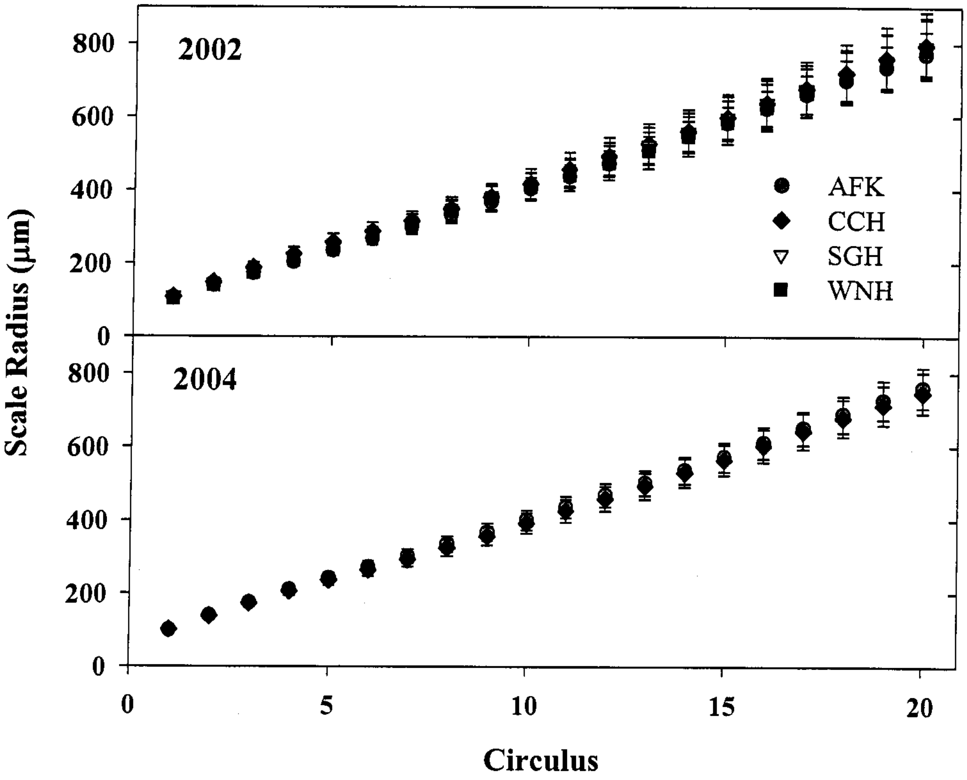

Figure 3.3. Mean size at circuli during the first growing season for adult pink salmon collected in Prince William Sound in 2002 and 2004. In 2002, scales were collected from adults captured at terminal fisheries in front of Armin F. Koernig (AFK), Cannery Creek (CCH), Solomon Gulch (SGH), and Wally Noerenberg (WNH) hatcheries. In 2004, adults were captured only at AFK and CCH. Error bars are ± cumulative 2SE.

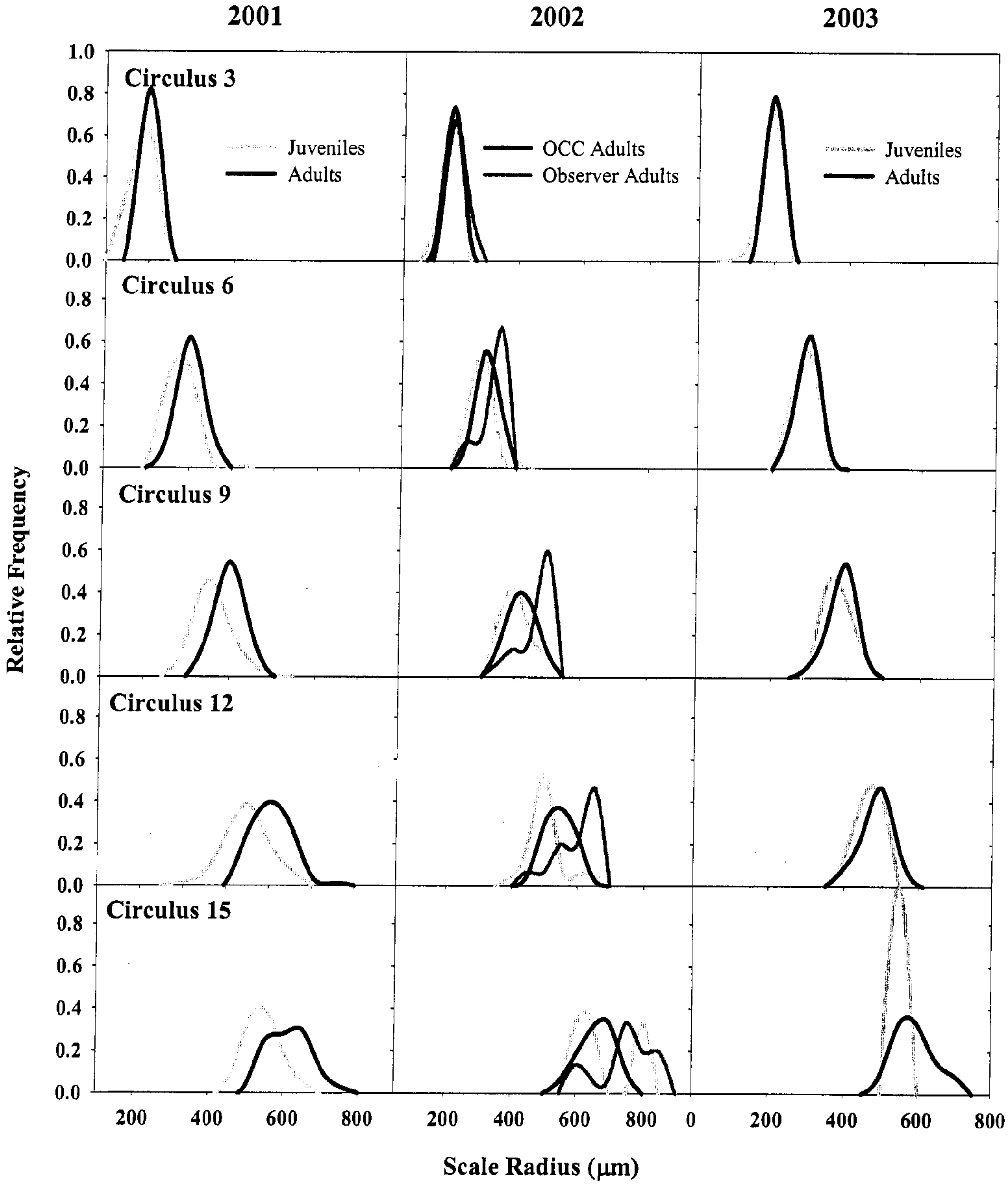

Figure 3.4. The frequency of scale measurements at every third circulus during the first growing season for juvenile pink salmon collected in Prince William Sound and the coastal Gulf of Alaska during July–September 2001-2003 and for pink salmon from the same year-class that survived to adulthood. In 2002 and 2004, adult pink salmon were collected at terminal fisheries in front of four hatcheries in Prince William Sound. In 2003, adults were captured in the Gulf of Alaska by the Ocean Carrying Capacity (OCC) and Observer programs of the National Marine Fisheries Service.

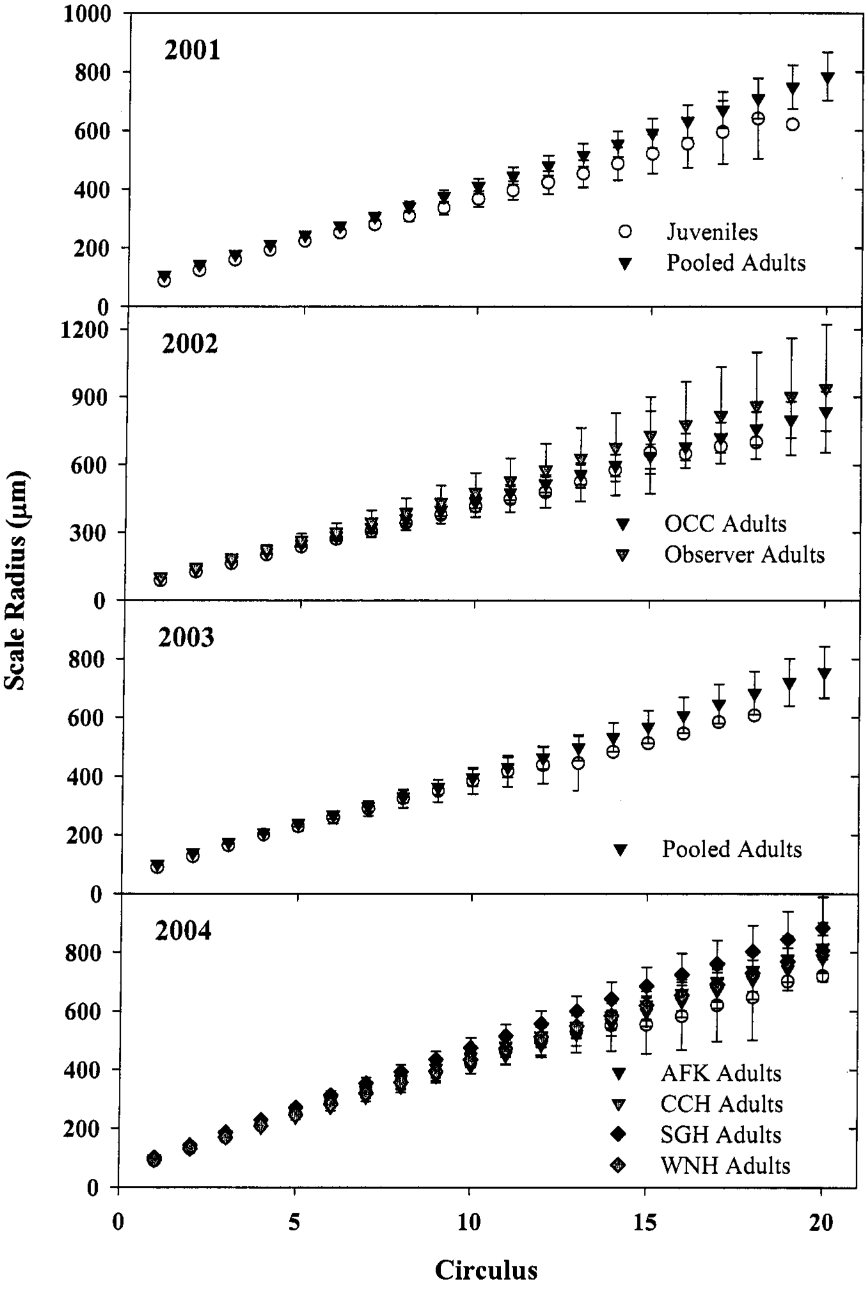

Figure 3.5. Mean size at circuli for juvenile pink salmon collected in Prince William Sound and the coastal Gulf of Alaska during July–September 2001-2004 and for pink salmon from the same year-class that survived to adulthood. During 2002, 2004, and 2005, adult pink salmon were collected at terminal fisheries in front of four hatcheries in Prince William Sound: AFK = Armin F. Koernig; CCH = Cannery Creek; SGH = Solomon Gulch; WNH = Wally Noerenberg. In 2003, adult pink salmon were captured in the Gulf of Alaska by the Ocean Carrying Capacity (OCC) and Observer programs of the National Marine Fisheries Service. Error bars are ± cumulative SE.

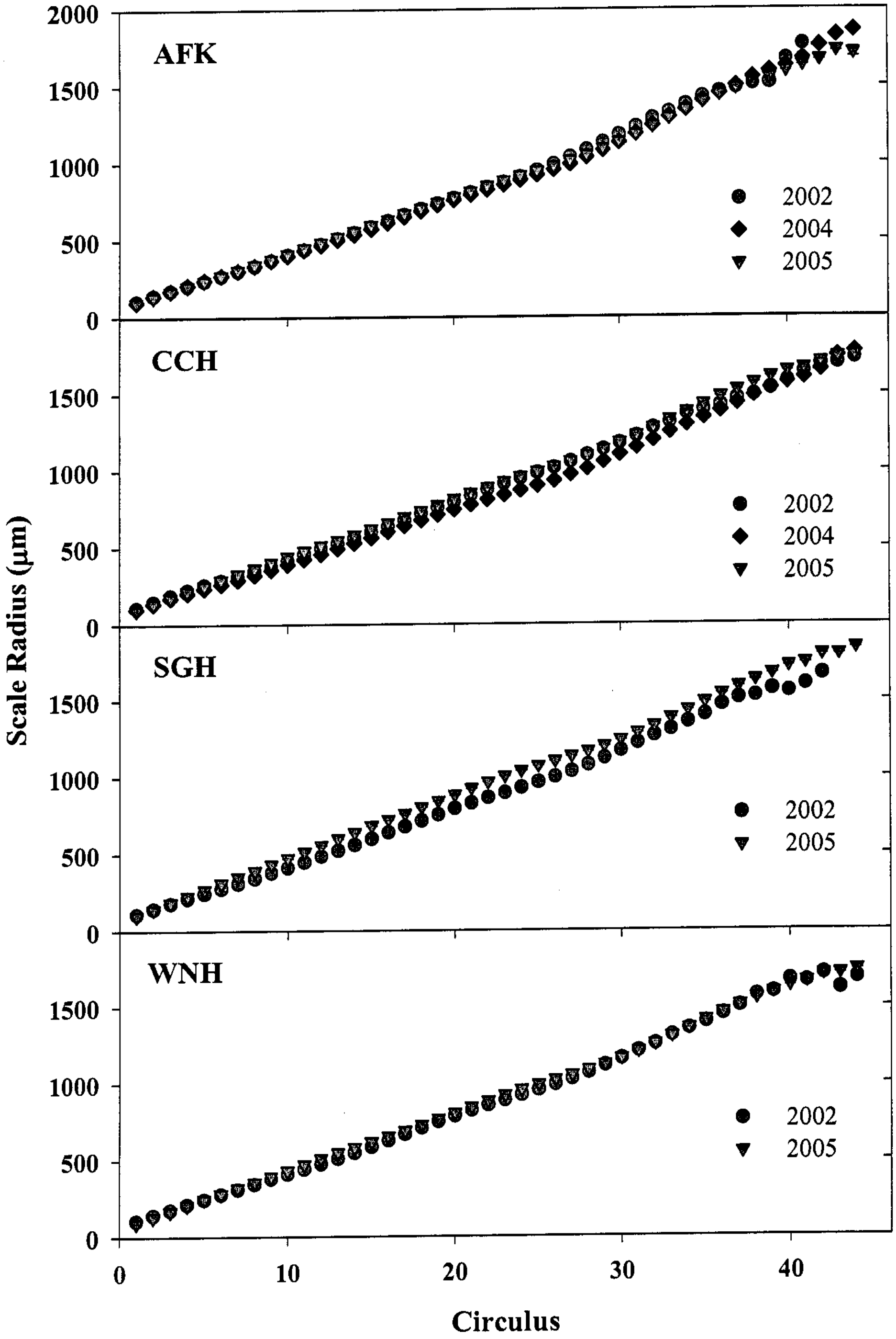

Figure 3.6. Mean size at circuli for adult pink salmon collected from terminal fisheries at Armin F. Koernig (AFK), Cannery Creek (CCH), Solomon Gulch (SGH), and Wally Noerenberg (WNH) hatcheries in Prince William Sound in 2002, 2004, and 2005. Error bars are ± 2SE.

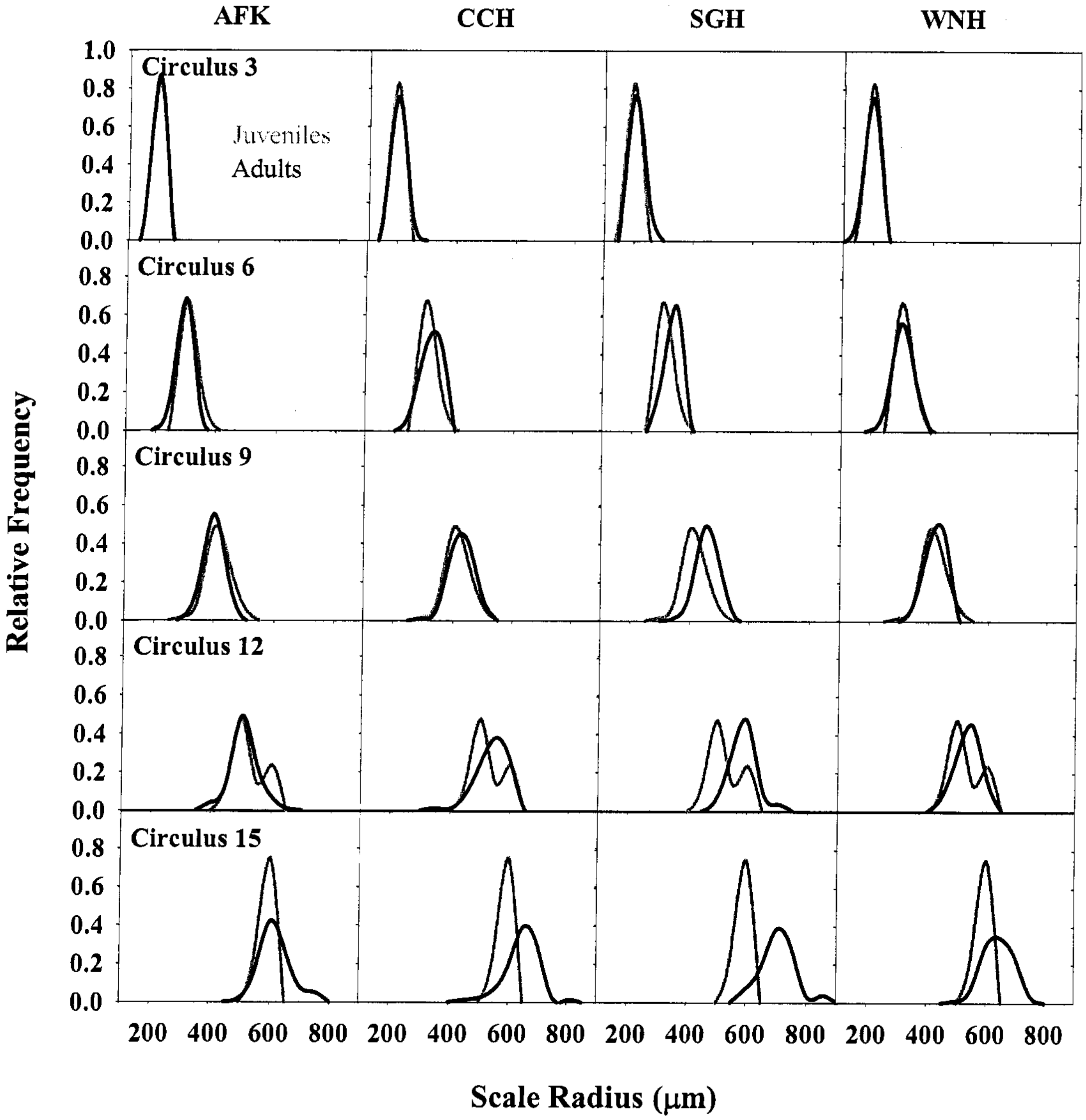

Figure 3.7. The frequency of scale measurements at every third circulus during the first growing season for juvenile pink salmon collected in Prince William Sound and the coastal Gulf of Alaska during July–September 2004 and for pink salmon from the same year-class that survived to adulthood. Adult pink salmon were collected at terminal fisheries in front of four hatcheries in Prince William Sound: AFK = Armin F. Koernig; CCH = Cannery Creek; SGH = Solomon Gulch; WNH = Wally Noerenberg.

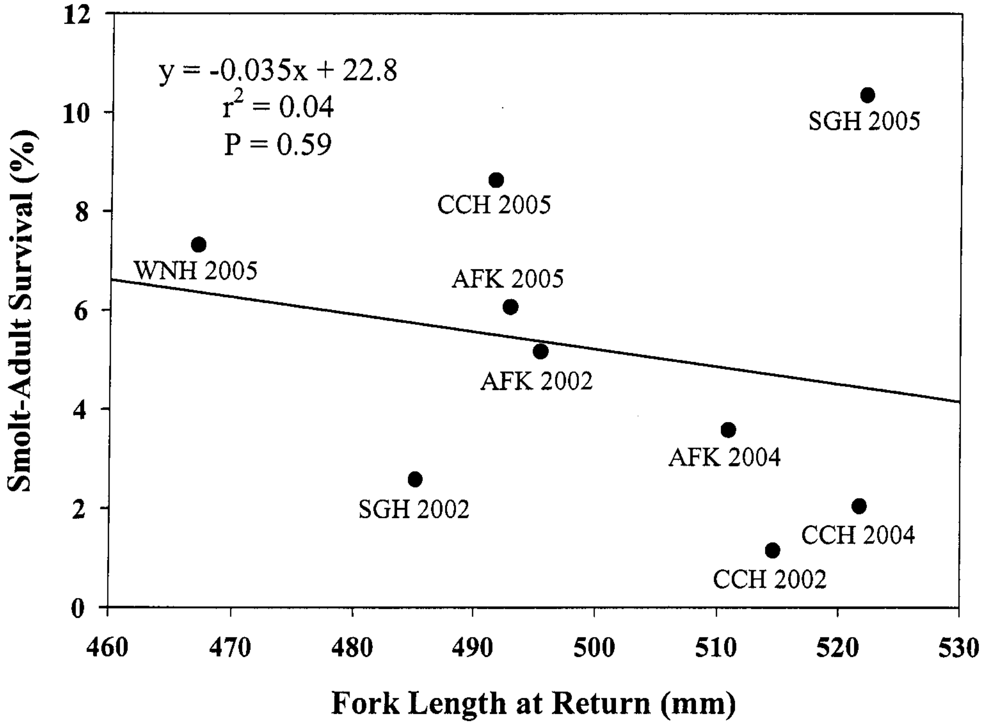

Figure 3.8. No relationship existed between size at return and smolt-to-adult survival for pink salmon returning to Armin F. Koernig, Cannery Creek, Solomon Gulch, and Wally Noerenberg hatcheries in Prince William Sound during 2002, 2004, and 2005.

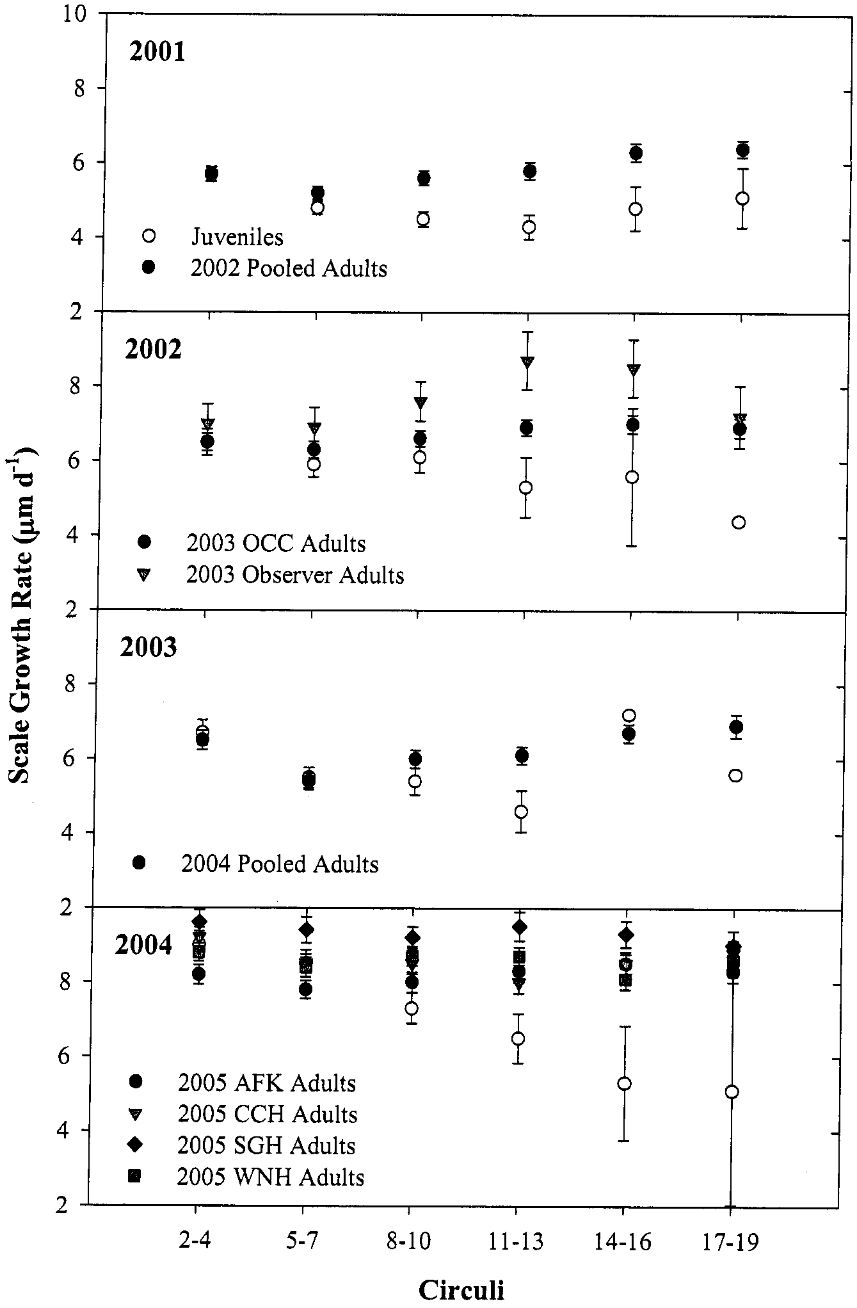

Figure 3.9. Mean growth rate between circuli ($\mu m \cdot d^{-1}$) for juvenile pink salmon collected in Prince William Sound and the coastal Gulf of Alaska during July–September 2001–2004, and for pink salmon from the same year-class that survived to adulthood. During 2002, 2004, and 2005, adult pink salmon were collected at terminal fisheries in front of four hatcheries in Prince William Sound: AFK = Armin F. Koernig; CCH = Cannery Creek; SGH = Solomon Gulch; WNH = Wally Noerenberg. In 2003, adult pink salmon were captured in the Gulf of Alaska by the Ocean Carrying Capacity (OCC) and Observer programs of the National Marine Fisheries Service. Error bars are ± 2SE.

NOTES TO CHAPTER 3

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Chapter 4. Consumption Demand of Juvenile Pink Salmon in Prince William Sound and the Northern Coastal Gulf of Alaska During Years of Low and High Survival

INTRODUCTION

The four hatcheries in Prince William Sound that release pink salmon (*Oncorhynchus gorbuscha*) fry represent one of the largest salmon hatchery programs in the world. Armin F. Koernig, Cannery Creek, Wally Noerenberg, and Solomon Gulch hatcheries have released a combined total of over 600 million fry since 2001 (Alaska Department of Fish and Game 2005). These hatchery releases average over three times more fry than the natural production of approximately 190 million wild pink salmon fry migrating into Prince William Sound (S. Moffitt, Alaska Department of Fish and Game, personal communication).

Whether sufficient prey are available in Prince William Sound and the coastal Gulf of Alaska to absorb the additional consumption demand by hatchery juvenile pink salmon is unknown. The increased abundance of juveniles from hatchery production has elicited concerns that the carrying capacity for juvenile pink salmon has been reached or exceeded; juvenile pink salmon could potentially become food-limited at one or more stages in their life cycle in one or more regions. Severe consequences, such as declining body size and survival, could result if carrying capacity is exceeded (Cooney and Brodeur 1998). This concern is especially timely because it stems from a human-initiated challenge to the ecosystem, and we can control the additional demand by regulating hatchery production. Therefore, future management of Prince William Sound hatchery operations should incorporate an understanding of the spatial and temporal nature of the additional demand on forage resources. This study examines interannual variability in the growth performance and consumption demand of juvenile pink salmon in years corresponding to low marine survival (3% for adult pink salmon returning to Prince William Sound in both 2002 and 2004) and high marine survival (9% in 2003; Alaska Department of Fish and Game 2005; Prince William Sound Aquaculture Corporation 2005; K. Morgan, Valdez Fisheries Development Association, personal communication).

Wild pink salmon fry enter the marine waters of Prince William Sound between mid-April and early June each year (Cooney 1993; Sharr et al. 1995). Prince William Sound hatcheries time the release of fry to coincide with the spring zooplankton bloom, which typically occurs in May (Cooney et al. 1995). Juvenile pink salmon migrate out of Prince William Sound to the coastal Gulf of Alaska by July or early August (Cooney 1993), move off the continental shelf by their first winter, and return to Prince William Sound the following summer as adults. Although some juvenile pink salmon remain in Prince William Sound through October, the most common strategy is to migrate to the coastal Gulf of Alaska around July. On account of their two-year life cycle, juvenile pink salmon that entered the ocean during 2001-2003 returned as adults in the following summers of 2002-2004.

Pink salmon fry migrate to sea at a smaller size than any other salmonid (Quinn 2005). Wild fish enter Prince William Sound at approximately 0.26 g (Bailey et al. 1976; Boldt and Haldorson 2002), and the average weight at release for the 2001-2003 hatchery cohorts was 0.53 g, 0.56 g, and 0.70 g respectively (Alaska Department of Fish and Game 2005). Throughout the summer and fall, juvenile pink salmon reside over the continental shelf and grow from roughly 7 g in July to larger than 90 g in October.

Due to their small size at ocean entry, juvenile pink salmon are highly vulnerable to predation during their first months in marine waters (Hunter 1959; Parker 1968), and consequent high juvenile mortality markedly affects adult year-class strength. Early marine growth has repeatedly been correlated with overall survival in salmon (Holtby et al. 1990; Murphy et al. 1998; Tovey 1999; Willette et al. 1999; Mortensen et al. 2000; Beamish et al. 2004; Moss et al. 2005), and rapid growth can reduce size-selective predation mortality (Hargreaves and LeBrasseur 1985; Heard 1991; Jaenicke and Celewycz 1994; Willette et al. 1999). The availability of small copepods, which compose the majority of the diet of pink salmon fry (Cooney et al. 1981; Parker 1997), will affect consumption rates of pink salmon and, subsequently, growth. If zooplankton availability is high enough for fry to grow rapidly and achieve a critical size, predation mortality could be reduced (Willette 2001).

Pink salmon are the dominant planktivorous fish species in the coastal Gulf of Alaska in terms of both numbers and biomass (L. Haldorson, University of Alaska Fairbanks–Juneau, unpublished data). Juvenile pink salmon feed primarily on small and large calanoid copepods in April and May (Parker 1997; Cooney et al. 2001b); small, surface zooplankton such as copepods, larvaceans, and pteropods during July and August; and larger prey such as euphausiids, crab megalopae, amphipods, and fish by fall (Sturdevant et al. 1996; Armstrong et al. 2005). Other planktivorous fishes, including walleye pollock (*Theragra chalcogramma*), Pacific herring (*Clupea pallasii*), capelin (*Mallotus villosus*), eulachon (*Thaleichthys pacificus*), sand lance (*Ammodytes hexapterus*), and other salmonids (*Onchorhynchus spp.*), utilize these resources as well. On account of such high dietary overlap and the large number of juvenile pink salmon released each year, both inter- and intraspecific competition for food resources could potentially influence the growth and subsequent survival of these species. Recent studies present evidence for the competitive dominance of pink salmon over other salmon species (Ruggerone et al. 2003; Ruggerone and Nielsen 2004). North American pink salmon significantly altered the abundance of prey available to other species of Pacific salmon, resulting in reduced consumption, growth, and survival (Ruggerone and Nielsen 2004). Asian pink salmon also appear to reduce the growth of Bristol Bay sockeye salmon (*O. nerka*) during odd years, when Asian pink salmon are most abundant (Ruggerone et al. 2003).

Although seasonal cycles of secondary prey production are similar in Prince William Sound and the coastal Gulf of Alaska, zooplankton composition differs between regions. Zooplankton biomass peaks in May in the northern Gulf of Alaska (Coyle and Pinchuk 2003; Coyle and Pinchuk 2005), and in June in Prince William Sound (Cooney et al. 2001a). In recent studies, copepods composed the majority of the zooplankton assemblage in both regions; however, large calanoid copepods (e.g. *Neocalanus*) were more prominent in the Gulf of Alaska (Coyle and Pinchuk 2003; Coyle and Pinchuk 2005), while smaller copepods (e.g. *Pseudocalanus*) dominated in Prince William Sound (Cooney et al. 2001a). Some dominant calanoid copepod species enter diapause and leave the water column in July, just when pink salmon disperse from Prince William Sound into the coastal Gulf of Alaska. In descending order of importance, cnidarians, euphausiids, pteropods, and chaetognaths comprise much of the zooplankton biomass in the northern Gulf of Alaska between May and October (Coyle and Pinchuk 2003; Coyle and Pinchuk 2005). Pteropods and larvaceans compose the majority of the non-copepod biomass in Prince William Sound during this time, while euphausiids, amphipods, and chaetognaths are also important (Cooney et al. 2001a; Eslinger et al. 2001).

Comparing the consumption demand of the population to the biomass of exploitable prey in localized areas allows us to identify and quantify ecological bottlenecks, such as periods of prey depletion. Knowing the amount of prey required by juvenile pink salmon to exceed minimum size thresholds for survival during the first summer and fall at sea is critical in determining the health of the species and its habitat. Moreover, by quantifying the consumption demand of both wild and hatchery pink salmon, we can begin to evaluate their role within the larger trophic dynamics of the Prince William Sound and coastal Gulf of Alaska region. A greater understanding of these issues is particularly significant at present, given the ongoing debate regarding the value of hatcheries (Meffe 1992; Smoker and Linley 1997; Hilborn and Eggers 2000; Wertheimer et al. 2001; Wertheimer et al. 2004a) and increasing evidence of global warming's effect on the world's oceans (Beamish et al. 1995; Hill 1995; Roemmich and McGowan 1995; Welch et al. 1998).

Two previous studies examined the amount of juvenile pink salmon production that Prince William Sound can support and found no evidence for food limitation (Cooney 1993; Boldt and Haldorson 2002). Boldt and Haldorson (2002) used bioenergetics models to estimate consumption by juvenile pink salmon in Prince William Sound during their first three months at sea. They found that pink salmon consumed only 0.06–0.45% of the total secondary production in the region, as determined from a general estimate of primary production in a non-tropical, coastal region and a transfer efficiency of 20%. Cooney (1993) estimated the demand of juvenile pink salmon in Price William Sound during their first four months at sea based on literature values of growth rate, growth efficiency, and survival, and determined that juvenile pink salmon consume 0.8–3.2% of total herbivore production and 3.0–10.0% of macrozooplankton production.

One prior study examined juvenile pink salmon consumption in both Prince William Sound and the open continental Gulf of Alaska shelf region just beyond Prince William Sound and observed the potential for food limitation in these regions (Cross et al. 2005). This study improves on that analysis by incorporating more accurate growth inputs, comparisons among multiple years, and comparisons between the juvenile pink salmon population at-large and the fraction that survived to adulthood. Prince William Sound hatcheries thermally mark the otoliths of 100% of their pink salmon fry prior to release, providing a unique opportunity to track the growth history of each hatchery fish recovered to a specific entry date, location, and size. As in Cross et al. (2005), this study uses region-specific data to follow known cohorts of juvenile pink salmon in specific water masses over their first growing season to further improve the accuracy of consumption estimates. Additionally, prior supply-demand comparisons in Prince William Sound (Cooney 1993; Boldt and Haldorson 2002) did not consider the supply of specific prey taxa consumed by juvenile pink salmon. This study compares the modeled consumption demand of juvenile pink salmon in both Prince William Sound and the coastal Gulf of Alaska to observed abundances of key prey types.

Growth rates provide an integrative history of foraging success and metabolic response to environmental conditions (Mason et al. 1995). Species-specific growth rates can reflect habitat quality and indicate oceanographic change, with higher growth rates signifying better growth conditions (Mason et al. 1995; Brodeur et al. 2004). Both biological (prey availability and quality) and physical (temperature, salinity, light intensity, and turbidity) characteristics determine habitat quality (Mason et al. 1995).

Environmental factors can affect spacing between scale circuli by changing somatic growth rates (Fukuwaka and Kaeriyama 1997). Changes in temperature, zooplankton availability, and competitor abundance could result in periods of slower or faster growth that would be recorded in the growth of scales and otoliths. Thus, salmon can record the general history of ocean growth conditions in their scales (Welch 1997).

Because of variability in the timing of ocean entry, using scales to study growth allows more accurate comparisons among different cohorts at certain points in their life history than by tracking mean sizes of fish captured at sea.

The primary intent of this study was to use scale circulus patterns to estimate consumption and growth efficiency for the average juvenile pink salmon in Prince William Sound and the coastal Gulf of Alaska during years of low and high survival. My specific objectives were to: 1) use bioenergetics model simulations to estimate the consumption demand of hatchery and wild pink salmon over their first five months in Prince William Sound and the coastal Gulf of Alaska, and 2) compare population-level consumption estimates to localized prey biomass to gain insight on possible ecological bottlenecks that limit growth and survival. Consumption and growth efficiency were compared among hatchery- and wild-origin juvenile pink salmon and hatchery pink salmon cohorts that survived to adulthood at comparable stages in their life history. I hypothesized that food limitation occurs during one or more critical periods in Prince William Sound and the coastal Gulf of Alaska, and is expressed as reduced feeding and growth. I also expected food limitation to vary among seasons or years due to differences in thermal regime and the quantity or quality of prey.

METHODS

Field sampling

Juvenile pink salmon, zooplankton, and data on physical oceanographic conditions were collected in 2001, 2002, and 2003 at three stations in southwest Prince William Sound and stations 1–6 on the GLOBEC-delineated Seward (GAK) Line (Figure 2.1). Stations were sampled during 6–10 d cruises monthly from July to October (Table 2.1) with the following exceptions: An early October 2002 cruise was scheduled in place of the two cruises held in mid-September and mid-October 2001. Because October catches were very low in 2001 and 2002, no October cruise was scheduled during 2003. We sampled out to station 10 on the Seward Line in August 2002, and to station 7 in September 2003. In 2003, we also sampled a transect extending south from Cape

Fairfield, east of the Seward Line, during all months (Table 2.1, Figure 2.1). Two stations west of the Seward Line were also sampled in August 2003. This sampling scheme encompassed the Prince William Sound to coastal Gulf of Alaska migration period for juvenile pink salmon and allowed reasonably high spatial and temporal data resolution during the first growing season.

Juvenile pink salmon

At each station, two or more trawls were performed during daylight hours using a Nordic 264 surface rope trawl with 3 m doors and a 1.2 cm mesh liner in the cod end. The net fished a depth of approximately 11.4 m and a width of approximately 14.3 m (S. Patterson, Net Systems, personal communication) for 30 min at 3.5–5 knots (6.5–9.3 $km \cdot h^{-1}$). If juvenile pink salmon were present, but fewer than 10 were caught in a single haul, the tow was repeated. Catches were sorted to species and counted; large catches were subsampled. The fork lengths of up to 200 fish of each species were measured. Up to 50 juvenile pink salmon from each tow were frozen in seawater for subsequent analysis.

Zooplankton Abundance

At the mid-point of each station, a 1 m^2 NIO/Tucker net was towed horizontally alongside the vessel in undisturbed surface water to collect surface zooplankton. Three 2-5 min trawls were conducted at each station where juvenile pink salmon were collected by the surface trawl. A digital flowmeter centered in the net opening quantified the distance traveled. In 2001 and 2002, we used 505 μm mesh; 333 μm mesh was used in 2003.

In July and August 2002, we also performed three surface tows and three vertical tows from 10 m depth at two stations using a Bongo net (60 cm diameter, 333 and 505 μm mesh = 12 tows per station) to compare the effects of our methods and trawl gear on estimates of zooplankton density. During 2003, both horizontal Tucker trawls and two

10 m vertical tows with a 333 μm mesh Bongo net were deployed at each sampling station.

Samples from all tows were preserved in a 5% buffered formalin solution at sea and sent to the University of Alaska Fairbanks – Juneau for analysis.

Ocean Conditions

At each station, vertical profiles of conductivity and temperature were recorded with a Seabird Seacat SBE-19 CTD. The CTD recorded depth, temperature, salinity, and fluorescence at 1 m intervals over 0–100 m depths or to 5 m above the sea floor in shallower waters. Sea surface temperature was measured with a thermometer placed in a bucket of water collected from the sea surface (at approximately 1 m) because the CTD did not function well at this depth.

Adult pink salmon

Adult pink salmon were collected in terminal cost-recovery fisheries during the summers of 2002 and 2004 upon return to Armin F. Koernig (AFK), Cannery Creek (CCH), Solomon Gulch (SGH), and Wally Noerenberg (WNH) hatcheries in Prince William Sound (Table 3.1). Adult fish were captured by purse seine at hatchery-specific terminal fishery sites, located directly in front of each hatchery.

Laboratory analyses

Personnel at the University of Alaska Fairbanks – Juneau recorded lengths and weights of all juvenile pink salmon collected and examined otoliths for thermal marks that indicated hatchery origin (L. Haldorson, J. Boldt, J. Piccolo, personal communication). Prince William Sound hatcheries thermally mark 100% of their pink salmon fry prior to release, providing a unique opportunity to trace each hatchery fish recovered to a specific entry date, location, and size.

Several scales were collected from the preferred area of both the juvenile and adult pink salmon. Preferred scales were located in a rectangular area located one to four scale rows above the lateral line between two vertical lines drawn from the posterior edge of the dorsal fin and halfway between the posterior edge of the dorsal fin and the anterior edge of the adipose fin. Scales were collected from up to 15 juvenile pink salmon captured at each station during each year. Scales were collected from 50 adult pink salmon at each hatchery (AFK, CCH, SGH, and WNH) in 2002 and from 50 pink salmon at AFK and CCH hatcheries in 2004. Because no adult scales were collected by Prince William Sound hatcheries in 2003, scales from adult pink salmon collected during the summer of 2003 by the Ocean Carrying Capacity (OCC) program of the National Marine Fisheries Service were used as surrogate scales for adults returning to Prince William Sound during this year (Table 3.1). Scales collected by the OCC program and used in this analysis were obtained from pink salmon captured just west of Prince William Sound during late July and early August (Figure 3.1). Thermal otolith markings were not read to determine the origin of these adult pink salmon; however, due to the location of these fish on the capture date and the large number of pink salmon released by Prince William Sound hatcheries, many of these fish were presumably returning to Prince William Sound. Recent studies show that environmental processes during the early marine period are related to juvenile salmon survival and affect survival at regional (up to 1000 km) rather than ocean basin-wide scales (Pyper et al. 2001; Mueter et al. 2002; Pyper et al. 2005). This suggests that even if fish from the OCC program were not bound for Prince William Sound, they likely experienced similar early marine conditions.

The scales from each pink salmon were placed on gummed cards, sculptured surface up, and impressed in transparent acetate at a pressure of 5000 psi for 3 min. Acetate impressions were read using a computerized video digitizing system (Optical Pattern Recognition System, Model OPR-512). The first scale from each fish showing clear, unbroken circulus bands, an unbroken scale edge, and no signs of regeneration was measured. Scale circuli were measured along the anterior-posterior axis, from the back of the focus to the scale edge—the most commonly used measurement (Martinson et al. 2000). Each circulus that crossed the measurement axis was automatically marked by the digitizing system and errors were manually edited.

Total scale radius equaled the distance from the mid-point of the focus (focus/2) to the scale edge. To remove outliers, measurements from fish with a fork length to scale radius ratio of > 0.45 or a focus > 250 μm were deleted (K. Myers, University of Washington High Seas Salmon Research Program, personal communication). Between 3–15% of juvenile scales were removed as outliers, while 3–43% of adult scales were removed. Scales were analyzed from a total of 135 hatchery pink salmon juveniles caught during July–September 2001, from 37 hatchery juveniles caught during July and August 2002, and from 40 hatchery juveniles caught during July–September 2003 (Tables 3.2-3.5). Scales were analyzed from 94, 102, and 81 adult pink salmon captured during 2002, 2003, and 2004, respectively (Table 3.2-3.5).

Energy densities for a subsample of juvenile pink salmon from each monthly cruise (n = 13–117) were measured with a Parr semi-micro bomb calorimeter. We analyzed stomach contents from up to 15 individuals from each station per month, and determined the proportional contribution of each prey category to the diet by volume (Armstrong et al. 2005).

Laboratory personnel at the University of Alaska – Juneau identified zooplankton samples to the lowest taxonomic category possible. For every replicate sample at each station, the areal density of each taxon in the top 1 m of the water column was calculated in terms of mean number·m^{-2}. Total density was calculated for all zooplankton combined and for only those sizes and species typically ingested by juvenile pink salmon.

Salinity measurements were obtained from the CTD cast at each station. Because salinity gradients can affect the distribution of forage fishes (Abookire and Piatt 2005), and because sea-surface salinity prior to migration can affect the survival of pink salmon fry (Mueter et al. 2005), we assigned a water mass category to each station on the Seward Line according to the salinity at 2 m depth: salinity < 30 psu in the Alaska Coastal Current (ACC); 30 psu ≤ salinity < 31.5 psu in the frontal zone (Front), and salinity ≥ 31.5 psu in the mid-shelf transition zone (Trans). All stations in Prince William Sound were classified as the Prince William Sound (PWS) water mass (range 19.4-30.1 psu). In July 2003, the range of salinity values declined between ACC and transition waters, with consistently low salinity in the transition zone. Consequently, we distinguished ACC and front regions by reviewing the salinity profiles for a number of stations that were sampled contiguously, and defined the transition zone as being ≥ 31.0 psu for these cruises.

Bioenergetics modeling

The bioenergetics modeling approach describes how consumed energy flows through a fish and is partitioned into growth, metabolism, and waste over time (Kitchell et al. 1977). The model calculates the consumption of a consumer using the energy-balance equation:

$$C = G + M + W,$$

where C is total energy consumed, G is growth, M is metabolic costs (e.g. respiration, activity, and specific dynamic action (SDA)), and W is waste (egestion and excretion). Species-specific functions for M, W, and maximum specific consumption rate (C_{max}) are built into the model (Hanson et al. 1997). Mass consumed by a predator is converted to energy and first allocated to metabolism and waste. Surplus energy is then converted to growth based on the energy density of the consumer. The model updates the physiology of the consumer on a daily time-step over the simulation period, and accounts for observed changes in body size, temperature, diet, and energy density, linearly interpolating user-input data when necessary.

I used the Pink/Sockeye salmon parameter set in the Wisconsin Bioenergetics Model (Hewett and Johnson 1992; Hanson et al. 1997), which has performed well for juvenile Pacific salmon (Beauchamp et al. 1989; Brodeur et al. 1992; Ruggerone and Rogers 1992). Model parameters were developed from juvenile and subadult sockeye salmon (Beauchamp et al. 1989), but are listed as a surrogate for pink salmon in the Wisconsin model (Hanson et al. 1997). Because juvenile pink and sockeye salmon exhibit similar distribution and life history traits (both are pelagic and highly planktivorous), this is a natural extension of the model, and is identified as such (Hanson et al. 1997). Boldt and Haldorson (2002) previously used this approach to model the bioenergetics of juvenile pink salmon in Prince William Sound.

Model simulations

Field- and laboratory-derived estimates of the weight change, thermal experience, energy density, and diet composition of juvenile pink salmon, and the energy density of their prey, were used as inputs to the model to estimate the amount of prey that individual fish consumed to achieve observed growth rates from May–September 2001–2003. I supplemented data from the GLOBEC cruises with May hatchery release data (Alaska Department of Fish and Game 2005), and used literature values as model inputs when necessary. Except for initial and final weights for each simulation, model input data were identical for the average hatchery juvenile pink salmon and the hatchery cohort that survived to the adult stage.

A linear scale-length relationship most closely characterized the early marine growth of juvenile pink salmon in Prince William Sound and the coastal Gulf of Alaska during 2001–2003 ($r^2 = 0.77$-0.80, $P < 0.001$ for all years; Figure 2.2; Chapter 2). Because of the linear relationship between scale size and fish length and between circulus spacing and fish growth rate, fish length can be inferred directly from scale radius and growth rate from scale circulus spacing. Scales began to form when pink salmon are approximately 44-48 mm in length, and the first circulus appeared during mid-June, approximately one month after marine entry (Chapter 2). After initial formation, circuli continued to develop at a rate of one every 4.4-6.1 d (Chapter 2).

Because scale-based growth trajectories were not significantly different among juvenile pink salmon from different hatcheries during May–September 2001–2003, I pooled all hatchery juveniles within each year (ANOVA: $P > 0.05$; Chapter 2). Additionally, no significant differences were apparent among adult pink salmon from AFK, CCH, SGH, and WNH hatcheries during 2001-2002 or from AFK and CCH hatcheries during 2003-2004 (Chapter 2). Adult pink salmon captured in 2002 and 2004 were therefore also pooled for growth analyses.

Because Prince William Sound hatcheries thermally mark 100% of their fry prior to release, individuals with no otolith marks were assumed to be of wild origin. However, immigration of unmarked hatchery or wild fish from Southeast Alaska or other sources into the study area could have biased growth estimates for unmarked fish in September or October. Through August, we could be reasonably confident that any unmarked fish captured in our trawls were wild fish originating from Prince William Sound. Studies on the incidence of thermally marked juvenile pink salmon in the coastal Gulf of Alaska found that only 0–2% of marked pink salmon caught west of Prince William Sound in July and August originated from Southeast Alaska (Farley and Munk 1997; Farley and Carlson 2000). However, hatcheries in Southeast Alaska do not mark all of their pink salmon fry. By September or October, unmarked fish from Southeast Alaska could have moved into Prince William Sound and across the Seward Line. Consequently, the unknown origin of unmarked fish caught during these latter months added uncertainty to comparisons between hatchery and wild fish at larger sizes.

To adequately model the experience of the average juvenile pink salmon during May–September of each year, I examined catch per unit effort (CPUE) data from the 2001–2003 cruises to determine which water mass(es) contained peak densities of juvenile pink salmon during each month (Chapter 2). Model inputs of thermal experience, diet, and consumer energy density were specific to the water mass with modal CPUE. However, in August 2001, CPUE was similar across PWS, ACC, Front, and Trans water masses. A weighted average of diet, temperature, and energy density in all water masses was used when modeling this month. Due to small sample sizes, fish caught in October were not included in this analysis.

During August and September 2003, the spatial distribution of juvenile pink salmon had clearly diverged into different non-adjacent regions. In August 2003, CPUE was high in PWS and the transition zone, but low in the ACC and Front. Pink salmon had to occupy one or the other distinct region, and could not have averaged their experience over all four regions. In this case, separate model simulations were run for PWS and Trans water masses to capture regional differences in growth and consumption. In September 2003, pink salmon were modeled in both ACC and Trans water masses.

Consequently, I produced 12 growth sequences depicting the bioenergetics for the juvenile stage of the average hatchery, average wild, and adult hatchery pink salmon:

1. Remaining in Prince William Sound through July, distributing throughout all water masses in August, and migrating to the transition zone by September during 2001;
2. Remaining in Prince William Sound through July and migrating to the transition zone by August during 2002;
3. Remaining in Prince William Sound throughout May–August and migrating to the ACC by September 2003; and
4. Remaining in Prince William Sound through July, migrating to the transition zone by August, and remaining in the transition zone through September 2003.

This allowed me to compare rearing strategies between the two regions in terms of consumption, growth, growth efficiency, and origin (hatchery vs. wild). Because no September cruise was conducted in 2002, simulations for this year encompass May–August. Simulations for juvenile fish during 2003 also only encompassed May–August due to low sample sizes in September, but the juvenile stages of the surviving adults were modeled through September.

To estimate consumption under each migration scenario, I ran separate model simulations from May–July, July–August, and August–September. Day 1 of the first simulation was designated as the day at which pink salmon fry entered the marine environment. The average day of release from all hatcheries (weighted by number released per day) was used as Day 1 for juvenile and adult hatchery cohorts: 18-May in 2001, 21-May in 2002, and 12-May in 2003. The average date of entry for wild fish was estimated based on the growth trajectory in back-calculated weight for the wild cohort each year and an initial weight of 0.26 g. The back-calculated entry dates of 17-Apr-2001, 28-Apr-2002, and 30-Apr-2003 fell within the estimated marine entry period for wild pink salmon (Cooney 1993; Sharr et al. 1995). The weighted average dates of monthly sampling cruises, calculated from the number of hatchery and wild juvenile pink salmon caught per day during each cruise, were used for the starting and ending dates of each successive simulation. I then merged the simulations for each origin-region combination into a continuous growth sequence from marine entry in May until the mean August or September sampling date. The model estimated both daily and cumulative consumption for every day of the simulation period.

Consumer weight change

Because the first circulus formed approximately one month after pink salmon were released from hatcheries (Chapter 2), the average size at marine entry was used as the initial weight for the May–July model simulation period. The average weight at release for the 2001-2003 hatchery cohorts from Prince William Sound was 0.53 g, 0.56 g, and 0.70 g, respectively (Alaska Department of Fish and Game 2005), whereas a mean weight of 0.26 g at marine entry was assumed for wild fish (Bailey et al. 1976; Boldt and Haldorson 2002).

Initial and final weights for hatchery juvenile, wild juvenile, and hatchery adult pink salmon for each model simulation period between July and September were derived from the scales of fish collected at sea. The weight of juvenile pink salmon at each circulus was estimated by first back-calculating fish length at each circulus. The effect of origin (hatchery versus wild) and scale size on fork length was significant in 2001 (ANCOVA, $P < 0.05$) but not in 2002-2003 ($P = 0.06$-0.42). Therefore, the fork length-scale size relationship for 2001 was determined using only hatchery fish, but the pooled group of hatchery and wild fish was used in the regressions for 2002 and 2003. Regressing fork length (FL) against total scale size at capture (SS) determined that the relationship between fish length and scale radius for juvenile pink salmon was linear throughout their first growing season:

2001 Hatchery: $FL = 0.216 \cdot SS + 44.49$ ($r^2 = 0.78$; $P < 0.001$)
2001 Unmarked: $FL = 0.188 \cdot SS + 61.35$ ($r^2 = 0.79$; $P < 0.001$)
2002 Pooled: $FL = 0.202 \cdot SS + 47.42$ ($r^2 = 0.77$; $P < 0.001$)
2003 Pooled: $FL = 0.202 \cdot SS + 46.60$ ($r^2 = 0.80$; $P < 0.001$)

(Chapter 2; Figure 2.2).

Back-calculations based on a linear relationship between scale radius and fork length that does not pass through the origin (because scales don't begin to grow until some unspecified time following ocean entry) can be made using the Fraser-Lee equation:

$$L_i = \frac{L_c - a}{S_c} \cdot S_i + a ,$$

where $(L_c-a)/S_c$ is the slope of the linear regression of scale radius on fork length of the fish, a is the intercept of the regression, L_i the fish length at which the i^{th} increment formed, L_c the fish length at capture, S_c the scale radius at capture, and S_i the scale radius at the i^{th} increment (Fraser 1916; Lee 1920). Since growth rate or size at scale formation can vary among populations of the same species (Lee 1920), only cohorts of fish with similar growth trajectories were used in the regression for each year, and the intercept parameter a was obtained from the regression for each cohort (Figure 2.2). The back-calculated size at each complete circulus for juvenile pink salmon was calculated using the fork length and scale size at capture for individual fish. Any growth that occurred between the last complete circulus and the scale margin was not included in the estimation of average size at circuli.

Due to differences in the morphology of juvenile and mature adult salmon, the relationship between scale size and fork length at capture for juvenile pink salmon does not hold for the adult cohort. The Fraser-Lee equation, which requires measurements of both total fish length and scale size at capture, is thus flawed for the purpose of back-calculating the size of adult fish at the juvenile stage. To adjust for this issue, I used a constant final scale size of 800 μm (approximately the average scale size at circulus 20 for adult survivors during the juvenile stage in September) and a final fork length estimated by using this constant final scale size in the FL-SS regression equation for the corresponding juvenile cohort. For example, for 2001:

$$L_c = 0.216 \cdot (800) + 44.49 .$$

This estimated L_c and $S_c = 800$ μm were then used in the Fraser-Lee equation to back-calculate size-at-circuli for the adult fish. Therefore, the same pooled fork length and scale size were used in the Fraser-Lee equation for all adults within each year, while individual measurements of fork length and scale size were used for juveniles.

Back-calculated lengths at each circulus were then converted to weights using the regression for wet weight (without stomach contents) on fork length for each cohort:

2001 Hatchery: $WW = 0.0000073 \cdot FL^{3.064}$ ($r^2 = 0.99$; $P < 0.001$)
2001 Unmarked: $WW = 0.0000061 \cdot FL^{3.104}$ ($r^2 = 0.99$; $P < 0.001$)
2002 Pooled: $WW = 0.0000059 \cdot FL^{3.121}$ ($r^2 = 0.98$; $P < 0.001$)
2003 Pooled: $WW = 0.0000062 \cdot FL^{3.092}$ ($r^2 = 0.99$; $P < 0.001$).

Initial and final weights for model simulations during July–September were the average back-calculated weight of each cohort on the average sampling date during each cruise (Tables 4.1–4.3). If a circulus did not coincide with the average sampling date during a particular month, the back-calculated weights at the two circuli that formed just before and after the sampling date and the number of days between circuli (6 d for all cohorts) were used to interpolate weight (see Chapter 2 for more information on the estimation of circulus formation rate). This method provided the best estimate of mean weight on the sampling date during each month.

Thermal experience

Because fry reside in surface waters shortly after marine entry (Bailey et al. 1975; Moulton 1997), literature values of sea surface temperature in Prince William Sound were used to estimate the temperature experienced by both hatchery and wild pink salmon fry on model day 1 (Cooney et al. 1995; Vaughan et al. 2001; Boldt and Haldorson 2002). I ran the model with a starting temperature of 5°C for wild pink salmon entering in late April, 7°C for the 2003 hatchery cohort released during the second week of May, and 8°C for the 2001 and 2002 hatchery cohorts released during the third week of May (Tables 4.1–4.3). As the season progresses, juvenile pink salmon increase their vertical distribution in the water column (Heard 1991). Therefore, a conservative average of temperatures from 1–10 m depth was used for thermal experience between July and September. Temperature data for July–September were obtained from CTD casts and averaged across all stations within each water mass (Tables 4.1–4.3).

Diet composition

Mean proportional diet composition by volume was estimated specific to the water mass(es) with the highest CPUE during each cruise from July–September (Table 4.4; Armstrong et al. 2005). An analysis of diel samples collected at sea showed that peak feeding by juvenile pink salmon occurred during daylight hours (Armstrong et al. 2005). Therefore, our July–September GLOBEC samples, collected in daylight, captured an accurate representation of juvenile pink salmon feeding behavior and diet composition. Since we did not sample during the May–July period, I used literature estimates of the diet of juvenile pink salmon in Prince William Sound during these months (Parker 1997; Table 4.4). Parallel model simulations accounted for regional differences in the proportion of prey items in the diet between fish collected in different salinity zones (Table 4.4).

Predator energy density

An energy density of 4102.3 $J \cdot g^{-1}$ wet weight was estimated from hatchery-raised fry just prior to release and used for the energy content of both hatchery and wild juvenile pink salmon upon entry to Prince William Sound in May (Boldt and Haldorson 2002). Differences in the energy densities of fish obtained in different water masses during each sampling cruise were large enough to be energetically significant in 2001 (ANCOVA, $P = 0.035$), so region-specific values were used in model simulations for all years (Tables 4.1–4.3). There were no significant differences in energy density between hatchery and unmarked fish during any cruise in 2001 and 2002 (ANCOVA, $P = 0.161$-0.365), so the data from these groups were pooled within all years. Boldt and Haldorson (2004) also found that the energy density of juvenile pink salmon in Prince William Sound and the coastal Gulf of Alaska varied among stations, but not between hatchery and wild fish.

Because no estimates were available for the energy density of juvenile pink salmon in either Prince William Sound or the transition zone during August 2003, the average estimate for fish caught in the Alaska Coastal Current and front was substituted for both values (Tables 4.1–4.3). For the adult cohort modeled as juveniles in September 2003, the average energy density in all regions in September 2001 was used because no estimates were available for 2003.

Prey energy density

Prey energy density values ($J \cdot g^{-1}$ wet weight) were obtained from the literature and from bomb calorimetry (Table 4.5; Davis et al. 1998; Davis 2003). Values for organisms obtained from the Gulf of Alaska were used when available (Davis et al. 1998; Davis 2003; M. Mazur, National Marine Fisheries Service Alaska Fisheries Science Center, personal communication), and supplemented with Bering Sea values when necessary (Nishiyama 1977; Davis et al. 1998). Insect energy density was obtained from a terrestrial study (Cummins and Wuycheck 1971). The insect value reflects the approximate percentage of aphids (90%) and larval Diptera (10%) consumed by juvenile pink salmon during 2001-2003. The energy density of the "other" prey category (Table 4.5) was estimated by proportionally weighting the energy density of each identifiable prey type that contributed to the diet in each month.

Energy densities for copepods, euphausiids, and hyperiid amphipods increase as lipid stores increase during summer and autumn (Higgs et al. 1995). Therefore, prey energy density inputs differed seasonally, but the same temporal pattern was applied to all regions (Table 4.5). Estimates of the percent indigestible for each prey type were obtained from the literature where possible, or otherwise assumed to be 10% (Table 4.5; Boldt and Haldorson 2002).

Model output

The model returned estimates of daily consumption ($g \cdot d^{-1}$), daily growth ($g \cdot d^{-1}$), and the average proportion of the theoretical maximum consumption (C_{max}) required for each fish to grow from the initial to final weight over the simulation period (Hanson et al. 1997). Growth efficiency was calculated by dividing the gain in body mass each day by the mass of prey consumed on that day. Growth efficiency reflects the net effect of prey quality and thermal experience, and increases with ration size under similar temperature and energy density regimes because a larger proportion of surplus energy can be allocated to growth. Growth efficiency thus provides a useful metric for comparing foraging conditions among different regions and months. I compared monthly growth, consumption, and growth efficiency between rearing scenarios for hatchery and wild juvenile and hatchery adult fish during their first growing season in marine waters.

Model sensitivity

To assess the influence of the input variables on the model's consumption estimates, I ran model simulations for hatchery, wild, and adult pink salmon cohorts from the largest size at release in May to the smallest observed size in September, and the smallest size at release in May to the largest observed size in September, under all migration scenarios (Tables 4.1–4.3). Even though these extreme growth scenarios are associated with very low probabilities compared to the average, this captured the extreme range of potential consumption for the sampled fish and allowed variability in consumption estimates to be addressed. Extreme growth scenarios were compared to nominal results from both this study to demonstrate the gain in accuracy and reduction in uncertainty from tracking individual growth trajectories rather than minimum/maximum weight changes through time.

I also modeled growth and consumption over the last complete circulus increment to estimate growth and consumption on a finer temporal scale. Model inputs specific to the water mass with peak CPUE were used to estimate the experience of the average pink salmon during each month (Tables 4.6–4.7). Hatchery and wild juveniles were pooled for this analysis.

Population-level consumption and prey biomass

I expanded estimates of consumption by individual fish to localized population-level consumption to determine the effect of juvenile pink salmon on the forage base in Prince William Sound and the coastal Gulf of Alaska. This analysis was conducted only for months in which zooplankton were sampled with more than one gear type in the water mass with peak CPUE of juvenile pink salmon: July 2003 and August 2003. During both months, zooplankton were collected with a horizontal Tucker trawl with 333 μm mesh and a vertical Bongo net with 333 μm mesh. Even though zooplankton were sampled with multiple gear types, August 2002 was not included in this analysis because the juvenile pink salmon catch was misidentified during this month, making it impossible to estimate density and population-level consumption.

Individual consumption estimates from simulations of hatchery cohorts were used in these calculations to minimize the potential uncertainty in tracking growth of mixed stocks that could be composed of fish with different times of marine entry and potentially different growth trajectories. Juvenile pink salmon consumption and prey biomass calculations were focused on four key prey types: large copepods (predominantly *Calanus* spp.), the pteropod *Limacina helicina*, amphipods (predominantly of the family hyperiidae), and larvaceans (genus *Oikopleura*). These prey items represented 89% of the diet of hatchery fish in Prince William Sound during July 2003, 60% of the diet of fish in Prince William Sound during August 2003, and 58% of the diet in the transition zone during August 2003.

To estimate the minimum density of juvenile pink salmon in each haul (fish·km^{-2}), I divided the catch by the area swept with the surface trawl. To determine area swept, I calculated the length of each haul using the Haversine formula, which uses start and end latitudes and longitudes to estimate distance while accounting for the spherical shape of the Earth (Sinnott 1984), and multiplied by net width (14.3 m = 0.0143 km). This approach assumed 100% capture efficiency and that the net followed the shortest distance between points and sampled the entire depth range of juvenile pink salmon. None of these assumptions are entirely true, so these calculations underestimate actual densities of pink salmon.

Both abundance and individual consumption (which is a function of body size, growth rate, temperature, and diet composition) affect the daily consumption demand by the juvenile pink salmon population. To estimate the total consumption of key prey types by juvenile pink salmon caught in Prince William Sound and the coastal Gulf of Alaska, I multiplied the average density of juvenile pink salmon in each water mass by the consumption of each key prey type by individual hatchery fish on the average sampling date during each month ($g \cdot d^{-1} \cdot fish$). This provided a two-dimensional localized estimate ($g \cdot km^{-2}$) of the consumption demand on key prey in specific water masses during each month.

To estimate the average density of key prey types co-occurring with juvenile pink salmon in each localized tow area during each month, I multiplied the average $number \cdot km^{-2}$ of each key prey species in the zooplankton trawls by the biomass of an average individual of that species at the approximate size found in the diet of juvenile pink salmon (Boldt and Haldorson 2002). Zooplankton densities from all tows in each water mass were averaged for each month. Because juvenile pink salmon reportedly feed to a depth of approximately 10 m (Heard 1991), I assumed that zooplankton composition in the volume of water sampled by both the Tucker and Bongo nets was representative of the top 10 m, and multiplied prey density estimates by 0.01 km. This gave an estimate of the biomass of key prey ($g \cdot km^{-2}$) available to juvenile pink salmon in water masses with peak CPUE on the average sampling day each month. I then compared estimates of daily consumption demand to the standing stock biomass of key prey estimated over 0–10 m during each month.

RESULTS

Growth Performance and Consumption Demand

Juvenile pink salmon required variable but high consumption rates, 66–106% of their theoretical maximum consumption (C_{max}), to satisfy the growth rates observed during the first four months in marine waters (Table 4.8). Average feeding rates for all cohorts were lowest from marine entry to July, ranging from 66–84% of C_{max} in 2001, 85–102% of C_{max} in 2002, and 67–77% of C_{max} in 2003. Consumption rates for all cohorts increased during July–August, ranging from 83–89% of C_{max} in 2001, 102–106% of C_{max} in 2002, and 78–85% of C_{max} in 2003. Compared to the July–August period, consumption rates during August–September 2001 remained constant for hatchery juveniles, decreased by 1% for wild juveniles, and increased 9% for hatchery survivors. Consumption rates during August–September 2003 increased 9% for hatchery survivors migrating from Prince William Sound to the ACC, and increased 13% for hatchery survivors in the transition zone (Table 4.8). Growth efficiency varied with changes in consumption rate, as would be expected for diets that offered minimal difference in composite energy density (Figure 4.1).

Juvenile hatchery, juvenile wild, and surviving hatchery pink salmon consumed more than 100% of their theoretical maximum consumption during July–August in 2002, the high-survival year, while feeding predominantly on *Limacina* (Figure 4.1). All cohorts were 40–72% larger in July and 55–143% larger in August during 2002 than during 2001 and 2003, low-survival years (Table 4.8). During 2002, all cohorts also consumed a larger percentage of their theoretical maximum consumption and more prey in total while feeding on large copepods during May–July and *Limacina* during July–August than during 2001 and 2003, when pink salmon diversified their diet and also consumed a large amount of *Limacina* during May–July and amphipods and larvaceans during July–August (Table 4.8, Figure 4.1). Juvenile pink salmon consumed an average of 20.5–25.6 g more large copepods and 47.1–66.1 g more *Limacina* during marine entry–August 2002 than during marine entry–August 2001 and 2003 (Table 4.8, Figure 4.1).

All cohorts were 4-16% larger by the sampling date in July 2003 than in July 2001, but 31-50% larger in August 2001 than in August 2003 (Table 4.8). The average consumption rate during May–July was 12–13% higher for hatchery juveniles at-large and hatchery survivors in 2001 than in 2003, but wild juveniles consumed a larger percentage of C_{max} during April–July in 2003 than in 2001 (77% versus 66%; Table 4.8). All cohorts consumed at a 1–6% higher rate during July–August 2001 than July–August 2003.

During July–August 2003, cohorts that remained in Prince William Sound consumed more than cohorts that migrated to the transition zone (Table 4.8; Figure 4.1). During August–September 2003, however, the surviving hatchery cohort that remained in the transition zone consumed more than cohorts that migrated from Prince William Sound to the ACC (Table 4.8; Figure 4.1).

Wild juvenile pink salmon and hatchery survivors were larger and consumed more prey in total than the average hatchery juvenile by the July sampling date during all years (Table 4.8). The largest discrepancy in size between the average and surviving hatchery pink salmon in August occurred in 2002, the high survival year, when adult survivors were 5.2 g larger than the average hatchery juvenile. Hatchery survivors were 4.8 g larger than the average hatchery juvenile by August 2001, 17.8 g larger than hatchery juveniles by September 2001, and 3.0 g larger than hatchery juveniles by August 2003 (Table 4.8). Hatchery survivors consumed 12% more prey during May – August 2002 than did the average hatchery juvenile, but consumed 22% more prey in 2001 and 20% more in 2003 than hatchery juveniles. Hatchery pink salmon that survived to adult return consumed a greater proportion of C_{max} than did both the average hatchery and wild juvenile pink salmon during marine entry–September 2001 and marine entry–July 2002 (Table 4.8). However, wild juveniles consumed a greater proportion of C_{max} than did hatchery juveniles at-large and hatchery survivors during July–August 2002 and marine entry–August 2003. Though cumulative individual consumption was greater for wild juveniles than for hatchery survivors during marine entry–July 2001, wild fish and hatchery survivors were approximately the same size on the July sampling date (Table 4.8). However, hatchery survivors consumed more prey and were 10.7 g larger than wild fish by September 2001 (Table 4.8). Surviving hatchery juveniles consumed more prey and were slightly larger than wild fish during July and August 2002, and wild fish consumed more prey and were larger than hatchery survivors in July and August 2003.

Responses to Different Growth Scenarios

Simulations modeling juvenile pink salmon growing from the largest size at release in May to the smallest observed size in August, and the smallest size at release in May to the largest observed size in August, showed that total consumption during 2001 ranged from 43.4–177.0 g, compared to the average nominal estimate of 94.8 g. During 2002, total consumption ranged from 97.3–249.0 g, compared to the average nominal estimate of 154.1 g. For pink salmon remaining in Prince William Sound during May–August 2003, total individual consumption ranged from 41.0–116.0 g, compared to the average nominal estimate of 64.4 g. For pink salmon migrating to the transition zone by August 2003, total individual consumption ranged from 40.7–115.1 g, compared to the nominal estimate of 63.9 g.

Fine-scale growth and consumption

Over the last full circulus increment, the average juvenile pink salmon captured in July and August consumed 1.7-2.4 $g \cdot d^{-1}$ more in 2002 than in 2001 and 2003 (Figure 4.2). Pink salmon consumed a greater percentage of C_{max} during July 2002 (94%) than during July 2001 and 2003 (73% and 77%, respectively), and a greater percentage of C_{max} during August 2002 (110%) than during August 2001 (84–95% in PWS, ACC, and Trans) and 2003 (75–77% in PWS and Trans). During all months, growth was more efficient in the ACC than in PWS, and more efficient in Trans than in the ACC.

Comparison of localized population-level consumption to prey biomass

During 2003, the average apparent density of juvenile pink salmon was largest in Prince William Sound in July (6338.7 $fish \cdot km^{-2}$) and smallest in the transition zone in August (950.2 $fish \cdot km^{-2}$; Figure 4.3). Peak density of pink salmon in Prince William Sound was nearly 6 times greater in July than in August (1111.1 $fish \cdot km^{-2}$).

Modeling growth between the final two complete circuli provided a snapshot of the daily consumption and growth performance of hatchery and wild juvenile pink salmon associated with the actual time and water mass of capture. Although individual consumption increased as juvenile pink salmon grew through time, daily population-level consumption of key prey (large copepods, amphipods, *Limacina*, and larvaceans) in Prince William Sound declined from July (7430.6 g·km^{-2}) to August (996.2 fish·km^{-2}) due to mortality and emigration from the area (Figure 4.3). Total demand by the population was slightly higher in the transition zone (1149.2 g·km^{-2}·d^{-1}) than in Prince William Sound in August.

A 15-30 fold discrepancy in estimates of exploitable prey biomass existed between zooplankton samples from the bongo nets, which integrated prey densities over the upper 10 m of the water column, versus the Tucker trawl, which collected zooplankton only from the surface meter. In Prince William Sound during July 2003, the local biomass of key prey was estimated at 487,090.1 g·km^{-2} from zooplankton samples collected with the vertical Bongo net with 333 μm mesh, but only 16,939.3 g·km^{-2} from samples collected with the horizontal Tucker trawl with 333 μm mesh (Figure 4.3). During August 2003, the biomass of key prey in Prince William Sound was 35,454.8 g·km^{-2} from the vertical Bongo net and 1190.5 g·km^{-2} from Tucker trawl samples, whereas in the transition zone, the biomass of key prey was 295,012.5 g·km^{-2} from the Bongo net and 17,120.8 g·km^{-2} from Tucker trawl samples.

The Bongo net collected an average of 11–40 times more large copepods than the Tucker trawl, 31.5 times more amphipods, 12-13 times more *Limacina*, and 5–1010 times more larvaceans (Figure 4.4). Neither gear type captured amphipods in Prince William Sound or the transition zone during August, and no *Limacina* were collected with the Tucker net in Prince William Sound in July. Where biomass estimates were available, the standing stock of key prey exceeded the daily consumption demand by pink salmon with two exceptions: estimates of consumption exceeded prey biomass when zooplankton were sampled with the Tucker trawl in both Prince William Sound and the transition zone during August 2003 (Figure 4.4). When zooplankton biomass was estimated using the Bongo net, juvenile pink salmon consumed 1.5% of the total standing stock per day in Prince William Sound in July, 2.8% per day in Prince William Sound in August, and 0.4% per day in the transition zone in August (Figure 4.3). When zooplankton biomass was estimated using the Tucker trawl, juvenile pink salmon consumed 43.9% of the standing stock per day in Prince William Sound in July, 83.7% per day in Prince William Sound in August, and 6.7% per day in the transition zone in August (Figure 4.3).

DISCUSSION

In all model simulations, juvenile pink salmon consumed a large proportion of their theoretical maximum consumption. Feeding at or near C_{max} can sometimes reflect the need to eat a higher ration of lower quality prey. Zooplankton prey such as large copepods, hyperiid amphipods, pteropods, and larvaceans, which composed the majority of the diet, have energy densities of less than approximately 3000 $J \cdot g^{-1}$ and provide a relatively poor energetic return. Low growth efficiencies reflect that juvenile pink salmon (with a body energy density of approximately 4000 $J \cdot g^{-1}$) must ingest large quantities of these low-quality prey types to obtain the energy needed for rapid growth. Also, gelatinous zooplankton are digested much more quickly than crustaceans (Arai et al. 2003), and juvenile pink salmon feeding on fast-digesting pteropods and larvaceans compensate by consuming at a high rate. The bioenergetics model for juvenile pink and sockeye salmon was developed using hatchery pellets, not natural prey; in reality, if the salmon consume prey that digest more quickly than hatchery pellets, the actual maximum daily consumption will be higher (D. Beauchamp, University of Washington, personal communication).

In early June, zooplankton density in Prince William Sound declined as blooms subsided and adult copepods migrated to winter depths (Cooney et al. 2001a). High consumption rates throughout the rest of the summer suggest that sufficient prey remained available to pink salmon that survived the first two months at sea. However, juveniles consumed a much larger proportion of their theoretical maximum consumption in 2002, the high-survival year, than during 2001 and 2003, low-survival years. This suggests that although the average juvenile pink salmon fed at high rates during all years, fish that consumed prey at a higher-than-average rate experienced higher survival.

Juvenile pink salmon fed at a relatively low proportion of their theoretical maximum consumption from May to mid-July during low-survival years. Juvenile pink salmon growth and survival can decline with decreasing zooplankton biomass (Perry et al. 1996). A decline in the availability or quality of food could require fish to expend more energy to find prey, thereby decreasing the net energy gained through consumption, decreasing growth efficiency, and potentially increasing vulnerability to predation, disease, and other environmental stressors. Although significant mortality occurs in pink salmon fry populations within days after entry into Prince William Sound, the population remains large until migration begins during summer. Prey availability in Prince William Sound may have limited individual growth when large populations of juvenile pink salmon occurred early in the growing season.

The increased abundance of juveniles from hatchery production has elicited concerns that we are reaching or exceeding the carrying capacity for juvenile pink salmon; juvenile pink salmon are potentially food-limited at one or more stages in their life cycle and in one or more regions. Wertheimer et al. (2004a, 2004b) contend that although density-independent ocean conditions primarily drive pink salmon spawner abundance and productivity (2004a), large-scale enhancement in Prince William Sound has contributed to reduced body size due to density dependent growth in the Gulf of Alaska (2004b). Farley and Carlson (2000) suggest that coastal waters of the Gulf of Alaska could be food limiting, and expressed concerns about density dependent growth when juvenile pink salmon first emigrate from Prince William Sound. The relatively high percentage of prey biomass consumed, more diversified diets in low-survival years, low feeding rates during May–July, the mid-summer decrease in growth efficiency, and the fact that growth and consumption rates are much higher for all cohorts in high-survival years and for surviving cohorts in all years indicate that juvenile pink salmon are food limited in Prince William Sound and the coastal Gulf of Alaska during their first summer at sea during some years.

Although standing stock biomass exceeded consumption demand on key prey by juvenile pink salmon during all months when estimated from Bongo net samples, the biomass of individual prey types was not always enough to sustain the high level of consumption that a localized population of pink salmon required to satisfy observed growth. Estimates of prey biomass presented in this study do not account for zooplankton production or advection and thus do not represent the actual flux of prey available per day; I simply presented a "snapshot" view of prey biomass and demand. Zooplankton production and advection affect the supply of prey available to juvenile pink salmon, as does prey patchiness, which we were unable to detect at the spatial scale of our zooplankton samples.

Production to biomass ratios (P/B) refer to the rate at which the biomass of a population is replaced by fresh production (Paloheimo and Dickie 1970; Tranter 1976). Knowing the daily weight-specific rate of production for local zooplankton allows us to estimate total production directly from an estimate of zooplankton biomass. Literature estimates of P/B vary widely for zooplankton (Cooney 1999), and very little is known about the production rates of pteropods, larvaceans, and hyperiid amphipods in subarctic regions. A recent study suggests that conservative monthly estimates of P/B ratios in Prince William Sound during July–September are: 1.2–1.5 for copepods; 0.2–0.3 for pteropods; 0.2–0.4 for amphipods; and 0.3 for larvaceans (Cooney 1999). These rates correspond to daily P/B ratios of 0.01–0.05 during July–September. Applying these rates to biomass estimates, the production of large copepods, amphipods, and pteropods appears to be capable of sustaining or exceeding the consumption demand by juvenile pink salmon and preventing a reduction in prey biomass or feeding rate during July and August. Most observed feeding rates for juvenile pink salmon therefore appear sustainable in terms of not depleting prey supply. However, daily consumption rates of juvenile pink salmon on larvaceans were greater than daily production rates during July and August 2003 in Prince William Sound; for some prey in some months, production alone could not sustain the consumption demand. Larvaceans would need P/B ratios of 0.04 in July and 0.09 in August to sustain feeding rates. Even in cases where prey production was enough to sustain feeding rates, production might not necessarily have allowed sufficient growth for juvenile pink salmon to avoid size-selective mortality.

In addition to accounting for zooplankton production, we must address the physical dynamics of this system. Advection in the deep Gulf of Alaska "feeds" inshore waters and influences the zooplankton stock in Prince William Sound (Kline, 1999; Eslinger et al., 2001). Coastal Gulf of Alaska waters generally flow into Prince William Sound through Hinchinbrook Entrance and back out through Montague Strait (Niebauer et al. 1994). Upper-layer inflow may also occur at Montague Strait in response to westward winds over the continental shelf (Vaughan et al. 2001). Zooplankton originating in the coastal Gulf of Alaska can therefore enter Prince William Sound at either entrance, causing a continuous exchange of zooplankton between regions. Approximately 40% of the volume of Prince William Sound is flushed into the northern Gulf of Alaska during May–September (Niebauer et al. 1994), but the impact of advection on the supply of key prey in both regions is unknown.

Although advection and production must replenish prey supply to some extent, high individual consumption rates together with the large abundance of juvenile pink salmon suggest that pink salmon have a considerable impact on the forage base in Prince William Sound and the coastal Gulf of Alaska. Juvenile pink salmon can potentially deplete the prey base under certain conditions, consequently influencing growth and survival. Trends observed in the occurrence of pteropods in the diet indicate that this prey type might play an important role for pink salmon and that its availability can fluctuate from year to year. A diet focused on large copepods during May–July and *Limacina* during July–August 2002 was associated with higher growth and survival rates, while growth was more limited during 2001 and 2003, when diets were more varied. *Limacina* were presumably not readily available to juvenile pink salmon during low-survival years, while the biomass of pteropods in the coastal Gulf of Alaska might have been higher in 2002. A recent study indicates that an increase in atmospheric carbon dioxide will within decades reduce ocean pH and the concentration of carbonate ions, leading to shell dissolution for high-latitude pteropods and a drastic change in both latitudinal and vertical distribution, if not complete disappearance (Orr et al. 2005). If *Limacina* are indeed vital to the growth and survival of pink salmon, the imminent and irreversible change in ocean chemistry and resulting decline in pteropod abundance could severely limit the health of the pink salmon population.

Growth efficiency was similar for the average hatchery juvenile and hatchery survivor during all years and did not reflect observed trends in growth and survival. An increase in habitat temperature increases metabolic costs and decreases the efficiency of converting energy consumed into growth. The observed decrease in growth efficiency from marine entry–July/August and subsequent increase from July/August–September, as well as the more efficient growth of fish that remained in Prince William Sound during July–August 2003 compared to fish that migrated to the transition zone, reflect habitat temperature seasonality in Prince William Sound and the coastal Gulf of Alaska (Tables 4.1–4.3). However, the direct effects of temperature on the growth of juvenile pink salmon are relatively minor over a broad range of temperatures. The difference in temperature among months is not large enough to have such a considerable effect on growth.

Over the range of temperatures observed during 2001–2003, different thermal regimes may have affected the growth performance of pink salmon more through indirect effects on prey availability and species composition than through direct metabolic responses to temperature. Cross et al. (2005) found that juvenile pink salmon growth, consumption, and growth efficiency were affected more by diet composition than by thermal experience. Prey consumed by pink salmon in Prince William Sound had a slightly higher average energetic return than prey consumed by pink salmon migrating to the transition zone, supporting more efficient growth. Under conditions of limited food availability, pink salmon might have expended more time and energy to find prey, consequently increasing foraging costs, decreasing the net energy gained through consumption, and decreasing growth efficiency. Variable periods of low and high consumption rates can also affect growth efficiency (Skalski et al. 2005). Conclusions from this analysis concerning growth efficiency assume that foraging costs do not vary among prey types.

Consumption estimates from this study are much higher than those produced by previous studies. Boldt and Haldorson (2002) concluded that in 1998, juvenile pink salmon residing in Prince William Sound for 93 d after marine entry reached a final wet weight of only 9.6 g, and consumed 27.9 g of prey to achieve this amount of growth (approximately 33% growth efficiency, assuming 0.26 g at entry). In this study, hatchery and wild juveniles and hatchery survivors averaged a much higher weight of 12.9–42.6 g after day 93 of the model simulation and consumed more prey (41.8–158.1 g at an average growth efficiency of approximately 28–29%). Total consumption during 2001–2003 was also much higher than predicted by Cooney (1993), who estimated that juvenile pink salmon consume 36.4 g of prey after 120 d in Prince William Sound and reach a final weight of 9.1 g (at 25% growth efficiency). Using the results of this analysis, estimates of the amount of annual secondary production consumed by juvenile pink salmon during a 93-d residence time in Prince William Sound would be much higher than the 0.06–0.45% estimate previously produced (Boldt and Haldorson 2002).

The disparity in average fish size three months after marine entry in the earlier study by Boldt and Haldorson (2002) and this study is striking. Boldt and Haldorson sampled during 1998, a warm El Niño year. The 2001–2003 cohorts of juvenile pink salmon were approximately 3.3–33.0 g (34–344%) larger after 93 d at sea than those observed in 1998. Differences in growth and consumption are likely due to interannual variation in climate and its effect on ocean conditions and the productivity of fish and zooplankton. Nutrient levels and advection between the Gulf of Alaska shelf and Prince William Sound cause zooplankton biomass to vary on spatial and temporal scales (Kline 1999; Eslinger et al. 2001; Coyle and Pinchuk 2003). Because juvenile pink salmon diet composition differs depending on the structure of the zooplankton community each year (Willette 2001), the composition of the forage base can potentially affect juvenile salmon growth. Climate variability must be accounted for when comparing consumption estimates from different years. Interannual differences in climate likely affect fish size, energy content, and diet, which consequently affect consumption estimates from model simulations.

Applying site- and year-specific input data to the model generated higher-resolution and more accurate estimates of juvenile pink salmon consumption than obtained by previous studies. Running the bioenergetics model at monthly intervals for each cohort increased the accuracy of our results by more precisely tracking growth rates that coincided with specific diet patterns and thermal experiences. In addition to relying on literature estimates for supply-demand comparisons, neither Boldt and Haldorson (2002) nor Cooney (1993) considered the specific taxa consumed by juvenile pink salmon. Previous studies comparing consumption by juvenile pink salmon to total prey biomass probably largely underestimated the impact of this species on the prey base, as juvenile salmon selectively consume specific prey (Schabetsberger et al. 2003) and therefore only consume a fraction of the total zooplankton biomass in an area.

Zooplankton samples collected using the Tucker surface trawl have recently been found unrepresentative of localized regions. Vertical Bongo tows conducted in 2002 and 2003 indicated that although zooplankton were concentrated in the top 10 m, density increased dramatically at depths below 1 m (L. Haldorson, unpublished data). The vertical 0–10 m bongo samples collected many taxa, including pteropods and large copepods, which are prominent in the diet of pink salmon, in densities 4–100 times higher than densities that the Tucker surface trawl collected concurrently. Surface tows therefore severely underestimated prey biomass.

Assuming 100% capture efficiency caused us to underestimate population-level consumption; our surface trawls conceivably captured much less than 100% of juvenile pink salmon encountered. This study also does not account for consumption by other potential competitors and nighttime planktivores, such as juvenile sockeye and chum salmon (*O. keta*), juvenile walleye pollock, and other species. Thus, the demand on the prey forage base must be significantly higher than presented in this analysis, based on pink salmon alone.

Several additional unanswered questions must be confronted before we can conclusively determine if ecological bottlenecks in salmon growth exist in Prince William Sound and the coastal Gulf of Alaska. Further studies regarding the effects of the density and size of specific prey types on encounter and consumption rates by juvenile pink salmon are necessary to create a more predictive framework for evaluating the effects of prey availability and limitation (Moss *in prep*). Complete assessment also requires understanding the fine-scale spatial and temporal overlap between juvenile pink salmon and their prey. Specifically, we need to determine the daytime distribution of exploitable sizes of key prey species and the spatial scale of prey patchiness. Also, this study estimated juvenile pink salmon and prey densities at a relatively crude spatial scale when compared to the search volume of a foraging juvenile salmon. It is unclear how representative these data are of other regions in Prince William Sound and coastal Gulf of Alaska and thus the extent to which these results can be extrapolated.

The Fraser-Lee method has performed well in many studies. Using scales, Klumb et al. (2001) observed that Fraser-Lee-based back-calculations underestimated actual length by a mean of only 1.8%. Horppila and Nyberg (1999) found that although the Fraser-Lee method overestimated lengths at young ages and underestimated lengths at older ages, the discrepancy was less than 5%. A major assumption of the Fraser-Lee method is that the relationship between hard part radius and fish growth is perfectly linear and does vary systematically with the growth rate of the fish. However, the growth of a fish may be higher than scale growth during earlier years, while the growth of scales may be higher as the fish gets older (Lee 1920). Individual fish do not likely maintain a constant growth rate through time (Campana 1990), and a bias in back-calculated body size may be due to variability in the hard part-body size relationship (Campana 1990; Ricker 1992). Because the ratio between parts is still nearly constant, however, this should cause only a negligible difference in the final length calculation. Minor errors in scale/otolith measurements may not change length estimates by much (Klumb et al. 2001), or may cause consistent underestimates of past growth (Campana 1990).

A bias in the intercept parameter a, sampling error, or environmental factors could affect back-calculated lengths of fish (DeVries and Frie 1996). An a value that deviates from reality leads to inaccurate back-calculated fish lengths, and can vary widely due to problems with collection, sampling, and measurement of the cohort. Looking at scales from the preferred region and eliminating outliers help to eliminate any such bias. Still, forcing a line for each individual fish through a common y-intercept constricts natural variability (Klumb et al. 2001). It is difficult to distinguish variability in the true length-scale relationship from variability introduced by sampling or measurement errors (Francis 1990; Ricker 1992).

The assumption that fish with no thermal markings were of wild origin could have biased our hatchery-wild comparisons. Without genetic analyses of fish origin, we are unable to evaluate the bias in our growth and consumption estimates due to the immigration of unmarked fish originating outside of Prince William Sound into the study area. However, the mixing of Prince William Sound fish with Southeast Alaska stocks was minimal throughout most of the growing season (Farley and Munk 1997; Farley and Carlson 2000). Even if some mixing occurred late in the growing season, survival rates of stocks from both regions were probably influenced by shared environmental effects (Pyper et al. 2001; Mueter et al. 2002; Pyper et al. 2005). The impact of any such mixing on this analysis was therefore most likely insignificant.

Although comparing population-level consumption to prey production rather than standing stock biomass would be ideal, this study makes a first attempt at comparing pink salmon consumption demand to the biomass of preferred prey in Prince William Sound and the coastal Gulf of Alaska. Studies focusing on the production rates of several key zooplankton species, the effect that other planktivores have on prey biomass, and the fine-scale spatial structure of the food base are needed to truly determine whether pink salmon are resource-limited (and, if so, when and where limitation occurs). Developing mechanistic links between climate, biophysical oceanography, and fisheries recruitment is important for developing more effective and economical harvest and management strategies and predicting the response of pink salmon to climate change. This study demonstrates an initial approach for quantifying the relative effects of prey supply, prey quality, and temperature on the growth and consumption of juvenile salmon, and consequences for subsequent ocean survival.

Conclusions

Bioenergetics models were used to compare spatial and temporal variation in the consumption demand and growth efficiency of the average hatchery juvenile pink salmon, hatchery fish that survived to adult return, and wild juveniles in Prince William Sound and the coastal Gulf of Alaska between May and September 2001–2003. Juvenile pink salmon consumed at 66–106% of their theoretical maximum consumption rate in order to achieve observed growth. All cohorts were larger, ate a larger proportion of their theoretical maximum consumption, and consumed more prey both in total and per day during 2002, a high-survival year, than during 2001 and 2003, low-survival years, while feeding predominantly on *Limacina*. Wild juvenile pink salmon and hatchery fish that survived to adulthood were larger than the average hatchery juvenile and consumed more prey in total throughout the model simulation period. The standing stock biomass of key prey (large copepods, amphipods, the pteropod *Limacina*, and larvaceans) exceeded the daily consumption demand of the juvenile pink salmon population during all months; however, the estimated prey biomass was not enough to sustain the high level of consumption required to satisfy observed growth over more prolonged feeding periods for some prey in some cases. The relatively high percentage of prey biomass consumed, more diversified diets in low-survival years, low feeding rates during May–July, the mid-summer decrease in growth efficiency, and the fact that growth and consumption rates are much higher for all cohorts in high-survival years and for surviving cohorts in low-survival years indicate that juvenile pink salmon are food limited in Prince William Sound and the coastal Gulf of Alaska during their first summer at sea during some years.

Appropriate environmental and resource management decisions affecting salmonid stocks require an immediate, more detailed understanding of the connections between salmon production and their ocean environment. This analysis should provide the basis for interannual and spatial comparisons of growth performance by pink salmon in response to different environmental and ecological conditions.

Table 4.1. Bioenergetics model inputs for the average hatchery and wild juvenile pink salmon during 2001 and the hatchery cohort that survived to adulthood. Pink salmon dispersed from Prince William Sound (PWS) across all water masses by August and migrated to the transition zone (Trans) by September. Model inputs refer to the body mass, thermal experience, and energy density of consumers. The number of fish from each cohort that were used to back-calculate body weight on each sampling date is also given. Minimum and maximum weights refer to the values used to calculate minimum and maximum consumption. All inputs were derived from sampling conducted during 2001 except for the estimate of consumer energy density in May, which was obtained from Boldt and Haldorson 2002.

Cohort	Simulation Date	Model Day	Water Mass	Back-calculated Wet Weight (g)				Thermal Exp. (°C)	Energy Density (J/g wet wt.)
				Avg.	Min.	Max.	n		
Hatchery Juvenile	18-May	1	PWS	0.53	0.71	0.32		8.0	4102.3
	11-Jul	55	PWS	8.4	4.6	23.7	133	12.0	3665.0
	15-Aug	90	All	23.4	15.1	40.9	68	14.1	4134.4
	19-Sep	125	Trans	51.1			12	11.7	4247.7
Wild Juvenile	17-Apr	1	PWS	0.26	0.26	0.26		5.0	4102.3
	11-Jul	86	PWS	9.7	4.6	17.4	172	12.0	3665.0
	15-Aug	121	All	27.0	11.3	48.8	146	14.1	4134.4
	19-Sep	156	Trans	58.2			45	11.7	4247.7
Hatchery Adult	18-May	1	PWS	0.53	0.71	0.32		8.0	4102.3
	11-Jul	55	PWS	9.7	6.1	13.2	94	12.0	3665.0
	15-Aug	90	All	28.2	18.4	46.4	94	14.1	4134.4
	19-Sep	125	Trans	68.9			94	11.7	4247.7

Table 4.2. Bioenergetics model inputs for the average hatchery and wild juvenile pink salmon during 2002 and the hatchery cohort that survived to adulthood. Pink salmon migrated from Prince William Sound (PWS) to the transition zone (Trans) by August. Model inputs refer to the body mass, thermal experience, and energy density of consumers. The number of fish from each cohort that were used to back-calculate body weight on each sampling date is also given. Minimum and maximum weights refer to the values used to calculate minimum and maximum consumption. All inputs were derived from sampling conducted during 2002 except for the estimate of consumer energy density in May, which was obtained from Boldt and Haldorson 2002.

Cohort	Simulation Date	Model Day	Water Mass	Back-calculated Wet Weight (g)				Thermal Exp. (°C)	Energy Density (J/g wet wt.)
				Avg.	Min.	Max.	n		
Hatchery Juvenile	21-May	1	PWS	0.56	0.69	0.39		8.0	4102.3
	21-Jul	62	PWS	14.3	6.1	18.9	41	12.8	4084.6
	22-Aug	94	Trans	38.5	26.8	55.1	16	12.6	4346.9
Wild Juvenile	28-Apr	1	PWS	0.26	0.26	0.26		5.0	4102.3
	22-Jul	86	PWS	15.9	6.9	25.6	27	12.8	4084.6
	22-Aug	117	Trans	42.1	27.0	66.2	16	12.6	4346.9
Hatchery Adult	21-May	1	PWS	0.56	0.69	0.39		8.0	4102.3
	21-Jul	62	PWS	16.7	9.1	21.1	87	12.8	4084.6
	22-Aug	94	Trans	43.7	31.4	62.7	87	12.6	4346.9

Table 4.3. Bioenergetics model inputs for the average hatchery and wild juvenile pink salmon during 2003 and the hatchery cohort that survived to adulthood. Pink salmon either remained in Prince William Sound (PWS) through August and migrated to the Alaska Coastal Current (ACC) by September, or migrated from PWS to the transition zone (Trans) by August. Model inputs refer to the body mass, thermal experience, and energy density of consumers. The number of fish from each cohort that were used to back-calculate body weight on each sampling date is also given. Minimum and maximum weights refer to the values used to calculate minimum and maximum consumption. All inputs were derived from sampling conducted during 2003 except for the estimate of consumer energy density in May, which was obtained from Boldt and Haldorson 2002, and consumer energy density in September, which was obtained from September 2001. Because no estimates of consumer energy density were available for PWS or Trans during August, models used the average value for fish caught in the ACC and front during 2003.

Cohort	Simulation Date	Model Day	Water Mass	Back-Calculated Wet Weight (g)				Thermal Exp. (°C)	Energy Density (J/g wet wt.)
				Avg.	Min.	Max.	n		
Hatchery Juvenile	12-May	1	PWS	0.70	1.09	0.41		7.0	4102.3
	16-Jul	66	PWS	8.8	5.3	12.3	39	14.0	3736.8
	4-Aug	85	PWS	15.9	12.2	26.8	29	14.2	3899.5
	4-Aug	85	Trans	15.9			29	13.8	3899.5
Wild Juvenile	30-Apr	1	PWS	0.26	0.26	0.26		5.0	4102.3
	16-Jul	78	PWS	11.3	6.0	17.8	70	14.0	3736.8
	4-Aug	97	PWS	20.7	14.1	33.6	63	14.2	3899.5
	4-Aug	97	Trans	20.7			63	13.8	3899.5
Hatchery Adult	12-May	1	PWS	0.70	1.09	0.41		7.0	4102.3
	16-Jul	66	PWS	10.2	6.5	14.4	81	14.0	3736.8
	4-Aug	85	PWS	18.9	12.0	27.4	81	14.2	3899.5
	4-Aug	85	Trans	18.9	12.0	27.4	81	13.8	3899.5
	15-Sep	127	ACC	59.4			81	12.7	4240.3
	10-Sep	122	Trans	59.4			81	12.6	4240.3

Table 4.4. The proportional contribution of prey types (by volume) to the diet of juvenile pink salmon during marine entry–September 2001–2003. July–September diet proportions were generated from sampling conducted during each year, while April/May diet proportions were obtained from Parker 1997. Diet contributions greater than 0.200 in any month and region are shown in bold.

Year	Month	Water Mass	Small Copepods	Large Copepods	Euphausiids	Amphipods	Crab Larvae	Shrimp Larvae	Limacina	Larvaceans	Insects	Fish	Other
2001	April/May	PWS	0.000	**0.742**	0.047	0.000	0.019	0.000	0.043	0.000	0.024	0.038	0.087
	July	PWS	0.022	0.028	0.014	0.192	0.033	0.021	**0.418**	0.196	0.012	0.006	0.057
	August	Avg	0.024	**0.260**	0.093	**0.330**	0.063	0.013	0.080	0.007	0.044	0.025	0.061
	September	Trans	0.001	**0.267**	0.073	0.147	0.020	0.005	0.174	0.113	0.049	0.108	0.043
2002	April/May	PWS	0.000	**0.742**	0.047	0.000	0.019	0.000	0.043	0.000	0.024	0.038	0.087
	July	PWS	0.002	**0.335**	0.016	0.120	0.029	0.005	**0.420**	0.020	0.000	0.020	0.034
	August	Trans	0.001	0.005	0.036	0.096	0.011	0.005	**0.685**	0.000	0.000	0.151	0.011
2003	April/May	PWS	0.000	**0.742**	0.047	0.000	0.019	0.000	0.043	0.000	0.024	0.038	0.087
	July	PWS	0.006	0.112	0.011	**0.339**	0.031	0.006	**0.281**	0.158	0.000	0.038	0.017
	August	PWS	0.001	**0.247**	0.089	0.053	0.193	0.014	0.002	**0.302**	0.005	0.047	0.047
	August	Trans	0.039	**0.311**	0.013	0.015	0.065	0.009	**0.238**	0.020	0.006	**0.263**	0.020
	September	ACC	0.015	**0.200**	0.098	0.100	0.108	0.018	0.002	**0.298**	0.008	0.107	0.046
	September	Trans	0.001	**0.415**	0.051	0.069	0.008	0.004	0.072	0.008	0.001	**0.225**	0.147

Table 4.5. The energy content and percent indigestible of prey types consumed by juvenile pink salmon during marine entry–September 2001–2003.

	Energy Density (J/g wet weight)				
Prey Type	April/May-July	August	September	Source	% Indigestible
Small Copepods	2624.6	2624.6	3040.0	Davis et al. 1998, M. Mazur pers. comm.	9.04
Large Copepods	2624.6	2624.6	3040.0	Davis et al. 1998, M. Mazur pers. comm.	9.04
Euphausiids	3110.2	3110.2	4259.0	Davis et al. 1998, M. Mazur pers. comm.	10.35
Amphipods	2465.6	2465.6	2787.0	Davis et al. 1998, M. Mazur pers. comm.	12.99
Crab Larvae	2980.4	2980.4	4458.0	Nishiyama 1977, M. Mazur pers. comm.	10.00
Shrimp Larvae	2980.4	2980.4	4458.0	Nishiyama 1977, M. Mazur pers. comm.	10.00
Limacina	2612.1	2612.1	2630.0	Davis et al. 1998, M. Mazur pers. comm.	8.50
Larvaceans	3177.2	3177.2	1434.0	Davis et al. 1998, M. Mazur pers. comm.	10.00
Insects	3117.5	3117.5	3117.5	Cummins and Wuycheck 1971	10.00
Fish	3760.0	3760.0	3760.0	M. Mazur pers. comm.	8.98
Other 2001	2655.2	2501.0	2995.2	Weighted avg. based on diet composition	10.00
Other 2002	2577.9	2752.4		Weighted avg. based on diet composition	10.00
Other 2003	2887.8	2826.4	2771.1	Weighted avg. based on diet composition	10.00

Table 4.6. Bioenergetics inputs of the average weight change, thermal experience, and energy density for fine-scale temporal-spatial modeling of hatchery and wild juvenile pink salmon during 2001–2003. Growth was modeled over the last full circulus increment in Prince William Sound (PWS), the Alaska Coastal Current (ACC), and the mid-shelf transition zone (Trans).

Year	Month	Water Mass	Initial Weight (g)	Final Weight (g)	Thermal Exp. (°C)	Energy Density (J/g wet wt.)
2001	July	PWS	6.7	8.2	12.0	3665.0
	August	PWS	19.5	22.6	14.1	4134.4
	August	ACC	25.3	28.7	14.1	4134.4
	August	Trans	20.1	23.2	14.1	4134.4
	September	Trans	49.5	56.0	11.7	4247.7
2002	July	PWS	15.7	18.8	12.8	4084.6
	August	Trans	37.7	44.5	12.6	4346.9
2003	July	PWS	11.1	13.1	14.0	3736.8
	August	PWS	13.6	16.0	14.2	3899.5
	August	Trans	21.1	24.5	13.8	3899.5
	September	ACC	33.4	37.8	12.7	4240.3
	September	Trans	35.6	39.9	12.6	4240.3

Table 4.7. Diet inputs for fine-scale bioenergetics modeling of the average hatchery and wild juvenile pink salmon during 2001–2003. Growth was modeled over the last full circulus increment in Prince William Sound (PWS), the Alaska Coastal Current (ACC), and the mid-shelf transition zone (Trans). Inputs for prey energy density were the same as in Table 4.5.

Year	Month	Water Mass	Small Copepods	Large Copepods	Euphausiids	Amphipods	Crab Larvae	Shrimp Larvae	Limacina	Larvaceans	Insects	Fish	Other
2001	July	PWS	0.022	0.028	0.014	0.192	0.033	0.021	0.418	0.196	0.012	0.006	0.057
	August	PWS	0.000	0.015	0.044	0.789	0.027	0.005	0.001	0.001	0.031	0.034	0.054
	August	ACC	0.043	0.429	0.112	0.128	0.117	0.002	0.029	0.000	0.007	0.028	0.106
	August	Trans	0.034	0.375	0.130	0.011	0.053	0.031	0.215	0.019	0.091	0.012	0.028
	September	Trans	0.001	0.267	0.073	0.147	0.020	0.005	0.174	0.113	0.049	0.108	0.043
2002	July	PWS	0.002	0.335	0.016	0.120	0.029	0.005	0.420	0.020	0.000	0.020	0.034
	August	Trans	0.001	0.005	0.036	0.096	0.011	0.005	0.685	0.000	0.000	0.151	0.011
2003	July	PWS	0.006	0.112	0.011	0.339	0.031	0.006	0.281	0.158	0.000	0.038	0.017
	August	PWS	0.001	0.247	0.089	0.053	0.193	0.014	0.002	0.302	0.005	0.047	0.047
	August	Trans	0.039	0.311	0.013	0.015	0.065	0.009	0.238	0.020	0.006	0.263	0.020
	September	ACC	0.015	0.200	0.098	0.100	0.108	0.018	0.002	0.298	0.008	0.107	0.046
	September	Trans	0.001	0.415	0.051	0.069	0.008	0.004	0.072	0.008	0.001	0.225	0.147

Table 4.8. Estimates of mean daily and specific growth and consumption, total consumption, consumption as a proportion of the theoretical maximum consumption rate C_{max}, and growth efficiency for hatchery and wild juvenile pink salmon during 2001–2003 and the hatchery cohort that survived to adult return.

Year	Cohort	Simulation Period	Water Mass	Daily Growth (g d^{-1})	Specific Growth (g g^{-1} d^{-1})	Total Growth (g)	Daily Consumption (g d^{-1})	Specific Consumption (g g^{-1} d^{-1})	Total Consumption (g)	Proportion of C_{max}	Growth Efficiency
2001	Hatchery	May - July	PWS - PWS	0.14	0.052	7.9	0.46	0.163	25.2	0.79	31.6%
		July - Aug	PWS - All	0.42	0.029	15.0	1.64	0.110	59.1	0.83	26.0%
		Aug - Sept	All - Trans	0.77	0.022	27.7	3.04	0.088	109.4	0.83	25.1%
	Wild	Apr - July	PWS - PWS	0.11	0.043	9.5	0.36	0.135	31.1	0.66	31.5%
		July - Aug	PWS - All	0.48	0.029	17.3	1.89	0.110	67.9	0.86	26.0%
		Aug - Sept	All - Trans	0.87	0.022	31.2	3.43	0.087	123.5	0.85	25.0%
	Adult	May - July	PWS - PWS	0.17	0.054	9.2	0.53	0.170	29.2	0.84	31.8%
		July - Aug	PWS - All	0.51	0.030	18.5	2.00	0.113	71.9	0.89	26.3%
		Aug - Sept	All - Trans	1.13	0.025	40.7	4.30	0.097	154.8	0.98	26.1%
2002	Hatchery	May - July	PWS - PWS	0.22	0.054	13.7	0.78	0.180	48.4	0.95	29.5%
		July - Aug	PWS - Trans	0.73	0.030	24.2	2.85	0.118	94.1	1.02	25.8%
	Wild	Apr - July	PWS - PWS	0.18	0.049	15.6	0.65	0.161	55.7	0.85	30.0%
		July - Aug	PWS - Trans	0.82	0.031	26.2	3.18	0.120	101.7	1.06	25.8%
	Adult	May - July	PWS - PWS	0.26	0.056	16.2	0.92	0.188	56.8	1.02	29.6%
		July - Aug	PWS - Trans	0.82	0.030	27.0	3.20	0.115	105.6	1.03	25.6%
2003	Hatchery	May - July	PWS - PWS	0.12	0.039	8.1	0.44	0.132	29.0	0.67	29.2%
		July - Aug	PWS - PWS	0.35	0.030	7.1	1.33	0.112	26.5	0.78	26.7%
		July - Aug	PWS - Trans	0.35	0.030	7.1	1.30	0.111	26.1	0.77	27.1%
	Wild	Apr - July	PWS - PWS	0.14	0.050	11.0	0.48	0.158	37.8	0.77	30.9%
		July - Aug	PWS - PWS	0.47	0.031	9.4	1.73	0.113	34.6	0.85	27.1%
		July - Aug	PWS - Trans	0.47	0.031	9.4	1.70	0.112	34.0	0.84	27.5%
	Adult	May - July	PWS - PWS	0.14	0.041	9.5	0.51	0.138	33.5	0.72	29.6%
		July - Aug	PWS - PWS	0.44	0.031	8.7	1.60	0.115	31.9	0.84	27.2%
		July - Aug	PWS - Trans	0.44	0.031	8.7	1.57	0.114	31.4	0.83	27.6%
		Aug - Sept	PWS - ACC	0.94	0.027	40.5	3.49	0.099	150.0	0.93	27.2%
		Aug - Sept	Trans - Trans	1.07	0.031	40.5	3.56	0.102	135.4	0.96	29.9%

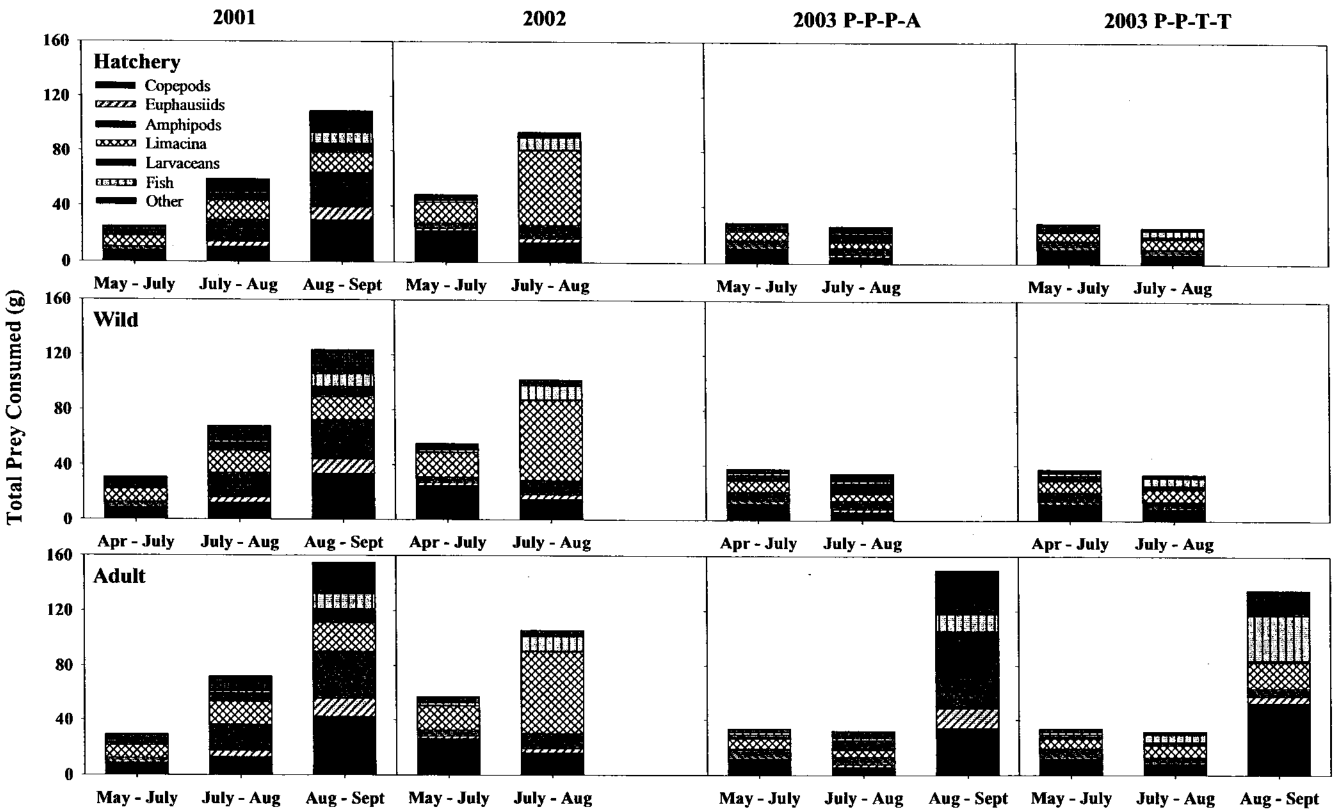

Figure 4.1. Total cumulative consumption of prey groups (g) during each bioenergetics model simulation period during May–September 2001–2003 by juvenile hatchery and wild pink salmon and hatchery pink salmon that survived to adulthood in Prince William Sound and the coastal Gulf of Alaska. During 2001, fish remained in Prince William Sound through July, distributed throughout all water masses in August, and migrated to the transition zone by September. During 2002, fish remained in Prince William Sound through July and migrated to the transition zone by August. During 2003, fish either remained in Prince William Sound throughout May–August and migrated to the Alaska Coastal Current by September, or remained in Prince William Sound through July, migrated to the transition zone by August, and remained in the transition zone through September.

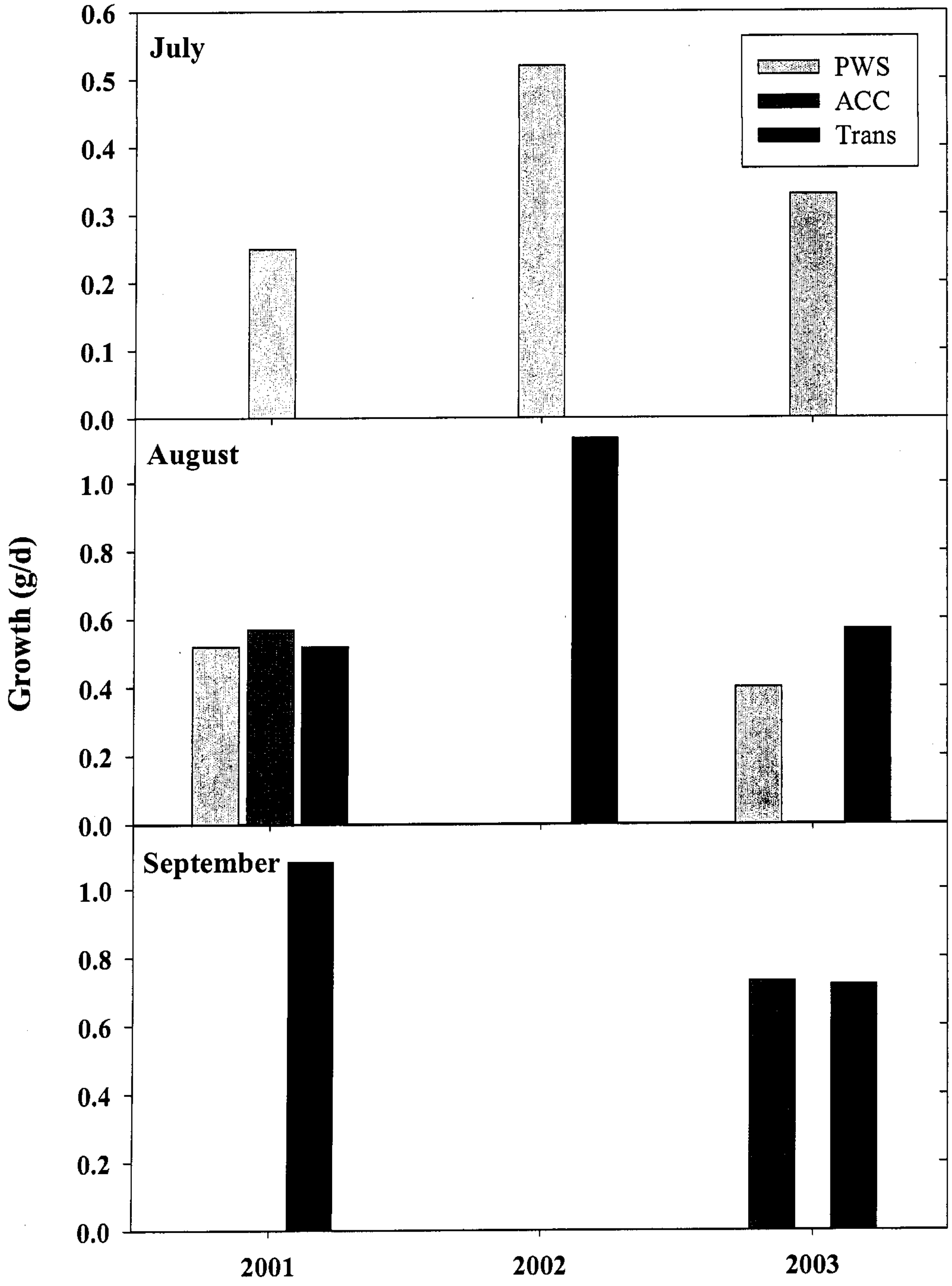

Figure 4.2. Daily growth (g·d^{-1}) of juvenile pink salmon just before capture during July–September 2001–2003.

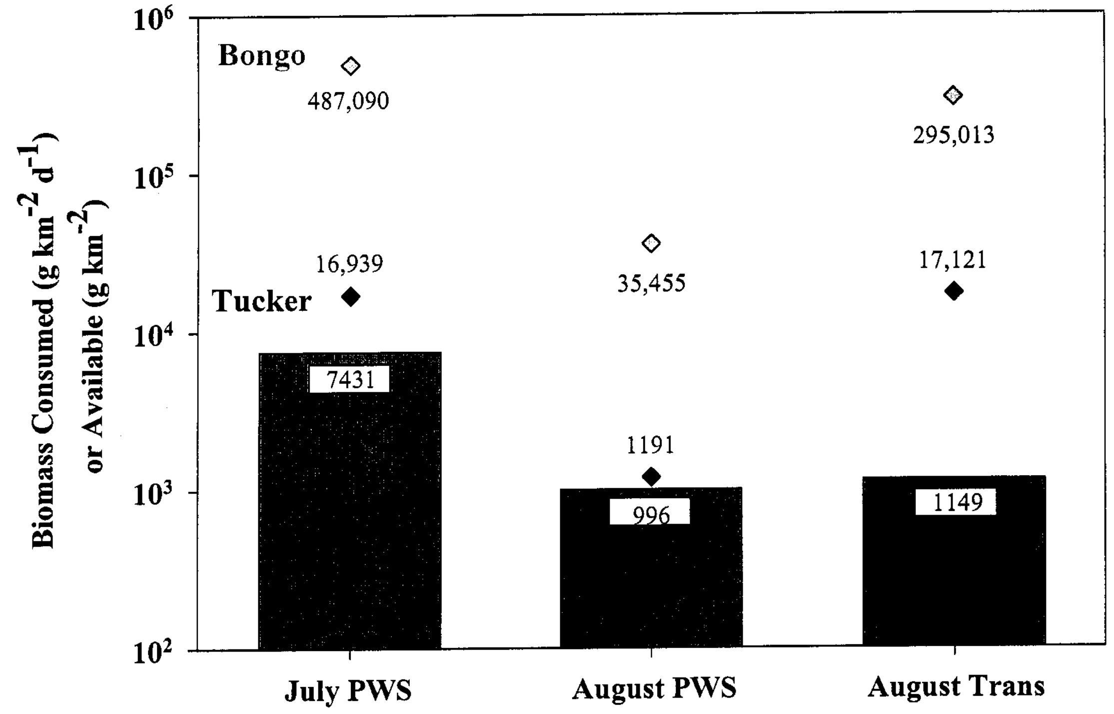

Figure 4.3. Daily consumption demand by juvenile pink salmon (bar) and the biomass of key prey (diamonds) during July 2003 in Prince William Sound (PWS), and August 2003 in PWS and the mid-shelf transition zone (Trans) of the coastal Gulf of Alaska. Key prey are large copepods, pteropods, hyperiid amphipods, and larvaceans. Zooplankton were collected with a horizontal Tucker trawl (black) and a vertical Bongo net (gray), both with 333 μm mesh. Note that the y-axis is on a log-scale.

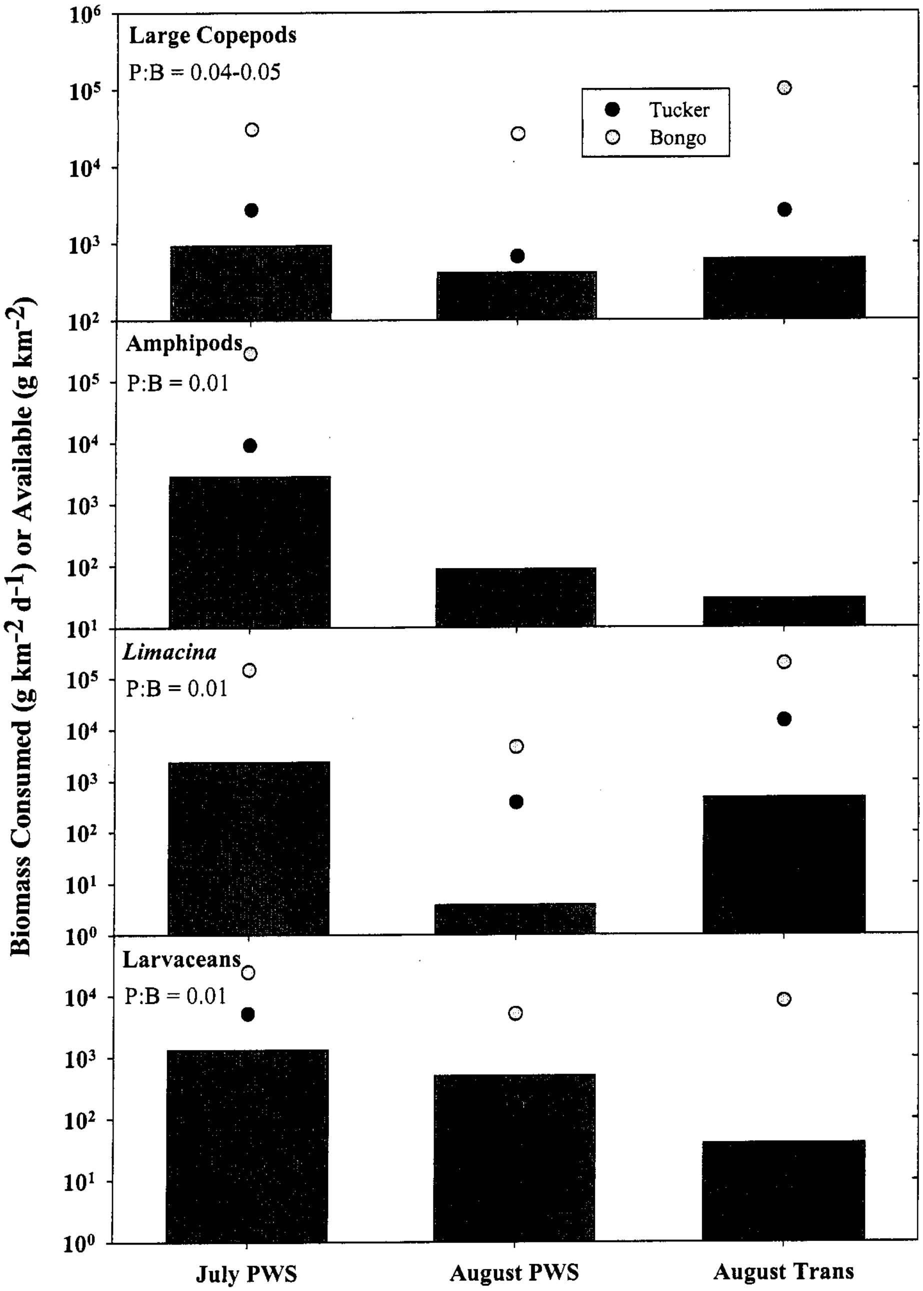

Figure 4.4. Daily consumption demand (bar) by juvenile pink salmon and standing stock biomass of individual key prey types (circles) during July 2003 in Prince William Sound (PWS), and August 2003 in PWS and the mid-shelf transition zone (Trans) of the coastal Gulf of Alaska. Production to biomass ratios (P:B), or the rate at which the biomass of a population is replaced by fresh production, are listed for each prey type. Zooplankton were collected with a horizontal Tucker trawl (black) and a vertical Bongo net (gray), both with 333 μm mesh. Note that the y-axis is on a log-scale.

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Chapter 5: Summary

This study used scale patterns and bioenergetics models to examine spatial and temporal patterns in the early marine growth and consumption demand of the average hatchery, average wild, and surviving hatchery pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound and the northern coastal Gulf of Alaska. Analyses focused on the first summer at sea, a critical period for growth and survival, during 2001 and 2003, years of low smolt-adult survival, and 2002 and 2004, years of high-survival. A better understanding of the relationship between early ocean growth and survival, demand on the prey forage base, and effects on prey supply provides insight on questions of carrying capacity and can ultimately lead to improved management of our ocean resources. In this chapter, I revisit my objectives, summarize the main findings, and present hypotheses regarding the early marine growth and survival of pink salmon in these regions.

Objective 1: Do the early marine growth and consumption demand of pink salmon differ between years of low and high survival? Between hatchery and wild pink salmon? Among Prince William Sound, the Alaska Coastal Current, and the transition zone? Between the population of juveniles at-large and juveniles that survive to adulthood?

Results

Low- vs. high-survival years

- Juvenile pink salmon were consistently larger throughout the summer and early fall of 2002 and 2004 than in 2001 and 2003 (Chapters 2 and 4).
- Both the average juvenile pink salmon and those that survived to adulthood grew faster during high-survival years than during low-survival years from mid-late June to mid-late August (Chapter 3).
- More differences in size at all circuli existed among adult hatchery cohorts during high-survival years than during low-survival years (Chapter 3).

- All cohorts ate a larger proportion of their theoretical maximum consumption and consumed more prey both in total and per day during 2002 than during 2001 and 2003 (Chapter 4).
- During 2002, all cohorts consumed primarily large copepods during May–July and the pteropod *Limacina helicina* during July–August, while pink salmon during 2001 and 2003 diversified their diet and also consumed a large amount of *Limacina* during May–July and amphipods and larvaceans during July–August (Chapter 4).
- Growth efficiency was similar for the average hatchery juvenile and hatchery survivor during all years and varied with changes in consumption rate, as would be expected for diets that offered minimal difference in composite energy density (Chapter 4).

Hatchery vs. wild cohorts

- Unmarked "wild" juvenile pink salmon were significantly larger than hatchery fish during low-survival years, but no significant difference was observed during high-survival years (Chapter 2).
- By the July sampling date in 2001, 2002, and 2003, wild juvenile pink salmon had consumed more prey than the average hatchery juvenile (Chapter 4).
- Surviving hatchery juveniles consumed more prey and were slightly larger than wild fish during July and August 2002, and wild fish consumed more prey and were larger than hatchery survivors in July and August 2003 (Chapter 4).
- No differences in size were found among hatchery groups during each year, although, in some cases, smolt-adult survival varied widely among these cohorts (Chapter 2).

Salinity zones

- Juvenile pink salmon migrated onto the continental shelf and out of the sampling area more quickly in years when they were of a larger average size (Chapter 2).

- During all months, growth was more efficient in the Alaska Coastal Current than in Prince William Sound, and more efficient in the transition zone than in the Alaska Coastal Current (Chapter 4).
- During July–August 2003, cohorts that remained in Prince William Sound consumed more prey than cohorts that migrated to the transition zone. During August–September 2003, the surviving hatchery cohort that remained in the transition zone consumed more than hatchery survivors that migrated from Prince William Sound to the Alaska Coastal Current (Chapter 4).
- No consistent pattern existed between thermal experience and growth for pink salmon during July–October (Chapter 2).

Average juveniles vs. survivors

- Hatchery pink salmon that survived to adulthood were larger at circuli, grew faster, and consumed more prey than the average hatchery juvenile during marine entry–September (Chapters 3 and 4).
- The largest difference in growth between the average hatchery juvenile and hatchery survivor was in 2002, the high-survival year (Chapter 4).

Objective 2: Do juvenile pink salmon need to achieve certain size thresholds at one or more life stages to have the potential to survive to adulthood? When do these critical periods in the growth of pink salmon occur? What is the relative importance of initial marine mortality versus mortality after the first growing season?

Results

- Larger, faster-growing juveniles experienced higher survival and possibly escaped a mid-summer bottleneck in growth (Chapter 3).
- Surviving fish began growing at a faster rate than the average juvenile by late July, but as early as late June, during all years (Chapter 3).

- Growth rate declined for both juveniles at-large and fish that survived to adulthood in early-mid July during all years (Chapter 3).
- The smallest surviving adult had smaller scales at circuli 1-18 than the average juvenile during 2001-2004, with one exception (Chapter 3).
- Scale size distributions of surviving fish and juveniles at-large were not aligned by September (Chapter 3).
- Differences in size among years were determined by some combination of growing conditions and early size-selective mortality, the strength of which could vary significantly among years (Chapter 2).

Objective 3: How much prey is necessary to achieve the amount of growth observed through September of the juvenile pink salmon's first year at sea?

Results

- In order to satisfy observed growth, juvenile pink salmon consumed at 66–106% of their theoretical maximum consumption rate (Chapter 4).
- During July–August 2002, all cohorts consumed more than 100% of their theoretical maximum consumption while feeding predominantly on *Limacina* (Chapter 4).
- Average cumulative consumption for all cohorts during May–August was 94.8 g during 2001, 154.1 g during 2002, 64.4 g for pink salmon remaining in Prince William Sound during 2003, and 63.9 g for pink salmon migrating to the transition zone by August 2003 (Chapter 4).
- Average daily consumption for all cohorts in all years ranged from 0.36–0.92 $g \cdot d^{-1}$ during marine entry–July, 1.30–3.20 $g \cdot d^{-1}$ during July–August, and 3.04–4.30 $g \cdot d^{-1}$ during August–September (Chapter 4).

Objective 4: Are juvenile pink salmon food-limited during May–September in Prince William Sound and the coastal Gulf of Alaska?

Results

- The localized standing stock biomass of key prey (large copepods, amphipods, *Limacina*, and larvaceans) exceeded the daily consumption demand of juvenile pink salmon during July–August 2003; however, for some prey in some months, production alone could not sustain the high level of consumption required to satisfy observed growth (Chapter 4).
- When zooplankton biomass was estimated using the Bongo net, juvenile pink salmon consumed 0.6–3.1% of the standing stock of large copepods per day, 1.0% of amphipods per day, 0.1–1.6% of *Limacina* per day, and 0.5–9.8% of larvaceans per day during July and August (Chapter 4).

Conclusions

- Larger, faster-growing juvenile pink salmon experienced higher survival.
- During low-survival years, wild pink salmon perhaps were more resilient in the face of some stress, experienced severe early size-selective mortality, or avoided some force that negatively affected the growth of hatchery fish.
- A diet focused on large copepods during May–July and *Limacina* during July–August 2002 was associated with higher growth and survival rates.
- Juvenile pink salmon must ingest large quantities of low-quality prey types to obtain the energy needed for rapid growth.
- Most observed feeding rates for juvenile pink salmon appeared sustainable in terms of not depleting prey supply. However, even in cases where prey production was enough to sustain feeding rates, production might not necessarily have allowed sufficient growth for juvenile pink salmon to avoid size-selective mortality.
- The high percentage of prey biomass consumed, more diversified diets in low-survival years, low feeding rates during May–July, the mid-summer decrease in circulus spacing and growth efficiency, and the fact that growth and consumption rates are much higher for all cohorts in high-survival years and for surviving cohorts

in all years indicate that juvenile pink salmon are food limited in Prince William Sound and the coastal Gulf of Alaska during their first summer at sea.

- Significant size-selective mortality occurs after the first growing season for pink salmon.
- The relative timing, importance and magnitude of early and late size-selective mortality varies significantly among years, and the results of the earlier phase might alter the severity of the later phase.
- Diversified distribution strategies or feeding strategies during later life stages could produce greater variability in the growth trajectories of surviving adults during high-survival years.
- A large discrepancy in estimates of prey biomass exists between zooplankton samples collected with a vertical Bongo net versus a horizontal Tucker trawl.

Future Work

Future studies will be necessary to fully address the issue of food limitation for juvenile pink salmon in Prince William Sound and coastal Gulf of Alaska. Some potential objectives are:

- Determine how representative these data are of other regions in Prince William Sound and the coastal Gulf of Alaska, and their applicability to the broader spatial region.
- Collect juvenile pink salmon during the May–July period to observe growth and mortality immediately after marine entry.
- Examine growth from juvenile pink salmon scales collected during and shortly after the first winter to provide additional insight into the rate and importance of ocean growth after the first growing season and when critical periods for growth and survival occur.
- Estimate the density of predators throughout the first summer at sea to gain insight on the magnitude and timing of size-selective mortality.

- Examine the fine-scale spatial and temporal overlap between juvenile pink salmon and their prey, including the daytime distribution of exploitable sizes of key prey species and the spatial scale of prey patchiness.
- Determine the impact of competitors of juvenile pink salmon on the forage base and rates of zooplankton production and advection to gain a better understanding of whether sufficient prey are available in Prince William Sound and the coastal Gulf of Alaska to sustain the pink salmon population.
- Continue side-by-side comparisons of zooplankton gear to determine which technique collects the most representative samples of the top 10 m.
- Further investigate the effects of local ocean conditions on growth and survival.
- Conduct genetic analyses of fish origin to examine the extent of immigration of unmarked fish originating outside of Prince William Sound into the study area.
- Determine the capture efficiency of the fish trawl to gain insight on the accuracy of population density estimates.

Significance

This study provides a basis for linking the growth performance and survival of juvenile pink salmon to the larger trophic dynamics of the Prince William Sound/coastal Gulf of Alaska region, which is especially importance for predicting the response of the population to climate change. Understanding the processes regulating growth, energetics, and survival will also lead to more accurate preseason forecasts, enabling more effective and economical harvest and management. Hatchery production may be overshooting carrying capacity, and continuing with current enhancement schemes could have severe ecological, economic and social ramifications. Prince William Sound hatchery operations can incorporate an understanding of the spatial and temporal nature of the additional demand on prey resources in production schemes.

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Appendix A: Additional Tables for Chapter 3

Table A.1. Mean scale size (SS) at each circulus throughout the first growing season for the average juvenile pink salmon during 2001 and the population from the same year-class that survived to adulthood, and the number of samples contributing to each measurement. Adult pink salmon from Armin F. Koernig, Cannery Creek, Solomon Gulch, and Wally Noerenberg hatcheries were pooled for analysis.

	Juveniles			Pooled Adults		
Circulus	Avg. SS (μm)	2SE SS (μm)	Count	Avg. SS (μm)	2SE SS (μm)	Count
1	87.5	1.7	135	106.9	1.9	94
2	123.5	2.5	135	143.0	3.0	94
3	159.1	3.4	135	177.6	3.7	94
4	192.3	4.0	134	211.4	4.3	94
5	222.8	4.6	133	243.1	4.8	94
6	252.0	5.2	130	275.3	5.3	94
7	279.9	6.2	120	306.6	5.8	94
8	308.3	7.5	109	340.5	6.3	94
9	335.1	8.7	102	375.4	7.2	94
10	366.0	10.0	94	409.7	7.9	94
11	395.4	10.4	82	444.2	8.6	94
12	422.5	13.1	62	479.7	9.3	94
13	452.3	14.9	45	515.5	9.8	94
14	485.7	19.4	26	553.1	10.2	94
15	519.7	21.2	20	590.6	11.1	94
16	553.6	28.0	13	631.1	11.9	94
17	593.9	54.3	6	669.7	12.4	94
18	640.3	60.3	4	709.1	13.2	94
19	620.5		1	748.1	13.4	94
20				784.7	13.8	94

Table A.2. Mean scale size (SS) at each circulus throughout the first growing season for the average juvenile pink salmon during 2002 and the population from the same year-class that survived to adulthood, and the number of samples contributing to each measurement. Adult pink salmon were collected by the Ocean Carrying Capacity (OCC) and Observer (OBS) programs of the National Marine Fisheries Service.

	Juveniles			OCC Adults			OBS Adults		
Circulus	Avg. SS (µm)	2SE SS (µm)	Count	Avg. SS (µm)	2SE SS (µm)	Count	Avg. SS (µm)	2SE SS (µm)	Count
1	87.2	2.9	43	99.5	2.5	87	104.1	6.2	15
2	125.7	4.5	43	137.1	3.2	87	146.4	10.4	15
3	163.2	6.0	43	175.4	4.2	87	187.7	10.9	15
4	200.9	7.0	43	213.4	5.0	87	226.0	13.0	15
5	236.9	8.7	43	248.6	5.8	87	265.8	17.4	15
6	271.0	9.6	43	285.3	6.6	87	303.3	20.0	15
7	304.3	10.8	42	322.4	7.2	87	346.5	21.1	15
8	341.8	12.1	41	360.9	7.8	87	389.9	23.4	15
9	377.9	13.8	40	398.9	8.4	87	434.7	24.6	15
10	415.0	16.7	36	437.3	8.7	87	478.6	25.3	15
11	447.6	20.5	28	477.3	8.8	87	529.3	28.1	15
12	478.3	25.0	19	516.7	9.2	87	578.2	31.0	15
13	523.1	33.6	12	557.5	9.7	87	629.7	34.0	15
14	575.7	51.1	8	597.1	10.5	87	678.2	35.8	15
15	654.5	143.1	3	637.8	11.0	87	730.1	38.6	15
16	648.5		1	679.5	11.5	87	777.1	41.3	15
17	681.5		1	720.6	12.3	87	819.5	43.7	15
18	699.5		1	760.6	12.9	87	861.9	45.4	15
19				799.0	13.6	87	901.7	47.1	15
20				837.3	14.3	87	938.1	48.3	15

Table A.3. Mean scale size (SS) at each circulus throughout the first growing season for the average juvenile pink salmon during 2003 and the population from the same year-class that survived to adulthood, and the number of samples contributing to each measurement. Adult pink salmon from Armin F. Koernig and Cannery Creek hatcheries were pooled for analysis.

	Juveniles			Pooled Adults		
Circulus	Avg. SS (μm)	2SE SS (μm)	Count	Avg. SS (μm)	2SE SS (μm)	Count
1	88.9	4.2	40	100.6	2.7	81
2	126.2	6.3	40	139.0	3.6	81
3	163.4	6.8	40	174.3	4.2	81
4	200.2	7.9	40	208.5	5.0	81
5	229.4	8.3	39	239.5	5.7	81
6	259.4	8.9	39	268.2	6.4	81
7	290.2	9.8	39	297.7	6.8	81
8	324.1	10.8	35	330.0	7.6	81
9	350.3	13.2	33	362.3	8.1	81
10	384.4	14.2	29	396.4	8.8	81
11	417.2	16.2	23	430.8	9.2	81
12	437.5	18.5	14	463.5	10.0	81
13	444.5	60.6	3	497.6	10.4	81
14	483.0		1	532.7	10.6	81
15	512.0		1	568.5	11.1	81
16	545.0		1	607.6	11.5	81
17	584.0		1	647.1	12.4	81
18	607.0		1	683.7	12.9	81
19				720.9	14.1	81
20				754.5	14.4	81

Table A.4. Mean scale size (SS) at each circulus throughout the first growing season for the average juvenile pink salmon during 2004 and the population from the same year-class that survived to adulthood, and the number of samples contributing to each measurement. Adult pink salmon were collected upon return to Armin F. Koernig (AFK), Cannery Creek (CCH), Solomon Gulch (SGH), and Wally Noerenberg (WNH) hatcheries.

	Juveniles			AFK Adults			CCH Adults		
Circulus	Avg. SS (μm)	2SE SS (μm)	Count	Avg. SS (μm)	2SE SS (μm)	Count	Avg. SS (μm)	2SE SS (μm)	Count
1	91.4	91.4	58	96.1	2.5	98	97.3	2.4	98
2	130.6	130.6	58	133.4	3.0	98	136.3	3.5	98
3	169.7	169.7	58	169.1	3.6	98	178.2	4.3	98
4	210.4	210.4	58	204.5	4.5	98	218.4	4.9	98
5	248.5	248.5	58	238.9	5.2	98	255.7	5.4	98
6	286.5	286.5	58	272.2	5.5	98	293.2	6.1	98
7	322.9	322.9	58	307.1	6.1	98	330.6	6.5	98
8	356.9	356.9	57	341.8	6.5	98	368.1	7.2	98
9	392.0	392.0	52	377.2	7.1	98	405.7	8.0	98
10	424.0	424.0	46	412.5	7.8	98	443.4	8.7	98
11	464.2	464.2	29	448.3	8.4	98	480.2	9.4	98
12	498.4	498.4	21	484.8	9.0	98	515.3	10.0	98
13	529.4	529.4	11	521.7	9.3	98	549.6	10.5	98
14	551.3	551.3	6	559.6	9.6	98	584.8	10.9	98
15	553.8	553.8	4	596.4	10.2	98	622.7	11.3	98
16	582.5	582.5	4	633.5	10.8	98	661.6	11.5	98
17	620.0	620.0	3	670.6	11.3	98	701.3	11.8	98
18	646.5	646.5	2	707.0	11.7	98	738.8	11.9	98
19	700.5	700.5	1	743.2	12.1	98	777.6	12.0	98
20	719.5	719.5	1	779.8	12.3	98	816.9	12.1	98

Table A.4 (continued)

	SGH Adults			WNH Adults		
Circulus	Avg. SS (µm)	2SE SS (µm)	Count	Avg. SS (µm)	2SE SS (µm)	Count
1	101.8	2.8	55	92.4	2.4	97
2	143.0	3.8	55	130.7	3.2	97
3	186.2	4.6	55	168.5	3.9	97
4	228.9	5.2	55	208.2	4.6	97
5	271.3	6.4	55	246.1	5.0	97
6	312.6	7.4	55	282.5	5.7	97
7	353.5	8.1	55	319.3	6.3	97
8	392.6	8.8	55	356.2	6.6	97
9	433.8	9.7	55	394.8	7.0	97
10	474.5	10.5	55	433.8	7.4	97
11	515.1	10.4	55	472.9	7.9	97
12	556.6	11.6	55	511.1	8.3	97
13	600.3	12.5	55	548.0	8.6	97
14	641.9	13.7	55	583.5	9.1	97
15	684.6	14.7	55	619.7	9.8	97
16	723.5	15.1	55	654.6	10.2	97
17	760.4	15.5	55	690.8	10.3	97
18	802.9	16.1	55	729.4	10.5	97
19	842.8	17.3	55	768.1	11.3	97
20	882.8	17.9	55	805.8	11.5	97

VITA

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