Chapter 2

Juvenile Salmon Predation

Exxon Valdez Oil Spill
Restoration Project Final Report

Sound Ecosystem Assessment: Juvenile Salmon Predation

Restoration Project 98320E
Final Report

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May 1999

Study History: This project was initiated under Restoration project 94320E and was continued under Restoration Projects 95320E, 96320E, 97320E. Annual reports were issued by Willette et al. under the title Sound Ecosystem Assessment: Juvenile Salmon Predation each year from 1994 through 1997. This is the final report for the project.

Abstract: This project is a component of the Sound Ecosystem Assessment (SEA) program which was designed to acquire an ecosystem-level understanding of the processes that constrain pink salmon and herring production in Prince William Sound (PWS). This project collected data needed to test several hypotheses related to predator-prey interactions affecting the mortality of pink salmon (*Oncorhynchus gorbuscha*) in PWS. Approximately 726 million juvenile pink salmon entered Prince William Sound, Alaska from bordering streams and hatcheries each year. Predation during the spring plankton bloom (May to mid-June) accounted for the mortality of 413 million juveniles (57%) and therefore appeared to be the primary mechanism causing mortality during this life stage. Two planktivorous fish, herring (*Clupea pallasi*) and walleye pollock (*Theragra chalcogramma*) probably consumed the greatest numbers of juvenile salmon. Several piscivorous fish (*Gadus macrocephalus, Microgadus proximus*, and *Salvelinus malma*) probably consumed the second greatest numbers and an assemblage of nearshore demersal fishes (Cottidae, Hexagrammidae, and *Sebastes spp.)* and seabirds (*Rissa tridactyla, Larus spp.*) probably consumed the smallest numbers of salmon. Relative attack|capture probabilities for planktivores feeding on juvenile salmon decreased over salmon lengths from 3-5 cm, but increased over this same length range for piscivores and demersal fishes feeding on salmon. Generally, juvenile pink salmon mortality probably increased from early May, (–0.0034) to early June (–0.0359) due to increasing depredation by herring and pollock and declining numbers of salmon. Mortality of pink salmon (release to adult return) from Wally H. Noerenberg Hatchery, adjacent to our study area, was greatest in 1994 (-0.0091), decreasing in 1995 (-0.0074), 1996 (-0.0070), and 1997 (-0.0056). This decline in mortality corresponded to a decline in adult pollock densities in our study area. Our results indicate that the copepod *Neocalanus* plays a unique role in modifying predation losses of juvenile pink salmon. Reduced large copepod densities probably caused (1) reduced growth when juvenile salmon densities were high, (2) greater predation losses to planktivores as these predators switched to alternative prey including salmon, and (3) dispersion of foraging juvenile salmon offshore leading to greater predation losses to piscivores and demersal fishes. Numerical model simulations indicated that predator size was an important factor modifying the predation process. Episodic periods of high juvenile mortality resulted when adult pollock switched to feeding on high-density groups of salmon as pteropod densities declined in June. Similar high depredation by immature pollock did not occur. Our results indicate that bottom-up processes affecting the spring *Neocalanus* bloom influence juvenile salmon growth rates and foraging behavior, but also modify top-down processes, through size-selective depredation of juvenile salmon and by altering the timing of a shift from planktivory toward piscivory among major predators on juvenile salmon. High mortality occurring after the *Neocalanus* bloom is reduced for juveniles that reach lengths exceeding 6-7 cm.

Key Words: *Exxon Valdez*, pink salmon, *Oncorhynchus gorbuscha*, Pacific herring, *Clupea pallasi*, walleye pollock, *Theragra chalcogramma*, Pacific tomcod, *Microgadus proximus*, mortality, predation, food habits.

Project Data: *Description of data* – Seven sets of digital data were developed during this project: (1) catches of various fish species in several types of nets, (2) lengths and weights of fish, (3) stomach contents of fish, (4) recoveries of tagged juvenile salmon, (5) zooplankton density and species composition estimated from nets, (6) ocean temperature and salinity measurements, and (7) light intensity measurements. Each data set is accompanied by documentation giving more information about their contents, including definitions of codes and terms, and other details that will facilitate access to and use of these data. All data are in R:Base format except ocean temperature\salinity and light intensity data which are in text files. *Custodian* – Contact Mark Willette, Alaska Department of Fish and Game, Commercial Fisheries Division, P.O. Box 669, Cordova, Alaska 99574 (work phone (907) 424-3214, fax (907) 424-3235, e-mail markw@fishgame.state.ak.us. *Availability* - copies of all data are available on diskette for the cost of duplication.

Citation: Willette, T. M., Carpenter, G., Hyer, K., Clapsadl, M., Saddler, P., and Powell, M. 1999. Sound Ecosystem Assessment: Juvenile Salmon Predation. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 98320E), Alaska Department of Fish and Game, Cordova, Alaska.

Chapter 2: 98320E
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Paul, A.J., and T.M. Willette. 1997. Geographical variation in somatic energy content of migrating pink salmon fry from Prince William Sound: A tool to measure nutritional status. Pages 707-720 in: Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems, Anchorage, Alaska, November 13-16, 1996. Lowell Wakefield Fisheries Symposium 14, Alaska Sea Grant College Program Report no. 97-01. University of Alaska Fairbanks, Fairbanks, Alaska.

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Willette, T.M., R.T. Cooney, and K. Hyer. 1999. Predator foraging mode shifts affecting mortality of juvenile fishes during the subarctic spring bloom. *Canadian Journal of Fisheries and Aquatic Sciences*, 56:364-376.

Willette, T.M., R.T. Cooney, V. Patrick, D.M. Mason, G.L. Thomas, and D. Scheel. 2001. Ecological processes influencing mortality of juvenile pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska. *Fisheries Oceanography* 10 (Suppl. 1):14-41.

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Objectives

1. *Estimate the juvenile salmon consumption rate for fish predators in Prince William Sound.*

This objective was addressed in the following journal articles:

Willette, T.M., Cooney, R.T., Patrick, V., Thomas, G.L., and Scheel, D. 1999. Ecological processes influencing mortality of juvenile pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska. Fish. Oceanogr. (in review).

Willette, T.M. 1999. Effects of juvenile salmon size and foraging behavior on predation risk. Fish. Oceanogr. (in review).

2. *Estimate the species and size composition of fish predators in Prince William Sound.*

This objective was addressed in the following journal articles:

Willette, T.M., Cooney, R.T., Patrick, V., Thomas, G.L., and Scheel, D. 1999. Ecological processes influencing mortality of juvenile pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska. Fish. Oceanogr. (in review).

Willette, T.M. 1999. Effects of juvenile salmon size and foraging behavior on predation risk. Fish. Oceanogr. (in review).

Willette, T.M., Cooney, R.T., and Hyer, K. 1999. Predator foraging mode shifts affecting mortality of juvenile fishes during the subarctic spring bloom. Can. J. Fish. Aquat. Sci. **56**: 364-376.

3. *Conduct preliminary tests of prey/predator (prey switching) hypotheses.*

This objective was addressed in the following journal articles:

Willette, T.M., Cooney, R.T., Patrick, V., Thomas, G.L., and Scheel, D. 1999. Ecological processes influencing mortality of juvenile pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska. Fish. Oceanogr. (in review).

Willette, T.M. 1999. Effects of juvenile salmon size and foraging behavior on predation risk. Fish. Oceanogr. (in review).

Willette, T.M., Cooney, R.T., and Hyer, K. 1999. Predator foraging mode shifts affecting mortality of juvenile fishes during the subarctic spring bloom. Can. J. Fish. Aquat. Sci. **56**: 364-376.

Willette, T.M., Cooney, R.T., and Hyer, K. 1999. Some processes affecting mortality of juvenile fish during the spring bloom in Prince William Sound, Alaska. In: Proceedings of an international symposium on ecosystem considerations in fisheries management. Alaska Sea Grant College Program Report, University of Alaska Fairbanks, Fairbanks, Alaska.

Willette, T.M. 1999. Limitation of feeding and growth rates of juvenile pink salmon (*Oncorhynchus gorbuscha*) in relation to foraging behavior and subsequent effects on mortality of wild- and hatchery-origin salmon. Can. J. Fish. Aquat. Sci. (in review).

Carpenter, G., and Willette, T.M. 1999. Diurnal changes in juvenile salmon foraging behavior and predation risk. J. Fish Biol. (in review).

Appendix 1: Journal articles produced during this project.

Willette, T.M., Cooney, R.T., Patrick, V., Thomas, G.L., and Scheel, D. 1999. Ecological processes influencing mortality of juvenile pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska. Fish. Oceanogr. (in review).

Willette, T.M., Cooney, R.T., and Hyer, K. 1999. Predator foraging mode shifts affecting mortality of juvenile fishes during the subarctic spring bloom. Can. J. Fish. Aquat. Sci. **56**: 364-376.

Willette, T.M., Cooney, R.T., and Hyer, K. 1999. Some processes affecting mortality of juvenile fish during the spring bloom in Prince William Sound, Alaska. In: Proceedings of an international symposium on ecosystem considerations in fisheries management. Alaska Sea Grant College Program Report, University of Alaska Fairbanks, Fairbanks, Alaska.

Willette, T.M. 1999. Effects of juvenile salmon size and foraging behavior on predation risk. Fish. Oceanogr. (in review).

Willette, T.M. 1999. Limitation of feeding and growth rates of juvenile pink salmon (*Oncorhynchus gorbuscha*) in relation to foraging behavior and subsequent effects on mortality of wild- and hatchery-origin salmon. Can. J. Fish. Aquat. Sci. (in review).

Carpenter, G., and Willette, T.M. 1999. Diurnal changes in juvenile salmon foraging behavior and predation risk. J. Fish Biol. (in review).

Diurnal changes in juvenile salmon foraging behavior and predation risk

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FOR SUBMISSION TO THE JOURNAL FISH BIOLOGY

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May 1999

Abstract

Analyses of field data were used to examine diurnal changes in foraging behavior and the risk of predation for juvenile pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska. Juvenile pink salmon fed continuously throughout the day, but feeding rate was greatest at dawn and stomach fullness peaked at dusk. Juvenile pink salmon formed very dense aggregations in shallow water at night to avoid predators in deeper water. Total food consumption of potential predators on salmon increased during twilight and at night due to higher abundances and feeding rates for several taxonomic groups. Predation on juvenile salmon in nearshore habitats was probably greatest during near dawn and dusk when light intensities were between 0.1 and 100 lux. As light intensities declined below 1000 lux, the profitability of feeding for juvenile salmon declined relative to the risk of predation. Juvenile salmon in PWS may have been vulnerable to predation for a shorter period of time each day in early May than later in the season, because surface light intensities were within the range of greatest vulnerability for a shorter time each day.

Introduction

Juvenile salmon and their predators exhibit diurnal patterns of distribution and feeding that affect their interaction. Juvenile pink salmon (*Oncorhynchus gorbuscha*) feed continuously throughout the day (Godin 1981), exhibit peaks in activity at various times during the day (Godin 1979), and migrate vertically into shallower waters at night (Godin 1984). Several potential predators on juvenile salmon migrate from deep water into the surface layer at night (Clark and Green 1990; Sogard and Olla 1993; Grant and Brown 1997). These behavioral patterns result in an overlap in the distributions of predator and prey that affect juvenile salmon mortality. Diurnal behavior patterns result from the need to concentrate vital activities to the time of day when the balance between food availability and predation risk is optimal for survival (Helfman 1993). This balance is often a function of the variable responses of predator and prey to light intensity.

In some cases, fluctuations in light intensity may be more important than prey density in controlling predation and thus prey mortality (Aksnes and Giske 1993). The variability in light intensity in aquatic environments can be extreme often changing more than seven orders of magnitude between bright daylight and night (Whitney 1969). Reactive distances decline with light intensity at different rates for various fishes affecting their interaction (Gerking 1994). At twilight, fish activity generally increases, and piscivores tend to be more successful at capturing prey (Helfman 1993). Juvenile salmon may be especially vulnerable to predators during brief periods at dawn and dusk. At these times, surface-oriented preys are silhouetted against the sky, but prey cannot distinguish bottom dwelling predators from the dark background (Pitcher and Turner 1986).

The presence of a predator may modify the foraging behavior of small fish by restricting feeding time and location, and reducing feeding rate. In the presence of predators, juvenile pink salmon occupied vegetation with less prey, but predator avoidance behaviors were relaxed when hungry

(Magnhagen 1988). Feeding rates (Metcalfe et al. 1987a), the efficiency of prey selection (Metcalfe et al. 1987b), and growth (English 1983) are generally reduced in the presence of predators, because more time is spent scanning for them. These effects on foraging behavior may significantly effect population size and structure (Jakobsen et al. 1988).

In the present study, we will test the following hypotheses related to these processes: (1) juvenile salmon diet composition is correlated with time of day and feeding rate is greater at dawn and dusk, (2) juvenile salmon aggregate nearshore at night and disperse offshore at dawn, (3) predator relative abundance and feeding rate is greater at dawn and dusk, (4) predation on juvenile salmon is greater at dawn and dusk and correlated with light intensity.

Methods

Field sampling and laboratory analysis

Nearshore fishes and their prey were sampled at several sites in western PWS from early May to mid June 1995 (Figure 1). Diel sampling was conducted approximately every 3 hours over a 24-hour period from 1 to 4 times per month at each site. Samples aggregated by site and date formed "sample units". A mid-water wing trawl (40 m x 28 m) equipped with a net sounder was used to sample pelagic fish in the passages of PWS. The net was towed at about 1.5 $m \cdot sec^{-1}$ for approximately 30 min in the 0-60 m layer of the water column. Nearshore fishes were sampled with 'anchovy' purse seines (250 m x 20 m, 1.5 cm stretch mesh) set in an approximate semi circle with the net open in the direction of the prevailing current for 20 min. Anchovy seine sampling was conducted within 1 km of the shore and up to the 20-m isobath. Nearshore fishes were also sampled with variable-mesh gill nets set out from shore at two stations within each site. Juvenile salmon were sampled inshore of the 20-m isobath with a small-mesh purse seine (60 m x 10 m, 0.5 cm stretch mesh) deployed from a skiff, and the relative abundance of juvenile salmon (low, moderate, or high) nearshore was estimated from visual shoreline surveys. In each study area, temperature and salinity were measured with a conductivity-temperature-depth profiler (CTD) to a depth of 100-m. A pyrometer equipped with a quantum sensor (Li-Cor Model LI-1000) was used to measure light intensity at 30-min intervals throughout each diel study.

The diet composition of nearshore fishes was estimated from specimens collected in 1995 (n=10,155). At least 30 specimens from each fish species were randomly selected from each net set for stomach contents analysis. Fork length and wet weight were measured, and stomachs excised and preserved in formalin for later analysis. In the laboratory, total stomach contents wet weight and the weight of juvenile salmon in the stomachs was measured. The number of juvenile salmon in each stomach was estimated by dividing the weight of juvenile salmon in the stomach by the mean wet weight of whole individual juvenile salmon found in the stomach. At least 20 specimens of juvenile pink salmon were randomly selected from each net set for stomach contents analysis and preserved in formalin or frozen. In the laboratory, fork length (FL), wet weight, and total stomach content weight were measured. The proportion of the diet composed on large copepods (>2.5 mm), small copepods (<2.5 mm), amphipods, euphausiids and cladocerans, pteropods, and 'other' zooplankters was visually estimated.

Nearshore fishes were placed into 9 taxonomic groups: immature (<30 cm) and adult (>30 cm) walleye pollock (*Theragra chalcogramma*), herring (*Clupea pallasi*), gadids (*Gadus macrocephalus, Microgadus proximus*), adult salmon (*Oncorhynchus spp.*), trout (*Salvelinus malma, Salmo mykiss*), benthic fishes (Cottidae, Hexagrammidae, Stichaeidae, Cyclopteridae, Zoarcidae, Bathymasteridae), pelagic rockfish (*Sebastes melanops, S. flavidus, S. ciliatus*), and demersal rockfish (*Sebastes nebulosus, S. caurinus. S. maliger, S. rubberimus,* and others). Several other taxonomic groups of fishes (Osmeridae, Ammodytidae, Gasterosteidae, Zaproridae, Pleuronectidae, Anarhichadidae, Anoplopomatidae, and Lamnidae) were not included in the analysis because they were relatively rare and did not consume significant numbers of juvenile salmon.

Diurnal changes in juvenile salmon foraging and distribution

We conducted several analyses of variance (ANOVA) to test the hypothesis that juvenile salmon diet composition is correlated with time of day and feeding rate is greater at dawn and dusk. The dependent variables in the analyses were the proportion of the diet (arcsine square root transformed) composed of various prey and an index of stomach fullness. The independent variables in the analyses were sample site-date and time of day (0000-0300 hrs, 0300-0600 hrs, 0600-0900 hrs, 0900-1200 hrs, 1200-1500 hrs, 1500-1800 hrs, 1800-2100 hrs, and 2100-2400 hrs). Preys were aggregated into 5 taxonomic groups: (1) large copepods, (2) small copepods, (3) amphipods, euphausiids and cladocerans, (4) pteropods, and (5) 'other zooplankton'. The residuals from a linear regression of mean stomach content weight (natural logarithm transformed) on juvenile salmon FL was used as an index of stomach fullness (Perry et al. 1996). Only stomach data from habitats inshore of the 20-m isobath were used in these analyses. All two-way interaction terms were initially included in each analysis, and a stepwise procedure was used to develop the most parsimonious model.

We used data from underwater video cameras to test the hypothesis that juvenile salmon aggregate nearshore at night and disperse offshore at dawn. Fixed up-looking video cameras were used to estimate the relative abundance of juvenile salmon in nearshore habitats. Cameras were installed at 2 locations where juvenile salmon were relatively abundant and were operated continuously for several days. A cable running to a pulley on the bottom and back to shore held each camera. The cable was adjusted periodically to maintain the camera 2.5-m below the surface as the water level changed with the tide. After the field season, videotapes were reviewed manually, and the relative abundance (low, moderate, or high) and length of time juvenile salmon were present in the field of view was recorded. An index of the relative abundance of juvenile salmon during each 3-hr time period was calculated from the product of salmon relative abundance during each salmon observation event and the length of time of the event. This index was then divided by the total time of video observation during each 3-hr time period, because total observation time during each period was not constant. We also conducted an ANOVA to test for a difference in catch per net set of juvenile salmon by time of day in anchovy seines offshore of the 20-m isobath. The dependent variable in the analysis was the catch per net set (natural logarithm transformed), and the independent variables were sample site-date and time of day.

Diurnal changes in relative abundance and feeding rates of nearshore fishes

We conducted two ANOVAs to test the hypothesis that predator relative abundance and feeding rate is greater at dawn and dusk. The independent variables in the analyses were sampling site-day and time of day. In the first analysis, the dependent variable was catch per net set (natural logarithm transformed) of predators in various gear types. Catch data from mid-water trawls was used for adult pollock, small mesh purse seines for herring and salmon, and variable-mesh gillnets for all other predator groups. In the second analysis, the dependent variable was the ratio (arcsine square root transformed) of total stomach content weight to fish body weight. A stepwise procedure was applied when appropriate.

Diurnal changes in predation on juvenile salmon

We conducted two ANOVAs to test the hypothesis that predation on juvenile salmon is greater at dawn and dusk and correlated with light intensity. The dependent variable in both analyses was the number of juvenile salmon in predator stomachs (natural logarithm transformed). We estimated the mean time of day at which the salmons found in each predator stomach were captured, because light intensity at the time the predator was sampled may have been different from when the salmon was captured by the predator. The mean time of day that the salmon were captured was calculated by subtracting the time since prey capture (t) from the time of day when the predator was sampled. The time since prey capture was estimated from mean prey weight at capture (w_t), mean initial prey weight (w_o, back calculated from length), and temperature-specific gastric evacuation rate, i.e. $t = \frac{\log(w_t) - \log(w_o)}{\alpha}$. The independent variables in the first analysis were time of day and predator taxonomic group. The independent variables in the second analysis were light intensity defined as a class variable (0.01-0.1, 0.1-1.0, 1.0-10, 10-100, 100-1,000, 1,000-10,000, and 10,000-100,000 lux) and predator taxonomic group. Data collected during 1996 and 1997 (Willette 1999) were included in these analyses to increase sample size.

Results

Diurnal changes in juvenile salmon foraging and distribution

Feeding rates of juvenile salmon peaked at dawn and dusk, and diet composition was correlated with time of day. Stomach fullness indices were correlated with time of day with maximum values near noon and midnight (Fig. 2). Juvenile salmon also consumed more pteropods in the evening and 'other zooplankton' at night (Fig. 2). The sample site\date by time-of-day interaction term in the model was significant for large copepods (R^2=0.932, df=203, p=0.005), small copepods (R^2=0.819, df=203, p=0.042), and amphipods, euphausiids, and cladocerans (R^2=0.771, df=203, p=0.052). Large copepods dominated juvenile salmon diets during early May, but small copepods generally dominated the diet later in the season (Fig. 3). The percent of the diet composed of large copepods was significantly different by time of day at site 525 on May 8 (*p* = 0.001) and at site 509 on June 13 (*p*=0.026). The percent of the diet composed of small copepods was significantly different by time of day at site 525 on May 8 (*p*=0.013) and at site 504 on June 9 (*p* =0.001). The percent of the diet composed of amphipods, euphausiids and cladocerans was significantly different by time of day at site 525 on May 13 ($p < 0.001$), site 506 on June 1 ($p=0.013$) and at site 525 on June 3 ($p=0.014$). The percent of the diet composed of other zooplankton was significantly different by time of day at site 525 on May 13 ($p=0.033$).

Underwater video observations indicated that juvenile salmon aggregated nearshore at night and dispersed offshore at dawn. The relative abundance of juvenile salmon estimated from these observations increased by a factor of 4 from mid day to evening (Fig. 4). Video cameras were operated in nearshore habitats for approximately 90 hours, but observations were hindered by extremes in light intensity during the darkest part of the night and at mid day. Visual observations during shoreline surveys conducted every 3 hours were consistent with this pattern of change in abundance, but catch per net set of juvenile salmon in the anchovy seines offshore of the 20-m isobath were not significantly different by time of day.

Diurnal changes in relative abundance and feeding rates of nearshore fishes

Predator relative abundance was greater at dawn and dusk for 5 taxonomic groups of fishes. From mid day to dusk, geometric mean catch per net set increased by a factor of 2 for adult pollock, 8 for immature pollock, 4 for gadids, 6 for demersal rockfish, and 3 for benthic fish (Fig. 5). The sample site by time of day interaction term in the model was only significant for benthic fish. Mean catch per net set for benthic fish reached a minimum between 0900 to 1500 hrs at 10 of 16 sites sampled.

Diel patterns of feeding differed among the 9 taxonomic groups of fishes, but many groups were feeding actively at dawn. Stomach fullness was significantly different among 3-hr sampling periods and the interaction term in the model was not significant for 6 of the groups (Fig. 6). Stomach fullness of immature pollock, gadids, trout, salmon, and pelagic rockfish increased in the morning. Immature pollock, gadids, and trout exhibited a second peak in stomach fullness in the evening. The sample site by time of day interaction term in the model was significant for herring (R^2=0.307, df=4956, p<0.001) and adult pollock (R^2=0.254, df=4177, p<0.001). Stomach fullness of herring was high during early May and varied considerably by time of day with peaks during the evening hours in some cases. Later in the season, stomach fullness of herring declined and was less variable. Conversely, stomach fullness of adult pollock was low in early May and varied little by time of day. In June, pollock stomach fullness was generally higher and more variable than in May.

Diurnal changes in predation on juvenile salmon

The numbers of juvenile salmon found in stomachs of 5 taxonomic groups of fishes were significantly correlated with light intensity or time of day, but light intensity always accounted for a greater amount of variance (Fig. 7). The relationships between number of salmon consumed and light intensity and time of day were significantly different (p<0.001) among predator groups. The greatest numbers of salmon were consumed by pollock and trout at light intensities from 0.1-10 lux and by gadids and pelagic rockfish from 10-100 lux. The number of salmon consumed was significantly correlated with time of day for immature pollock and gadids, and both predators consumed the greatest number of salmon during the darkest part of the night.

Discussion

Juvenile pink salmon fed continuously throughout the day, but feeding rate was greatest at dawn and stomach fullness peaked at dusk. Similar diel patterns of stomach fullness have been observed for pink salmon in other areas (Simenstad et al. 1980; Godin 1981). The minimum light intensity for juvenile pink salmon feeding on live prey is between 1.0 and 0.1 lux, but feeding rate declines with light intensity below 1000 lux (Bailey et al. 1975). High feeding rates at dawn probably resulted from hunger, because feeding at night was negligible. A second peak in feeding rate at dusk may be a genetic adaptation to maximize growth by maximizing stomach fullness before the nighttime fast. It is unlikely that high feeding rates at dusk result from greater prey vulnerability, because reactive distance declines with light intensity (Gerking 1994). Also, the diel pattern of feeding we observed was not associated with consumption of specific prey types that may at times become more vulnerable due to their behavior. An increase in consumption of pteropods during mid day suggested that the reactive distance for salmon feeding on pteropods declined below peak light intensities at mid day.

Juvenile pink salmon formed very dense aggregations in shallow water at night to avoid predators in deeper water. We could not observe juvenile salmon with underwater video cameras during the darkest part of the night (Figs. 4 & 8), but observations made during shoreline surveys using spotlights indicated that salmon aggregations were maintained at night. Our visual observations also indicated that this behavior was clearly related to light intensity, because the aggregations became larger and denser as light intensity declined and vice versa. Juvenile salmon and other fishes cannot generally maintain school formations at light intensities below 10^{-3} lux (Blaxter 1970). But, the aggregations we observed were not schools, because polarization among individuals was not maintained. Mechanical stimuli through the lateral line system resulting from the very close proximity of individuals may have been involved in maintaining these aggregations at very low light intensities. Juveniles probably formed these aggregations to avoid predators that increased in abundance at night (Fig. 5). Seine catches of juvenile salmon offshore were not correlated with time of day suggesting that aggregations observed nearshore were largely composed of individuals that had been inshore of the 20-m isobath as dusk approached. Mimic shiners (*Notropis volucellus*) also migrate inshore at night to avoid predators, but their behavior is highly variable depending on predator abundance (Hanych et al. 1983).

Total food consumption of fishes in nearshore habitats increased during twilight and at night due to higher abundances and feeding rates for several taxonomic groups. Higher catches during this time of day were probably due in part to vertical migrations into surface waters (Clark and Green, 1990; Sogard and Olla 1993). However, the magnitude of the changes in mean catch per net set we observed may not accurately reflect changes in abundance due to gear avoidance during the day or greater activity at night causing higher gill-net catches. Low stomach fullness during the darkest part of the night indicated that feeding rate was reduced at low light intensities (Blaxter 1970). Total food consumption by several groups may have been greatest at dawn, because relative abundances remained high and feeding rates were at their daily maximum (Figs. 5 & 6).

Predation on juvenile salmon in nearshore habitats was probably greatest during twilight and at night. Consumption of salmon by immature pollock and gadids was relatively high during this time of day. Although, predation on salmon by demersal rockfish and benthic fish was not correlated with time of day, higher relative abundances or activity levels during twilight and at night probably increased encounter rates with juvenile salmon. Our analysis indicated that predation on salmon was greatest when light intensities were between 0.1 and 100 lux (Fig. 7). In laboratory studies, predation on juvenile salmon by northern squawfish and rainbow trout increased as light intensities declined from 2.0-3.0 lux to 0.1 lux (Ginetz and Larkin 1976; Peterson and Gadomski 1994). Our method of estimating the actual time of day and thus light intensity when juvenile salmon were captured was not as accurate as was possible in the laboratory, but any error was probably random and thus did not bias our results. Our results suggest that predation on juvenile salmon was greatest at higher light intensities than observed in the laboratory, but we do not know the actual water depth where the salmon were captured. It is likely that the predation occurred anywhere within the upper 20-m of the water column. Light intensities were an order of magnitude lower within the deeper portions of this layer compared to the surface.

As light intensities declined below 1000 lux, the profitability of feeding for juvenile salmon declined relative to the risk of predation. Feeding often involves a tradeoff between predation risk and the growth needed to reach a viable size for later survival (Walters and Juanes 1993). As light intensities decline, reactive distances for juvenile salmon feeding on zooplankton decline (Bailey et al. 1975; Gerking 1994). Our data indicated that juvenile salmon stopped feeding when light intensities fell below about 10 lux (Fig. 2 & 8), and juveniles in nearshore habitats sought refuge from predation by forming large aggregations in shallow water. This behavior probably resulted from a declining profitability associated with feeding in risky habitats.

Juvenile salmon in PWS may have been vulnerable to predation for a shorter period of time each day in early May than in late May and June, because surface light intensities were within the range of greatest vulnerability for a shorter period of time each day in early May. Surface light intensities were between 0.1 and 100 lux for about 3-5 hrs each day in early May, but during late May and early June surface light intensities were within this range for 6-7 hours each day (Fig. 8). Juvenile salmon may reduce their vulnerability during this twilight period by migrating to depths where light intensities are below the minimum visual threshold for most predators. But, our data indicated that this did not occur, because catches of juvenile salmon in anchovy seines did not decline at night. Although juvenile salmon size and availability of alternative prey are important factors affecting predation losses of salmon (Willette et al. 1999), seasonal patterns of light intensity may in part explain increasing individual predation rates on juvenile salmon from early May to June (Willette 1999).

Acknowledgements

We would like to thank the numerous staff of the Alaska Department of Fish and Game, University of Alaska Fairbanks, Prince William Sound Science Center, and our charter vessel operators who endured very long work hours and often difficult conditions to obtain the samples used in this study. The Prince William Sound Aquaculture Corporation provided much appreciated logistical support for our vessels and staff. This project was funded by the *Exxon Valdez* Oil Spill Trustee Council through the Sound Ecosystem Assessment project. However, the findings presented by the authors are their own and do not represent the position of the Trustee Council.

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List of Figures

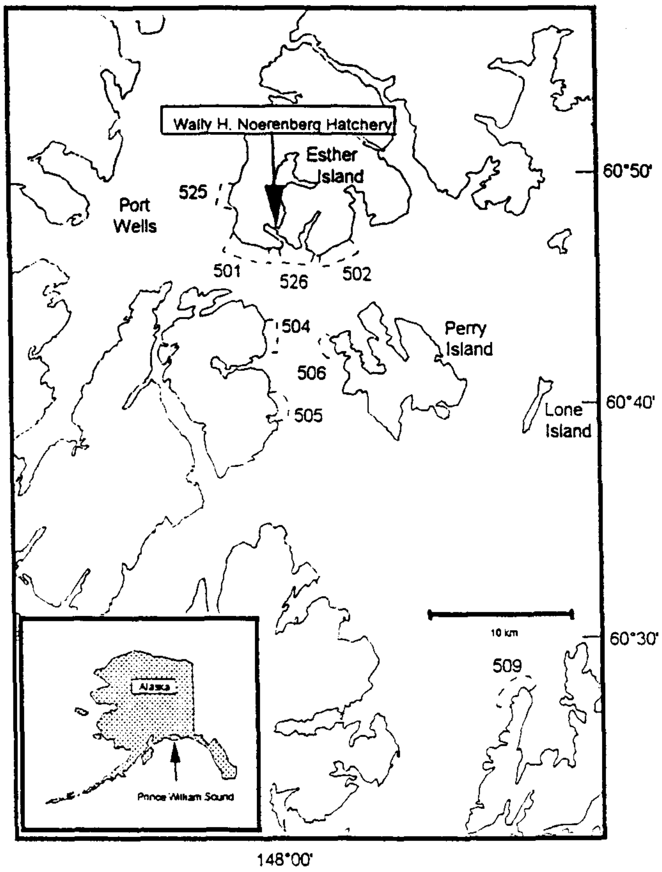

Wally H. Noerenberg Hatchery
Esther Island
Port Wells
525
501
526
502
504
506
505
Perry Island
Lone Island
60°50'
60°40'
60°30'
10 km
509
Alaska
Prince William Sound
148°00'

Figure 1

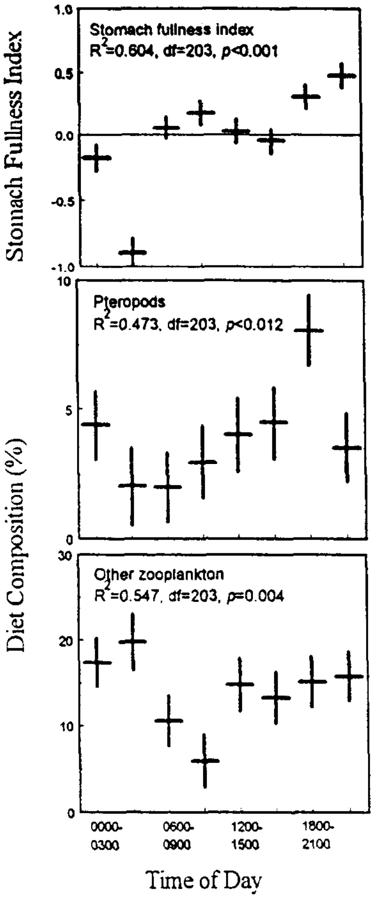

Stomach Fullness Index
1.0
0.5
0.0
-0.5
-1.0
Stomach fullness index
R^2=0.604, df=203, p<0.001
Diet Composition (%)
10
5
0
Pteropods
R^2=0.473, df=203, p<0.012
30
20
10
0
Other zooplankton
R^2=0.547, df=203, p=0.004
0000-0300
0600-0900
1200-1500
1800-2100
Time of Day

Figure 2

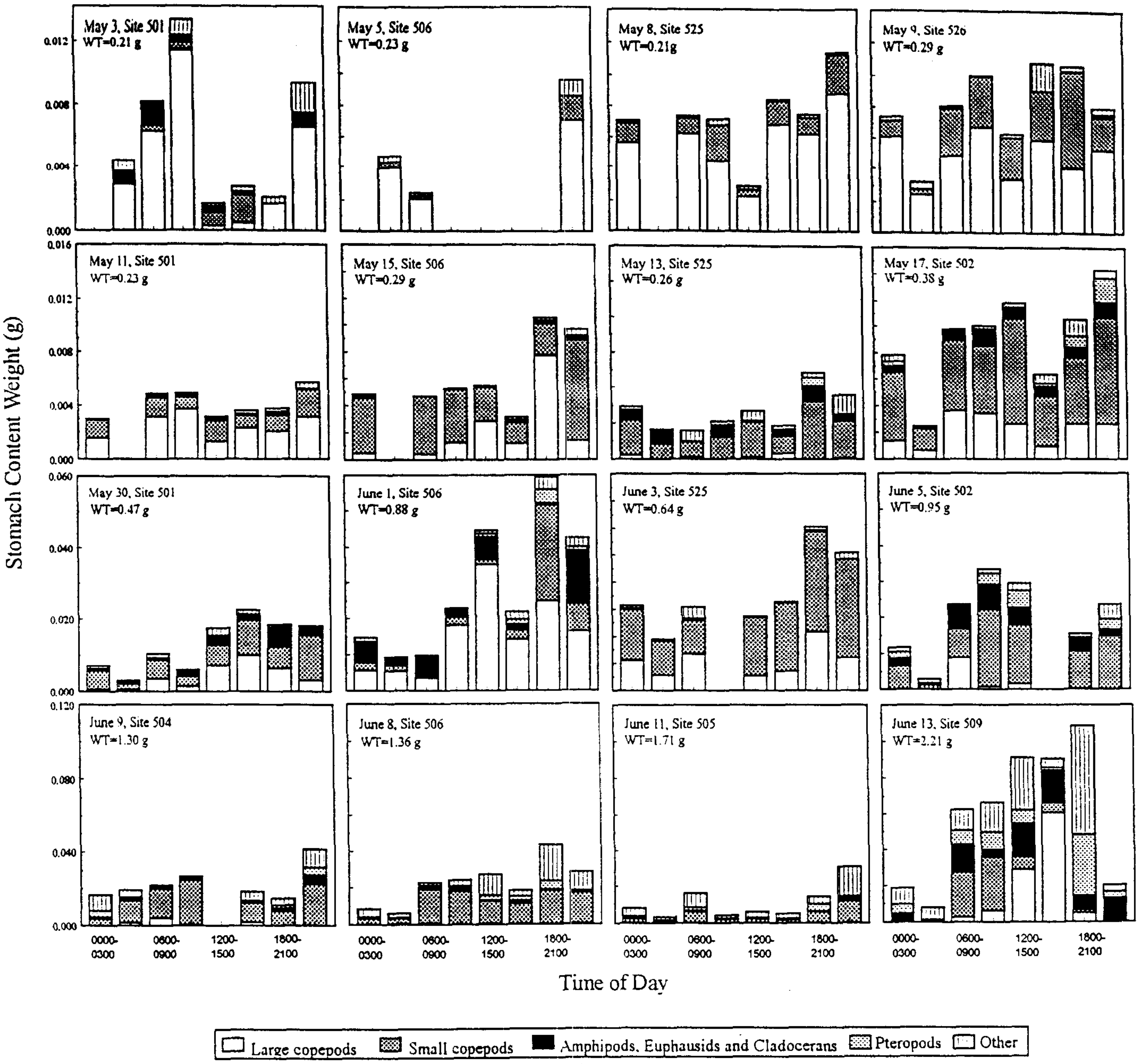
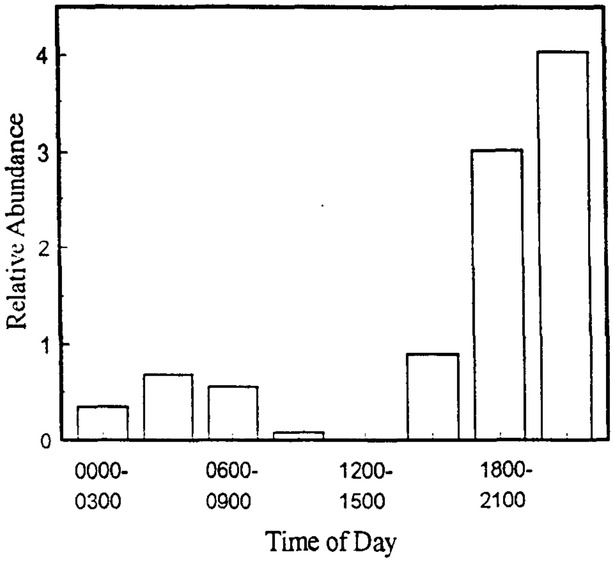
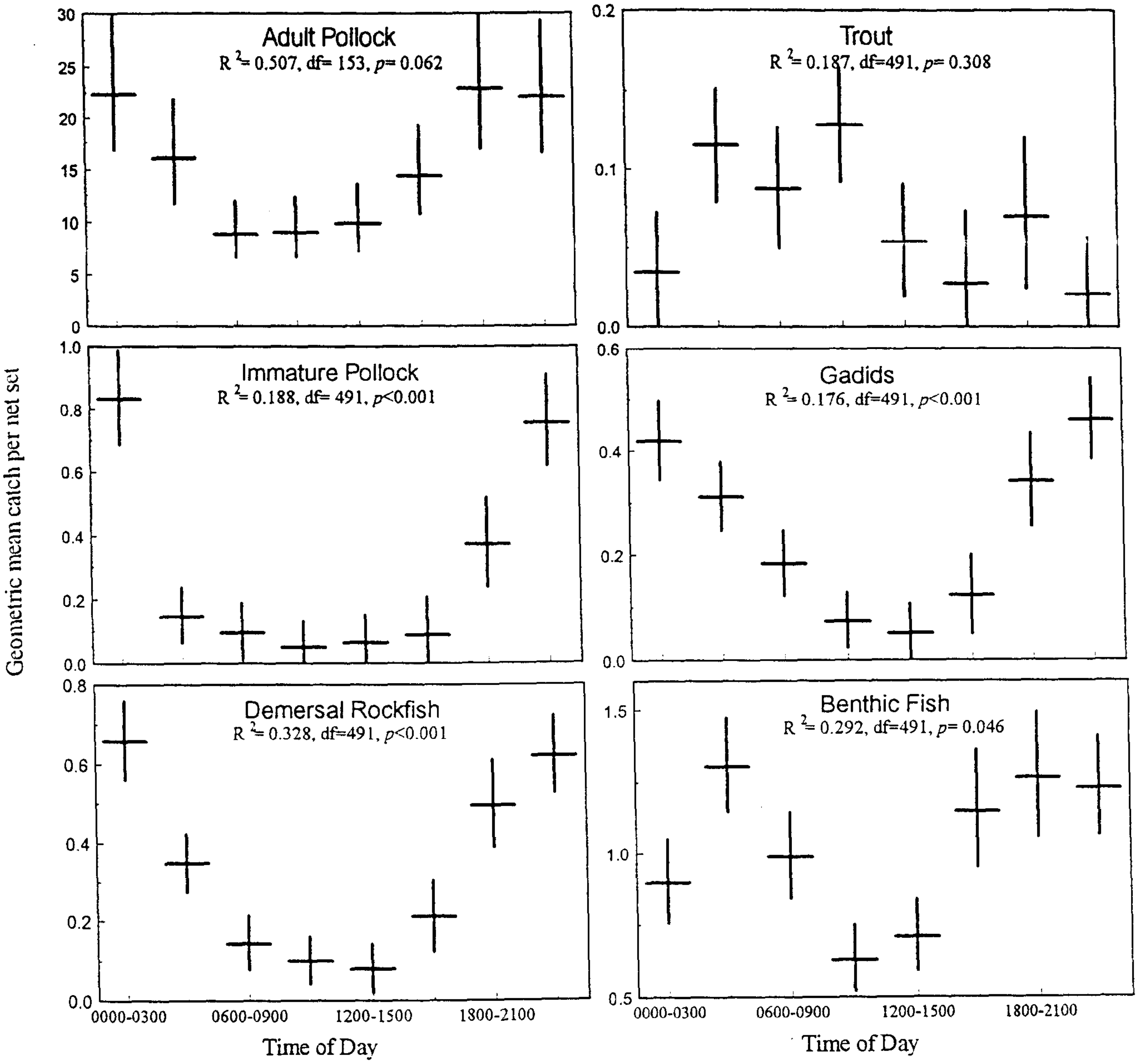

May 3, Site 501
WT=0.21 g
May 5, Site 506
WT=0.23 g
May 8, Site 525
WT=0.21g
May 9, Site 526
WT=0.29 g
May 11, Site 501
WT=0.23 g
May 15, Site 506
WT=0.29 g
May 13, Site 525
WT=0.26 g
May 17, Site 502
WT=0.38 g
May 30, Site 501
WT=0.47 g
June 1, Site 506
WT=0.88 g
June 3, Site 525
WT=0.64 g
June 5, Site 502
WT=0.95 g
June 9, Site 504
WT=1.30 g
June 8, Site 506
WT=1.36 g
June 11, Site 505
WT=1.71 g
June 13, Site 509
WT=2.21 g
0.000
0.004
0.008
0.012
0.016
0.020
0.040
0.060
0.080
0.120
Stomach Content Weight (g)
0000-0300
0600-0900
1200-1500
1800-2100
Time of Day
Large copepods
Small copepods
Amphipods, Euphausids and Cladocerans
Pteropods
Other

Figure 3



Relative Abundance
4
3
2
1
0
0000-
0300
0600-
0900
1200-
1500
1800-
2100
Time of Day

Figure 4



Adult Pollock
R^2= 0.507, df= 153, p= 0.062
Trout
R^2= 0.187, df=491, p= 0.308
Immature Pollock
R^2= 0.188, df= 491, p<0.001
Gadids
R^2= 0.176, df=491, p<0.001
Demersal Rockfish
R^2= 0.328, df=491, p<0.001
Benthic Fish
R^2= 0.292, df=491, p= 0.046
Geometric mean catch per net set
0000-0300
0600-0900
1200-1500
1800-2100
Time of Day
0
5
10
15
20
25
30
0.0
0.1
0.2
0.4
0.6
0.8
1.0
0.5
1.5

Figure 5

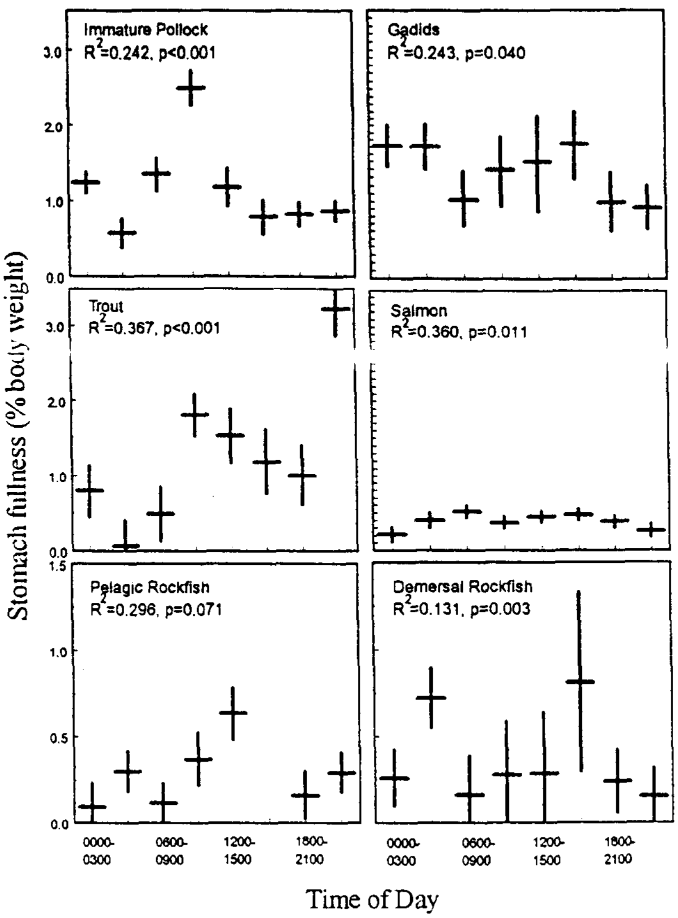

Immature Pollock
R^2=0.242, p<0.001
Gadids
R^2=0.243, p=0.040
Trout
R^2=0.367, p<0.001
Salmon
R^2=0.360, p=0.011
Pelagic Rockfish
R^2=0.296, p=0.071
Demersal Rockfish
R^2=0.131, p=0.003
Stomach fullness (% body weight)
0.0
0.5
1.0
1.5
2.0
3.0
0000-0300
0600-0900
1200-1500
1800-2100
Time of Day

Figure 6

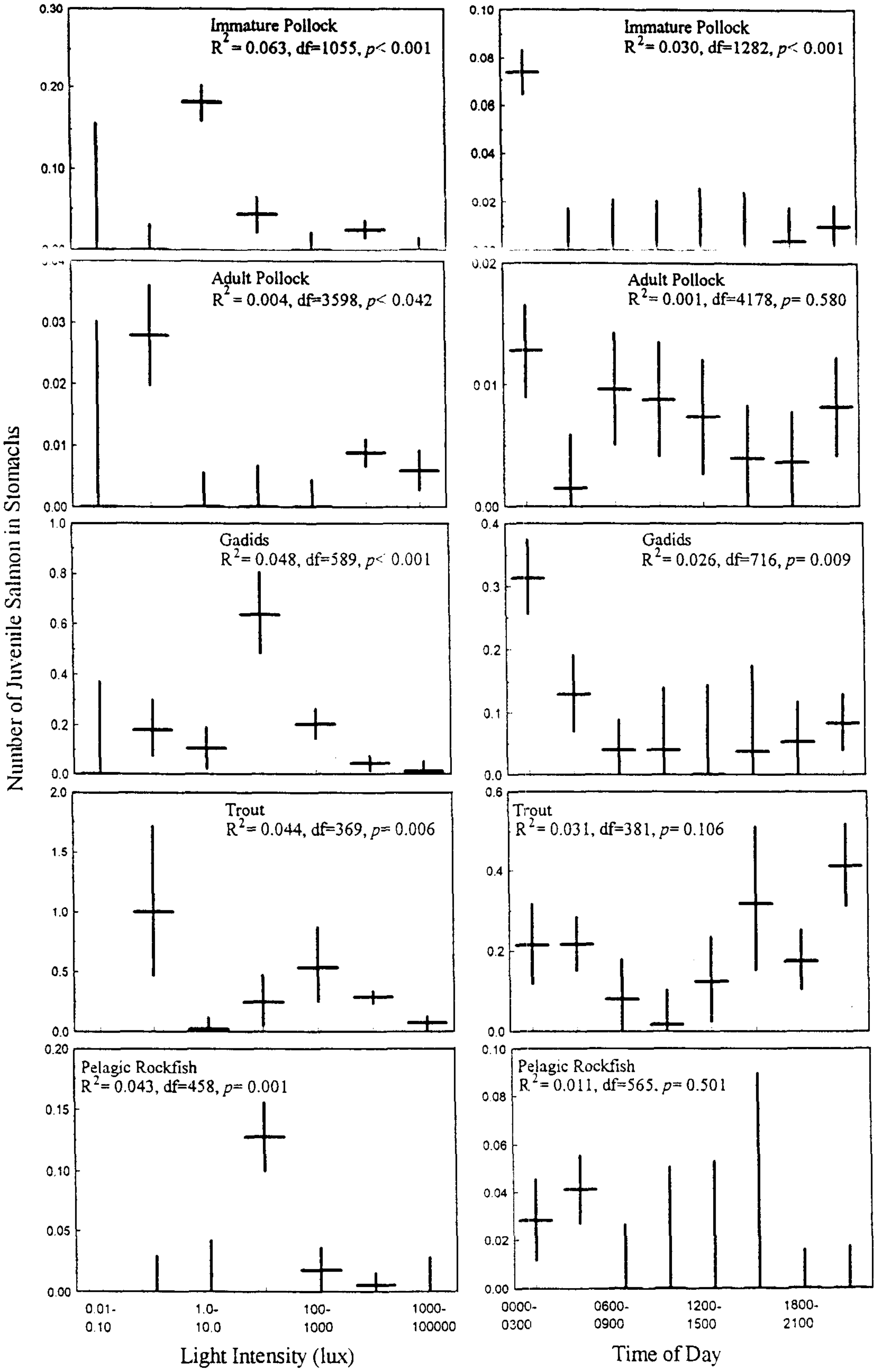

Immature Pollock
$R^2 = 0.063$, df=1055, $p < 0.001$
Immature Pollock
$R^2 = 0.030$, df=1282, $p < 0.001$
Adult Pollock
$R^2 = 0.004$, df=3598, $p < 0.042$
Adult Pollock
$R^2 = 0.001$, df=4178, $p = 0.580$
Gadids
$R^2 = 0.048$, df=589, $p < 0.001$
Gadids
$R^2 = 0.026$, df=716, $p = 0.009$
Trout
$R^2 = 0.044$, df=369, $p = 0.006$
Trout
$R^2 = 0.031$, df=381, $p = 0.106$
Pelagic Rockfish
$R^2 = 0.043$, df=458, $p = 0.001$
Pelagic Rockfish
$R^2 = 0.011$, df=565, $p = 0.501$
Number of Juvenile Salmon in Stomachs
0.30
0.20
0.10
0.10
0.08
0.06
0.04
0.02
0.03
0.02
0.01
0.00
0.02
0.01
0.00
1.0
0.8
0.6
0.4
0.2
0.0
0.4
0.3
0.2
0.1
0.0
2.0
1.5
1.0
0.5
0.0
0.6
0.4
0.2
0.0
0.20
0.15
0.10
0.05
0.00
0.10
0.08
0.06
0.04
0.02
0.00
0.01-
0.10
1.0-
10.0
100-
1000
1000-
100000
0000-
0300
0600-
0900
1200-
1500
1800-
2100
Light Intensity (lux)
Time of Day

Figure 7

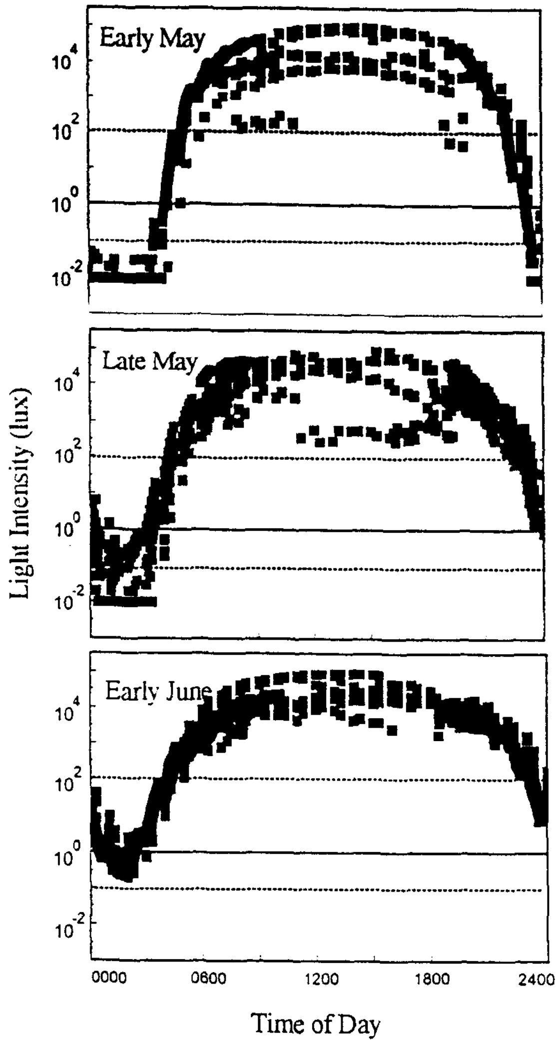

Early May
Late May
Early June
10^4
10^2
10^0
10^-2
Light Intensity (lux)
0000
0600
1200
1800
2400
Time of Day

Figure 8

Limitation of feeding and growth rates of juvenile pink salmon (*Oncorhynchus gorbuscha*) in relation to foraging behavior and subsequent effects on mortality of wild and hatchery-origin salmon

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FOR SUBMISSION TO THE CANADIAN JOURNAL OF FISHERIES AND AQUATIC SCIENCES

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May 1999

Abstract: Several hypotheses were tested regarding processes affecting foraging behavior, growth and size-dependent mortality of wild- and hatchery-origin juvenile pink salmon (*Oncorhynchus gorbuscha*) rearing in Prince William Sound, Alaska. Daily rations of juvenile pink salmon averaged over large spatial scales were often near maximum ration, and feeding and growth rates of juveniles were only weakly density dependent. Juvenile pink salmon that consumed large copepods (primarily *Neocalanus* and *Calanus*) probably achieved high growth rates, and juveniles dispersed from nearshore predation refugia when copepod densities declined. The higher feeding and growth rates achieved by juveniles consuming *Neocalanus* reduced their mortality by minimizing their foraging times in risky habitats, and their vulnerability to size-selective predation. Interactions among wild- and hatchery-origin juveniles resulted more from differential size-dependent predation losses among groups than from limitation of feeding and growth. Differential predation losses among groups are probably amplified when *Neocalanus* densities or ocean temperatures are low. Decadal oscillations in production of coastal and oceanic ecosystems in the Gulf of Alaska may cause changes in the carrying capacity of nearshore predation refugia amplifying mortality differences between wild- and hatchery-origin salmon.

Introduction

Limitation of feeding and growth rates of juvenile Pacific salmon (*Oncorhynchus*) during early sea life has been difficult to evaluate, yet variations in growth likely influence recruitment due to size-selective predation (Parker 1971; Healey 1982a). Model simulations (Walters et al. 1978), comparisons of prey production and juvenile forage demand (Bailey et al. 1975; Healey 1979; Brodeur et al. 1992; Cooney 1993; Simenstad and Salo 1980), comparisons of actual ration with maximum ration, and juvenile condition (Healey 1991; Perry et al. 1996) have all been used to examine this question. Most investigators concluded that juvenile salmon growth was not food limited during their first month of marine residence in nearshore habitats (Walters et al. 1978; Simenstad and Salo 1980; Cooney 1993), but food supply may have limited salmon production in some cases (Bailey et al. 1975; Healey 1979). Conversely, most investigators concluded that growth was at times limited by food abundance after juveniles migrated into the coastal zone (Healey 1991; Brodeur et al. 1992; Perry et al. 1996).

Walters et al. (1978) identified several questions that needed further investigation to improve our understanding of these processes: (1) how efficient are juvenile fish at finding food when it becomes scarce, (2) how much would food abundance have to be reduced to cause growth effects, and (3) are juvenile salmon strongly restricted to nearshore habitats or would they simply and safely move offshore in the face of competition ? Subsequently, Healey (1982) concluded that migration of juvenile salmonids from nearshore habitats was not related to foraging success, while Simenstad and Salo (1980) found that migration of chum salmon from nearshore habitats coincided with a decline in abundance of their preferred prey (harpacticoid copepods). Healey (1991) concluded that juvenile salmon aggregated on prey patches and migrated from the coastal zone when foraging success declined (Healey 1982b). More recently, reduced growth was observed among juvenile pink salmon (*O. gorbuscha*) in Prince William Sound (PWS), Alaska when zooplankton biomass was less than about 0.3 g m^{-3} and the number of juveniles in hatchery release groups exceeded 20 million (Willette et al. 1999). Dispersion of juveniles from nearshore predation refugia and higher predation losses were also observed when densities of large calanoid copepods (primarily N*eocalanus* and *Calanus*) in nearshore habitats declined (Willette 1999). Dispersion of juveniles offshore probably was not motivated by hunger, because it was not correlated with stomach fullness.

Walters and Juanes (1993) predicted that juvenile foraging time in risky habitats adjacent to refugia would be a function of the minimum needed for growth to a viable size for later survival plus an additional time inversely proportional to the predation risk per time. Foraging times should further be an inverse function of juvenile density and prey density assuming juveniles exhibit a heritable variation in behavioral traits that cause foraging times to vary with changes in prey density. Walters and Juanes (1993) did not explicitly consider effects of prey type on feeding and growth rates of juveniles, but Willette's (1999) results suggest that prey type has an important effect on the foraging behavior of juvenile salmon. Feeding rates of juvenile pink and chum salmon (*O. keta*) were 3-4 times higher when *Calanus* rather than *Pseudocalanus* were consumed, and each species selected for *Calanus* and against *Pseudocalanus* both in tanks studies (LeBrasseur 1969; Parsons and LeBrasseur 1973) and in situ (Simenstad and Salo 1980).

In the present study, I will test 4 hypotheses related to these processes: (1) juvenile pink salmon growth is not food limited, (2) feeding and growth rates of juvenile pink salmon are not related to prey type, (3) zooplankton species composition and juvenile salmon diet composition are not different between nearshore and offshore habitats, and (4) feeding and growth rates of juvenile pink salmon are not related to juvenile density. Finally, I will examine the overlap in distributions of wild- and hatchery-origin juvenile pink salmon and the relative size-dependent predation losses from each group in PWS.

Methods

Field sampling and laboratory analyses

This study was conducted in Prince William Sound (PWS), Alaska which is an approximately 8,800 km^2 semi-enclosed basin reaching depths to 750 m. Juvenile salmon and their prey were sampled in PWS from early May to September, 1994 (Willette et al. 1999) and from early May to mid June, 1995-1997 (Fig. 1). Each year in late April or early May, four hatcheries released approximately 500 million juvenile pink salmon into western and northern PWS, and these fish mixed with about 250-500 million wild pink salmon emigrating from nearly 1,000 local streams. As a result, juvenile salmon densities in nearshore refugia varied greatly from western to eastern PWS. This feature was used to examine effects of juvenile density on feeding and growth. In 1994, samples were collected at several sites each day. These samples were only used to evaluate whether juvenile pink salmon growth was food limited. In 1995, sampling was conducted approximately every 3 hrs throughout a 24-hr period at a single site each day. In 1996-1997, samples were collected every 3 hrs from about 21:00 to 09:00 hrs at each site. Each year, juvenile salmon were sampled with purse seines (250 m x 20 m, 1.5 cm stretch mesh) set in an approximate semi circle with the net open in the direction of the prevailing current for 20 min. Seine sampling was conducted within 1-km of the shore and up to the 20-m isobath. Inshore of the 20-m isobath, juvenile salmon were sampled with a small-mesh purse seine (40 m x 10 m, 0.5 cm stretch mesh) deployed from a skiff. In 1995-1997, visual shoreline surveys were conducted to estimate the relative density of juvenile salmon inshore of the 20-m isobath. At least 2 zooplankton samples were collected every 3 hours at each site at stations located near the 20-m isobath to estimate the density of large calanoid copepods and other macrozooplankton available to juvenile salmon. These samples were collected with a 0.5-m ring net (243 μm mesh) towed vertically from a depth of 20-m to the surface. In each study area, temperature and salinity were measured with a conductivity-temperature-depth profiler (CTD) to a depth of 100-m. One thousand and sixty-nine purse seine sets, 610 small-mesh purse seines sets, and 596 zooplankton casts were taken during the 4 years of the study.

The diet composition of juvenile pink salmon was estimated from at least 10 specimens randomly selected from each net set and preserved in formalin for later stomach contents analysis. In the laboratory, fork length (FL), wet weight, and total stomach contents wet weight was measured to 0.01 g. For samples collected in 1994, prey items in the gut were identified to the lowest possible taxonomic level and enumerated (Willette et al. 1997). For samples collected in 1995 and 1996, the proportion of total stomach contents weight in 8 taxonomic groups (large calanoid copepods, >2.5 mm; small calanoid copepods, <2.5 mm; cladocerans; ostracods; amphipods; euphausiids; pteropods and 'other zooplankton') was visually estimated. In 1997, cladocerans, ostracods, amphipods, euphausiids, and pteropods were further aggregated with the 'other zooplankton' group. In 1996 and 1997, at least 20 specimens were also randomly selected from each net set and frozen for later measurement of dry-weight condition and moisture content. The wet weight and dry weight of these fish was measured to 0.01 mg with the head and stomach removed. For juvenile pink salmon less than 8 cm FL, energy content was estimated from moisture content ($R^2=0.952$, df=53, $p<0.001$) using data provided by Parker and Vanstone (1966). Zooplankton samples were analyzed using standard subsampling techniques (Coyle et al. 1990) after measurement of total wet weight. Zooplankters were enumerated into three taxonomic groups as previously described, and biomass was calculated as the product of abundance and the mean individual wet weight for each taxonomic group (Coyle et al. 1990).

Juvenile growth and food limitation

I tested the hypothesis that the growth of juvenile pink salmon was not food limited by testing for a difference between the daily ration of juvenile pink salmon in PWS during 2-week periods and maximum daily ration (Table 1). Daily ration (I) of juvenile salmon in PWS was estimated from $I = 24\overline{S}\alpha$ (Eggers 1977), where $\overline{S}$ was the daily mean stomach content wet weight and α was the temperature-specific gastric evacuation rate. The sampling design was not adequate to estimate ration for each day, so the data were aggregated over 2-week sampling periods to insure that samples from throughout the day were available. Data from Brett and Higgs (1970) were used to estimate temperature-specific gastric evacuation rate. Brett and Higgs (1970) starved the fish in their study before and after measurement of evacuation rate, but gastric evacuation rate of juvenile Atlantic salmon (*Salmo salar*) doubled when the fish were fed continuously rather than starved before and after measuring evacuation rate (Talbot et al. 1984). Therefore, I increased gastric evacuation rates estimated from Brett and Higgs (1970) by a factor of 2 to account for the effect of continuous feeding which is common in juvenile pink salmon under natural conditions (Godin 1981). I did not correct evacuation rates for fish size, because juvenile Atlantic salmon within the size range of those in PWS did not exhibit a difference in evacuation rate related to fish size (Talbot et al. 1984). The energy content of the daily ration (kJ g^{-1} wet weight) was estimated from the product of wet weight and energy density of prey. Energy densities and percent dry weight of zooplankton were estimated from data provided by Norrbin and Bamstedt (1984), Harris (1985), and Higgs et al. (1995): large calanoid copepods (27.6 kJ g dry wt^{-1}, 23.1% dry wt), small copepods (24.7 kJ g dry wt^{-1} , 17.7% dry wt), cladocerans and ostracods (25.8 kJ g dry wt^{-1}, 25.5% dry weight), amphipods and euphausiids (22.7 kJ g dry wt^{-1}, 22.7% dry wt), pteropods (14.0 kJ g dry wt^{-1}, 12.8% dry wt), and other zooplankters (19.3 kJ g dry wt^{-1}, 25.5% dry wt). Maximum daily ration was estimated from temperature- and size-specific growth at maximum ration for juvenile sockeye salmon fed a commercial food (Brett 1974). I increased Brett's estimates of sockeye growth by 1.45, because his data indicated that juvenile pink salmon grew faster than sockeye on the same ration. I assumed a gross growth conversion efficiency of 30%, which is near the upper range for juvenile salmonids considering interacting effects of temperature, ration size and type, and body size (Brett et al. 1969; Biette and Geen 1980; Brett et al. 1982). Overlap between the 95% confidence interval on the estimated daily ration of juvenile pink salmon in PWS and maximum daily ration was used to determine whether the rations were different. The 95% confidence intervals on the daily ration were calculated from confidence intervals on mean stomach content weight.

Growth rates of juvenile pink salmon in PWS were estimated from recoveries of coded-wire tagged (CWT) juveniles (0.25-0.35 g) released from the Wally H. Noerenberg Hatchery in late April and early May, 1994-1995 (Willette 1996). Growth rates of these 'early-release' groups were adjusted for size-selective predation using relative attack-capture probabilities for pollock and herring preying on juvenile salmon (Willette 1999) and mortalities estimated from recoveries of CWT adults (Geiger 1990). During both years, 2 CWT groups of pink salmon (1.0-1.5 g) were also released from the Wally H. Noerenberg Hatchery (WHN) in mid-June. Mortality of the early-release groups during the initial 45-days of marine residence was estimated from mortalities of the late-release groups assuming that the mortality of both groups was the same after mid-June. Seine sampling indicated that both groups occurred together and were similar in size after mid-June. Growth rates (kJ day^{-1}) were estimated assuming an energy density of 3.34 kJ g wet weight^{-1} for juvenile pink salmon (Paul and Willette 1997). Gross growth conversion efficiencies under natural foraging conditions were then calculated from growth and daily ration estimates. Mean energy content of juvenile pink salmon during each sampling period was estimated during 1996 and 1997 for comparison with daily rations.

Effect of prey type on feeding and growth rates

I conducted an analysis of covariance (ANCOVA) to test hypothesis that juvenile salmon feeding rate was not different when large versus small calanoid copepods were consumed. I estimated feeding rate (kJ hr^{-1}) from the increase in mass of large and small copepods in the stomachs of juvenile salmon between samples collected during the night and those collected about 3-hours later shortly after dawn. Because feeding typically ceases at night (Godin 1981), juveniles were probably actively feeding at dawn. Estimated losses to gastric evacuation were added to the change in mass, and feeding rates were standardized to the mean FL of juveniles used in the analysis. The dependent variable in the ANCOVA was the feeding rate, and the independent variables were the biomass of large or small copepods and prey taxonomic group. No intercept term was included in the model. Only data from 1995 and 1996 were available for this analysis.

I also conducted an analysis of variance (ANOVA) to test the hypothesis that juvenile salmon stomach fullness indices were not related to diet composition. Data from all 4 years of the study were available for this analysis, because samples collected during and immediately after night were not required. The stomach fullness index was estimated from the residuals from a linear regression of mean stomach contents weight (natural logarithm transformed) on juvenile salmon FL (Perry et al. 1996). Separate analyses were conducted for large copepods, small copepods, and 'other zooplankton', because diet proportions were not independent among prey groups. The independent variable in the analysis was the proportion of the diet composed of each prey group. A class variable was established for diet composition (0-25%, 25-50%, 50-75%, and 75-100%), because graphical analysis indicated a non-linear relationship between stomach fullness index and diet composition.

Three additional ANCOVAs were conducted to test the hypothesis that juvenile salmon condition was not related to diet composition. The dependent variable in the analysis was the mean energy content of juveniles, and the independent variables were mean juvenile salmon FL, mean stomach fullness, and mean proportion (arcsine-square root transformed) of the diet composed of large copepods, small copepods, and 'other zooplankton'. Separate ANCOVAs were conducted for each of the 3 prey taxonomic groups, because diet proportions were not independent among prey groups. Juvenile salmon FL was included as an independent variable in the model, because moisture content of juvenile salmon declines steadily with size on a constant ration (Brett 1974). A class variable was established for the stomach fullness index as previously described based upon whether regression residuals were less than or greater than zero. All two-way interaction terms were initially included in the analysis. A stepwise procedure was used to develop the most parsimonious model. The variance inflation factor was calculated to assess whether multicollinearity may have affected estimation of regression coefficients and their statistical significance (Neter et al. 1989). Net set was used as the sample unit.

Foraging habitat and diet composition

I conducted several ANOVAs to test the hypothesis that zooplankton densities and juvenile salmon feeding rate and diet composition were not different between nearshore and offshore habitats. In the first set of analyses, the dependent variables were total zooplankton biomass, and the densities of large copepods, small copepods, and 'other zooplankton'. In the second set of analyses, the dependent variables were mean stomach fullness index, and mean proportion of the diet (arcsine square root transformed) composed of large copepods, small copepods, and 'other zooplankton'. In all analyses, net set was used as the sample unit, and the independent variables were sampling period and habitat (nearshore versus offshore). Only data from 1995 were used to test for a difference in zooplankton biomass and densities between habitats, because this was the only year that zooplankton sampling was stratified by habitat. In 1995, zooplankton samples were collected at two stations nearshore and two stations offshore every three hours during daylight at each study site. Nearshore zooplankton stations were located near the 20-m isobath, and offshore stations were approximately 2-km from shore in water generally exceeding 200-m depth. Samples of juvenile salmon collected inshore of the 20-m isobath were classified as nearshore.

Effect of juvenile density on feeding and growth rates

Four analyses were conducted to test the hypothesis that juvenile salmon feeding rate and condition were not related to juvenile density. Samples aggregated by site and date formed sample units for these analyses, because juvenile density was estimated over these units. In the first analysis, I tested for a difference in stomach fullness indices among sites with different juvenile salmon densities. The independent variables were mean total zooplankton biomass and juvenile density at each site. In the second analysis, I tested for a difference in the proportion of the diet (arcsine-square root transformed) composed of large calanoid copepods among sites with different juvenile densities. The independent variables were the mean density of large calanoid copepods and juvenile density at each site. In the third analysis, I tested for a difference in the energy content of juvenile salmon among sites with different juvenile densities. The independent variables were mean juvenile salmon FL and juvenile density at each site. Separate analyses were conducted using data from 1996 and 1997, because no sites with high juvenile densities were sampled in 1997. Finally, I also tested for a difference in total zooplankton biomass and density of large calanoid copepods among sites with different juvenile densities.

Interactions between wild- and hatchery-origin juvenile salmon

Two analyses were conducted to examine interactions between wild and hatchery-origin juveniles. In the first analysis, I evaluated the extent of overlap in the spatial distributions of wild- and hatchery-origin juveniles by sampling period and area. Origins of juvenile salmon were determined from recovery of CWT juveniles in 1994-1995 (Willette 1996) and otolith thermal marked juveniles in 1996-1997. In 1994-1995, ratios of tagged to untagged juveniles in each tag-code group were used to estimate the total number of juveniles from each hatchery in each net set. The number of wild juveniles in each net set was estimated by subtracting the number of hatchery juveniles from the total catch. The estimated total numbers of wild- and hatchery-origin juveniles captured were then summed by sampling period and area. In 1996 and 1997, stock composition was estimated by enumerating wild- and hatchery-origin juveniles in random samples taken from each net set and then summing by sampling period and area.

In the second analysis, I examined apparent size-dependent predation losses for wild- and hatchery-origin juveniles. I estimated the growth in length of wild- and hatchery-origin juveniles combined and predicted the length of each fish in the next sampling period assuming constant growth among all groups. I then used Chi-square analysis to test for differences between actual and predicted length-frequency distributions for each group separately. The magnitude of size-dependent predation on each group was then evaluated by comparing differences between actual and predicted length distributions with length distributions of juvenile salmon from predator stomachs collected at the same time. Willette (1999) described the methods used to sample predators and analyze stomach contents. Length distributions of juvenile salmon in stomachs of planktivores (*Theragra chalcogramma* and *Clupea pallasi*) and piscivores\demersal fish (Gadidae, Cottidae, Hexagrammidae, Stichaeidae, Cyclopteridae, Zoarcidae, Bathymasteridae, *Salvelinus spp*, and *Sebastes spp.*) were calculated separately, because Willette (1999) found that these two predator groups tended to select for different sizes of juvenile salmon.

This analysis was only conducted for groups of juvenile salmon that had fully recruited to nearshore habitats at the time samples were collected. In 1996, actual length distributions measured in early July were compared with distributions predicted from lengths measured in early June. In 1997, a unique otolith thermal mark was applied to about 76 million juveniles released from WHN Hatchery, so it was possible to compare actual and predicted length distributions over 4 sampling periods from early May to late June. Otherwise, the analysis for 1997 was limited to comparisons between early and late June.

Results

Juvenile growth and food limitation

Daily rations of juvenile pink salmon in PWS were less than maximum daily ration in late June 1994, late May 1996, and early May 1997 (Tables 1&2). Maximum rations estimated by Brett (1974) were less than daily rations of juveniles in PWS during early Sept. 1994, and early June 1995 and 1997. Growth rates of juveniles in PWS, adjusted for size-selective predation, ranged from 3.5-5.0% body wt day^{-1}. Mortality and apparent growth from size-selective predation during the initial 45-days of marine residence were about 4 times higher in 1994 ($z=-0.085$, $g=0.24$ mm FL day^{-1}) than in 1995 ($z=-0.020$, $g=0.07$ mm FL day^{-1}). Estimated gross growth conversion efficiencies for juveniles in PWS increased from about 30-75% from late May to June, 1994. This trend coincided with a decline in stomach fullness (Table 1), a decline in the proportion of large copepods in the diet (early May 64%; late May 59%; early June 9%; late June 9%; early July 22%; early Sept 43%), and an increase in the proportion of pteropods (early May 0%; late May 0%; early June 7%; late June 14%; early July 10%; early Sept 0%) and 'other' zooplankton (early May 13%; late May 20%; early June 33%; late June 51%; early July 51%; early Sept 35%) in the diet.

Effect of prey type on feeding and growth rates

Feeding rates of juvenile salmon consuming large versus small copepods were significantly different ($R^2=0.698$, df=28, $p<0.001$). The slope of the regression between feeding rate and zooplankton biomass was about 2 times higher for juveniles feeding on large versus small copepods (Fig. 2a). Mean stomach fullness indices were also significantly correlated with the proportion of the diet composed of large copepods ($R^2=0.019$, df=523, $p=0.018$), small copepods ($R^2=0.017$, df=523, $p=0.027$), and 'other zooplankton' ($R^2=0.029$, df=523, $p=0.001$).

Mean stomach fullness index was significantly higher ($p<0.050$) when the proportion of the diet composed of large copepods was greater than 50% compared to <25% (Fig. 2b). Mean stomach fullness index was also significantly higher ($p<0.050$) when the proportion of the diet composed of small copepods and 'other zooplankton' was <25% compared to 25-75%. The energy content of juvenile salmon was positively correlated with the proportion of large calanoid copepods in the diet and negatively correlated with the proportion of small copepods in the diet (Fig. 3). Juvenile salmon FL was also significantly correlated with energy content.

Foraging habitat and diet composition

The mean density of large copepods and the proportion of juvenile salmon diets composed of large copepods were about 50% greater offshore than nearshore during May 1995 (Table 3). In contrast, the proportion of the diet composed of small copepods was significantly higher nearshore than offshore in both May and June 1995, but densities of small copepods were not. During June 1995, total zooplankton biomass was higher offshore than nearshore, mean stomach fullness index was about 2 times higher offshore than nearshore, and the juvenile diets offshore were composed primarily of 'other zooplankton'. In 1996, the proportion of juvenile salmon diets composed of large copepods was again higher offshore than nearshore, and small copepods composed a greater proportion of the diet nearshore (Table 4). In 1997, there were no differences in diet composition of juvenile salmon between nearshore and offshore habitats during any sampling periods, but densities of large copepods in early May were very low and 'other zooplankton' were more abundant than in the previous 2 years (Table 4).

Effect of juvenile density on feeding and growth rates

The mean stomach fullness index of juvenile salmon was not significantly different among sites with different juvenile densities, and the proportion of large copepods in juvenile diets was positively correlated with copepod density (Fig. 4a). The regression slope for high-density sites was significantly lower ($p=0.002$) than for low- or moderate-density sites. Regression intercepts and least-squares mean diet proportions were not different among sites with different juvenile densities. In 1996 and 1997, least-squares mean energy content of juveniles was lower at sites with moderate compared to low juvenile densities, but the difference was only significant (*p*=0.023) in 1996 (Fig. 4b). Juvenile salmon FL was also significantly correlated with energy content. Total zooplankton biomass was significantly correlated (R^2=0.335, df=19, *p*=0.031) with juvenile density in 1996 (low: mean=0.28; moderate: mean=0.36; high: mean=0.56) but not in 1997. Large copepod densities were significantly correlated with juvenile density in 1996 (R^2=0.538, df=19, *p*=0.001; low: mean=3.6; moderate: mean=24.3; high: mean=104.1) and 1997 (R^2=0.251, df=23, *p*=0.013; low: mean=16.7; moderate: mean=36.4).

Interactions between wild- and hatchery-origin juvenile salmon

Juveniles originating from the WHN hatchery composed greater than 80% of the juvenile stock in the Wells\Perry passage area in early May, 1994-1997 (Table 5). In early June 1994, the proportion of WHN juveniles declined rapidly to <30%, and the proportion of wild juveniles increased to >50% of the stock. In 1995-1997, a temporal decline in the WHN stock was not observed, and wild juveniles composed <30% of the stock in this area. Wild juveniles and fish originating from the Cannery Creek Hatchery (CCH) generally composed about 15% and 50% of the stock in the Unakwik area. In eastern PWS, wild juveniles composed 99% of the stock during early May, but by late May fish originating from the Solomon Gulch Hatchery (SGH) composed >40% of the stock.

Comparison of predicted and actual length distributions of wild- and hatchery-origin juveniles indicated that predation losses were probably greater among the smaller individuals present during each sampling period. In early June 1996, CCH and WHN hatchery juveniles exhibited length modes near 4-5 cm FL and wild juveniles near 5-6 cm FL (Fig. 5). In early July 1996, predicted length distributions for CCH and WHN hatchery juveniles were skewed toward smaller sizes compared to actual distributions, whereas predicted length distributions for wild juveniles were skewed toward larger sizes. During this same period, the length modes for juvenile salmon found in the stomachs of planktivores and piscivore\demersal fish were around 4-5 cm FL (Fig. 6). During May 1997, length modes for WHN hatchery juveniles were <6 cm FL, and predicted length distributions were skewed toward smaller sizes compared to actual distributions (Fig. 5). During this same period, length modes for juvenile salmon found in planktivore stomachs were about 4 cm FL, and the length mode for salmon in piscivore\demersal fish stomachs was 5-6 cm FL (Fig. 6). From early to late June 1997, length modes were near 5 cm FL for CCH juveniles, 6 cm FL for wild juveniles, and 8 cm FL for WHN juveniles. In late June, predicted length distributions were skewed toward smaller sizes for CCH juveniles and toward larger sizes for WHN juveniles compared to actual distributions. During this same period, the length mode for juvenile salmon found in piscivore\demersal fish stomachs was around 5 cm FL (Fig. 6). Chi-square tests indicated that all predicted and actual length distributions were significantly different (p<0.004) from each other.

Discussion

Daily rations of juvenile pink salmon in PWS were often near maximum. This conclusion was based on comparison of rations estimated from stomach content analysis and growth rates of juvenile salmon fed to excess in the laboratory. Rations estimated from stomach content analysis were strongly dependent on assumed temperature-specific gastric evacuation rates. I examined the accuracy of my ration estimates by comparing gross growth conversion efficiencies with measured growth rates of tagged fish. Conversion efficiencies were within the expected range except in late June 1994 (Table 2). Actual conversion efficiencies probably vary with ration (Paloheimo and Dickie 1966) and temperature (Brett et al. 1969), but it is unlikely that conversion efficiencies often approach 75% (Biette and Geen 1980). It seems more likely that growth was overestimated in late June 1994. I corrected my growth estimates for size-selective predation by assuming constant predation losses throughout the juvenile period. In early June, juvenile pink salmon were beginning to migrate into neritic habitats and probably suffered strong size-selective predation (Healey 1982a; Willette et al. 1999) that biased growth estimates.

Juvenile pink salmon that consumed large copepods (primarily *Neocalanus*) probably achieved high growth rates, because their high feeding rates sustained high stomach fullness with lower feeding metabolic costs. When feeding rates exceeded gastric evacuation rates, juveniles were able to maintain full stomachs and thus consume higher daily rations. Ration is a function of mean stomach content weight (Eggers 1977), and gastric evacuation rate increases with meal size (Smith et al. 1989). Juveniles that consumed largely *Neocalanus* also exhibited higher estimated energy content (Fig. 3). Energy content estimated from moisture content probably reflected recent feeding rate, because diel changes in moisture content were correlated with stomach fullness and with daily ration when juveniles in the laboratory were fed between maintenance and maximum ration (Parker and Vanstone 1965; Brett et al. 1969). Juveniles consuming *Neocalanus* probably incurred lower feeding metabolic costs, because less active foraging time was required to obtain maximum ration. Metabolic rates of juvenile sockeye doubled from routine rates while feeding and declined by about 13% per hour after cessation of feeding (Brett and Zala 1975). Several investigators have concluded that the relation between food and growth is strongly dependent on the amount of energy required to search for and capture prey (Mann 1966; Paloheimo and Dickie 1966; Warren and Davis 1966; Kerr and Martin 1970).

Neocalanus and other similar size prey were probably more important for sustaining high growth when prey density was below that needed to obtain maximum ration. LeBrasseur (1969) observed no relation between prey size and growth of juvenile chum salmon fed *Calanus*, *Pseudocalanus*, and euphausiids at high ration levels. Similarly, Mills et al. (1989) found no relation between prey size and growth of yellow perch when the fish were fed 40% of their dry weight per day. However, when rations were reduced to 25% of dry weight per day, growth was a function of prey size with peak rates similar to those achieved at the higher ration. In situ growth of juvenile chinook salmon was correlated with densities of zooplankton 1.5-4.5 mm in length but not smaller prey (English 1983). Maximum daily rations were achieved when densities of this size range of prey exceeded about 0.5 g m^{-3}. Maximum rations for juvenile pink salmon in PWS were about 0.5 kJ day^{-1} (Table 2). If 20 hours of daylight were available for feeding each day, feeding rates near 0.025 kJ $hour^{-1}$ were required to achieve maximum ration. Juvenile pink salmon could have acquired this ration feeding on *Neocalanus* if prey densities exceeded 0.5 g m^{-3} or feeding on *Pseudocalanus* if prey densities exceeded 2.5 g m^{-3} (Fig. 2). During the 4 years of this study, peak *Neocalanus* densities measured from vertical net tows were about 0.6 g m^{-3}, but peak *Pseudocalanus* densities were only about 1.5 g m^{-3}. Thus during the *Neocalanus* bloom, juveniles could have probably acquired maximum ration by selecting for *Neocalanus* but without having to search for high-density prey patches. Juveniles feeding on *Pseudocalanus* probably could not have acquired maximum ration without finding very high-density prey patches.

Juvenile pink salmon searched for high-density patches of *Neocalanus* and other similar size prey after the copepod bloom. The proportion of salmon diets composed of large copepods and large copepod densities were typically higher offshore than nearshore (Tables 3 & 4). Juveniles dispersed offshore when *Neocalanus* densities nearshore declined, but dispersion offshore was not correlated with total zooplankton density or stomach fullness (Willette 1999). These observations support Walters et al. (1978) assumption that juveniles must exploit high-density prey patches to achieve the relatively high growth rates observed among juvenile salmon in situ. But, selection for prey sizes that sustain high growth rates is probably equally important when prey densities are within the range typically measured in situ using vertical net tows.

The higher feeding and growth rates achieved by juveniles consuming *Neocalanus* reduced their mortality by minimizing their foraging times in risky habitats, as well as the duration of their vulnerability to size-selective predation. Walters and Juanes (1993) predicted that juvenile foraging times in risky habitats adjacent to refugia are a function of the minimum time needed for growth to a viable size for survival upon emergence from the refuge plus an additional time inversely proportional to predation risk. Within this context, higher feeding rates achieved by juveniles consuming *Neocalanus* resulted in immediate benefits by reducing foraging time and thus predation risk. Additionally, the higher growth rates achieved by these individuals also increased their survival upon emergence from the refuge because of their larger size.

Observed feeding and growth rates of juveniles were only weakly density dependent. Dispersion or aggregation of juveniles in response to varying prey densities eliminated any expected inverse correlation between juvenile density and stomach fullness or diet composition resulting from food limitation (Fig. 4a). Although estimated daily rations were near maximum ration when data were pooled over large spatial scales (Table 2), juvenile energy content was reduced when juvenile densities were high (Fig. 4b). Behavioral responses of juveniles to varying prey availability probably resulted in strong size-dependent mortality rather than reduced growth, because low densities of preferred prey caused foraging juveniles to disperse from nearshore refugia and suffer higher predation losses (Walters and Juanes 1993; Willette 1999).

My analysis of differential size-dependent predation losses among various marked groups of juveniles indicated that smaller fish probably suffered higher mortality than larger fish. Predicted length distributions were always skewed toward smaller sizes compared to actual distributions for groups composed of relatively small fish during the previous sampling period (Fig. 5), and the small sizes of salmon in these groups was similar to the sizes of salmon in predator stomachs (Fig. 6). Actual length distributions resulted from both growth and size-dependent predation losses. I estimated growth from regression of ln(FL) on date for all groups combined, because behavioral responses of juveniles to varying prey densities probably led to minimal growth differences among groups rearing in the same area (Table 5). However, if mortality were higher among smaller individuals (Willette et al. 1999), growth was overestimated by this method. Predicted length distributions were skewed toward larger sizes compared to actual distributions for wild juveniles in 1996 and WHN juveniles in 1997. In both cases, these fish were the largest of the 3 groups during the prior sampling period, and they were generally larger than salmon found in predator stomachs. These differences between actual and predicted distributions probably resulted from overestimation of growth.

Interactions among wild- and hatchery-origin juveniles resulted more from differential size-dependent predation losses among groups than from limitation of feeding and growth rates. The interaction was a function of the relative sizes of individuals among groups after they mixed together. The larger fish within a school were probably sheltered from predation by the presence of smaller fish (Parker 1971). Wild juveniles were generally larger than juveniles released from CCH hatchery, but they were only slightly larger than WHN juveniles during May (Fig. 5). By late June and July, WHN juveniles were typically larger than wild juveniles. This may have resulted from continuing emigration of wild fry from streams bordering PWS (Cooney et al. 1995). During the 2 years of this study, interactions with hatchery-origin salmon probably did not cause higher predation losses among wild salmon. However, the nature of the interaction among groups of juvenile salmon is complex and probably changes from year to year.

Differential size-dependent predation losses are probably amplified when *Neocalanus* densities or ocean temperatures are low. Coherent decadal variations in ocean temperatures and zooplankton biomass affect both the coastal and oceanic ecosystems in the Gulf of Alaska (Emery and Hamilton 1985; Brodeur and Ware 1992; Sugimoto and Tadokoro 1997). The salmon enhancement program in Alaska was initiated after a period of low wild salmon returns and cold winters during the early 1970's. After a regime shift in 1977, ocean temperatures, zooplankton biomass, and salmon production in the region were relatively high (Brodeur and Ware 1992; Hare and Francis 1994). A return to lower salmon production and lower zooplankton stocks may have begun in the early 1990's (Beamish et al. 1998). Cooler winter temperatures will probably delay stream emigrations of wild salmon fry (Cooney et al. 1995) reducing their size relative to hatchery-reared salmon. Concurrent declines in *Neocalanus* density will reduce the carrying capacity of nearshore predation refugia causing juveniles to disperse offshore in search of prey (Willette 1999). Differences in sizes of wild and hatchery-origin juveniles may then lead to greater differential size-dependent predation losses among groups and more variable intra-annual adult returns to the 4 hatcheries and the various streams bordering PWS. Numerical models may enable us to further examine the nature of these processes and determine the efficacy of various hatchery release practices that may minimize differential mortality among groups of juvenile salmon.

Acknowledgements

I would like to thank the numerous staff of the Alaska Department of Fish and Game, University of Alaska Fairbanks, Prince William Sound Science Center, and our charter vessel operators who endured very long work hours and difficult conditions to obtain the samples used in this study. The Prince William Sound Aquaculture Corporation provided much appreciated logistical support for our vessels and staff. This project was funded by the *Exxon Valdez* Oil Spill Trustee Council through the Sound Ecosystem Assessment project. However, the findings presented by the authors are their own and do not represent the position of the Trustee Council.

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Table 1. Mean whole body wet weight (g) and stomach fullness (% body weight) of juvenile pink salmon, mean 2-m ocean temperature (°C), number of sites sampled, and number of specimens analyzed stomach contents and growth or condition during May-Sept., 1994-1997.

Year	Sampling Period	Mean Weight	Stomach Fullness	Ocean Temp.	No. Sites	Sample sizes Diet	Sample sizes Growth
1994	Early May	0.29	2.35	5.3	3	30	119
	Late May	0.57	2.31	7.6	9	74	25
	Early June	1.49	1.40	9.1	29	265	15
	Late June	3.53	0.99	9.9	8	89	14
	Early July	3.84	1.65	12.9	15	154	2
	Early Sept.	22.39	1.52	11.5[1]	8	71	0
1995	Early May	0.26	2.63	6.7	8	1,335	0
	Early June	1.11	2.54	8.8	8	2,112	109
1996	Early May	0.28	2.99	7.3	5	804	734
	Late May	0.56	2.03	10.5	7	968	487
	Early June	0.96	1.92	12.0	8	1,278	877
1997	Early May	0.44	1.56	7.9	1	127	127
	Late May	0.69	3.09	11.3	9	1,067	1,066
	Early June	1.66	2.93	12.7	9	988	982

[1] Mean 0-20 m temperature used due to deeper distribution of larger juveniles.

Table 2. Comparison of growth (kJ day^{-1}) and ration (kJ day^{-1}) of juvenile pink salmon in Prince William Sound with maximum growth (kJ day^{-1}) and ration (kJ day^{-1}) from Brett (1974). Significant differences between maximum and actual rations are indicated in bold. Energy content (kJ g wet weight^{-1}) and gross growth conversion efficiencies (CE) estimated from field data are also indicated.

	Sampling	Field Estimated				Max. (Brett 1974)		
Year	Period	Growth	Energy	Ration	CE (%)	Growth	Ration	Diff
1994	Early May	-	-	0.382 (±0.024)	-	0.108	0.358	0.024
	Late May	0.169	-	0.554 (±0.286)	30.5	0.140	0.467	0.087
	Early June	0.152	-	0.311 (±0.135)	48.7	0.129	0.431	-0.120
	Late June	0.163	-	0.219 (±0.069)	74.6	0.105	0.350	**-0.131**
	Early July	0.119	-	0.515 (±0.159)	23.2	0.138	0.460	0.055
	Early Sept.	-	-	0.550 (±0.155)	-	0.065	0.216	**0.334**
1995	Early May	-	-	0.537 (±0.065)	-	0.166	0.552	-0.015
	Early June	0.165	-	0.618 (±0.136)	26.7	0.133	0.442	**0.176**
1996	Early May	-	4.86	0.708 (±0.159)	-	0.186	0.620	0.088
	Late May	-	4.79	0.605 (±0.128)	-	0.221	0.736	**-0.131**
	Early June	-	4.69	0.656 (±0.155)	-	0.202	0.675	-0.019
1997	Early May	-	4.58	0.291 (±0.024)	-	0.169	0.562	**-0.271**
	Late May	-	4.87	0.853 (±0.367)	-	0.210	0.699	0.154
	Early June	-	4.82	0.903 (±0.232)	-	0.193	0.644	**0.259**

Table 3. Mean total zooplankton biomass (g m^{-3}) and density (no. m^{-3}) of large copepods, small copepods, and other zooplankters at nearshore and offshore stations during May and June, 1995. Also, mean stomach fullness index and proportion of the diet composed of large copepods, small copepods, and other zooplankters for juvenile pink salmon captured nearshore and offshore are indicated. Statistical tests are for a difference between means for nearshore and offshore stations.

Month	Variable	Mean Nearshore	Mean Offshore	*p*-value
Zooplankton density				
Early May	Lg. copepods	89 (14)	137 (9)	0.063
	Sm. copepods	2445 (298)	2578 (199)	0.712
	Other zooplankton	269 (39)	261 (26)	0.860
	Total biomass	0.50 (0.05)	0.58 (0.03)	0.188
Early June	Lg. copepods	15 (14)	54 (13)	0.045
	Sm. copepods	2666 (298)	3489 (267)	0.041
	Other zooplankton	425 (39)	545 (35)	0.025
	Total biomass	0.43 (0.05)	0.63 (0.04)	0.003
Diet composition				
Early May	Lg. copepods	0.44 (0.02)	0.66 (0.07)	0.002
	Sm. copepods	0.41 (0.02)	0.17 (0.07)	0.004
	Other zooplankton	0.14 (0.02)	0.16 (0.07)	0.747
	Stomach fullness index	0.005 (0.002)	0.008 (0.008)	0.726
Early June	Lg. copepods	0.12 (0.02)	0.05 (0.03)	0.042
	Sm. copepods	0.43 (0.02)	0.12 (0.03)	<0.001
	Other zooplankton	0.44 (0.02)	0.83 (0.03)	<0.001
	Stomach fullness index	-0.006 (0.002)	0.006 (0.003)	0.002

Table 4. Mean proportion of the diet composed of large copepods, small copepods, and other zooplankters for juvenile pink salmon captured nearshore and offshore, 1996-1997. Also, mean density (no. m^{-3}) of large copepods, small copepods, and other zooplankters at stations near the 20-m isobath are indicated. Totals refer to mean zooplankton biomass or stomach fullness indices for juvenile salmon. Statistical tests are for a difference between means for nearshore and offshore stations.

		Zoop.	Diet Composition		
Month	Variable	Density	Nearshore	Offshore	*p*-value
1996					
Early May	Lg. copepods	84 (7)	0.50 (0.02)	0.66 (0.06)	0.053
	Sm. copepods	3737 (426)	0.27 (0.03)	0.12 (0.08)	0.117
	Other zooplankton	290 (81)	0.23 (0.03)	0.22 (0.08)	0.870
	Total	0.46 (0.03)	0.004 (0.002)	0.002 (0.004)	0.613
Late May	Lg. copepods	19 (7)	0.06 (0.02)	0.15 (0.04)	0.025
	Sm. copepods	3824 (417)	0.48 (0.03)	0.18 (0.05)	<0.001
	Other zooplankton	680 (78)	0.44 (0.03)	0.66 (0.06)	0.001
	Total	0.35 (0.03)	-0.006 (0.001)	-0.008 (0.003)	0.444
Early June	Lg. copepods	5 (7)	0.01 (0.02)	0.05 (0.03)	0.005
	Sm. copepods	4740 (417)	0.33 (0.03)	0.16 (0.04)	<0.001
	Other zooplankton	1689 (78)	0.66 (0.03)	0.79 (0.04)	0.008
	Total	0.37 (0.03)	-0.013 (0.001)	-0.006 (0.002)	0.004
1997					
Early May	Lg. copepods	11 (8)	0.00 (0.04)	-	-
	Sm. copepods	3083 (1080)	0.22 (0.11)	-	-
	Other zooplankton	1602 (628)	0.77 (0.12)	-	-
	Total	0.26 (0.10)	-0.006 (0.01)	-	-
Late May	Lg. copepods	22 (4)	0.01 (0.01)	0.00 (0.02)	0.219
	Sm. copepods	3240 (571)	0.28 (0.03)	0.29 (0.05)	0.557
	Other zooplankton	1439 (317)	0.70 (0.03)	0.71 (0.06)	0.996
	Total	0.35 0.03)	-0.004 (0.004)	0.001 (0.006)	0.586
Early June	Lg. copepods	37 (4)	0.03 (0.01)	0.00 (0.01)	0.654
	Sm. copepods	4815 (558)	0.14 (0.04)	0.18 (0.03)	0.554
	Other zooplankton	2660 (310)	0.83 (0.04)	0.82 (0.03)	0.861
	Total	0.37 (0.03)	0.001 (0.005)	0.001 (0.004)	0.999

Table 5. Stock composition of juvenile pink salmon by sampling period and area in Prince William Sound, 1994-1997. Estimates based upon recoveries of coded-wire tags in 1994 and 1995 and otolith thermal marks in 1996 and 1997. Acronyms for hatcheries: Armin F. Koernig (AFK), Wally H. Noerenberg (WHN), Cannery Creek (CCH), and Solomon Gulch (SGH).

			Stock Composition (%)					No.	No.
Year	Period	Area	AFK	WHN	CCH	SGH	Wild	tags	Scan
1994	Early May	3	0	83	0	0	17	198	143.4
	Late May	2	0	46	1	2	51	49	59.9
	Early June	3	0	14	13	8	65	27	47.9
		2	0	25	1	3	71	109	226.7
	Late June	3	0	19	24	5	52	30	25.3
		2	0	15	19	4	62	154	226.4
		1	28	3	1	1	67	50	90.9
	Early July	2	0	3	33	0	64	20	31.4
		1	59	3	8	4	25	497	397.6
1995	Early June	3	0	89	1	0	10	271	180.7
1996	Early May	3	0	99	0	0	1	1643	-
	Mid. May	3	0	98	0	0	2	639	-
		4	72	0	17	461	-		
	Early June	3	0	82	0	0	18	832	-
		4	0	15	60	6	19	927	-
	Early July	1-3	18	11	29	10	32	916	-
1997	Early May	3	0	93	0	0	7	374	-
		4	0	2	58	4	36	399	-
		5	0	0	0	1	99	181	-
	Mid May	3	0	69	0	1	30	347	-
		4	0	5	66	16	13	700	-
		5	0	0	0	43	57	467	-
	Early June	3	0	65	11	4	20	567	-
		4	0	0	92	2	6	378	-
		5	0	0	0	25	75	473	-
	Late June	1	36	17	10	7	30	1216	-

List of Figures

Fig. 1. (a) Location of study areas in Prince William Sound, 1994-1997, and (b) total adult returns of wild- and hatchery-origin pink salmon to Prince William Sound, 1962-1998. Approximate numbers of juvenile pink salmon released from each hatchery in recent years is also indicated.

Fig. 2. (a) Feeding rates of juvenile pink salmon consuming large copepods (solid squares and heavy- solid regression line) and small copepods (open circles and light-solid line) in relation to zooplankton biomass. (b) Mean stomach fullness index (and SE) for juvenile pink salmon in relation to the proportion of the diet composed of large copepods (solid circles), small copepods (solid squares), and other zooplankton (open circles).

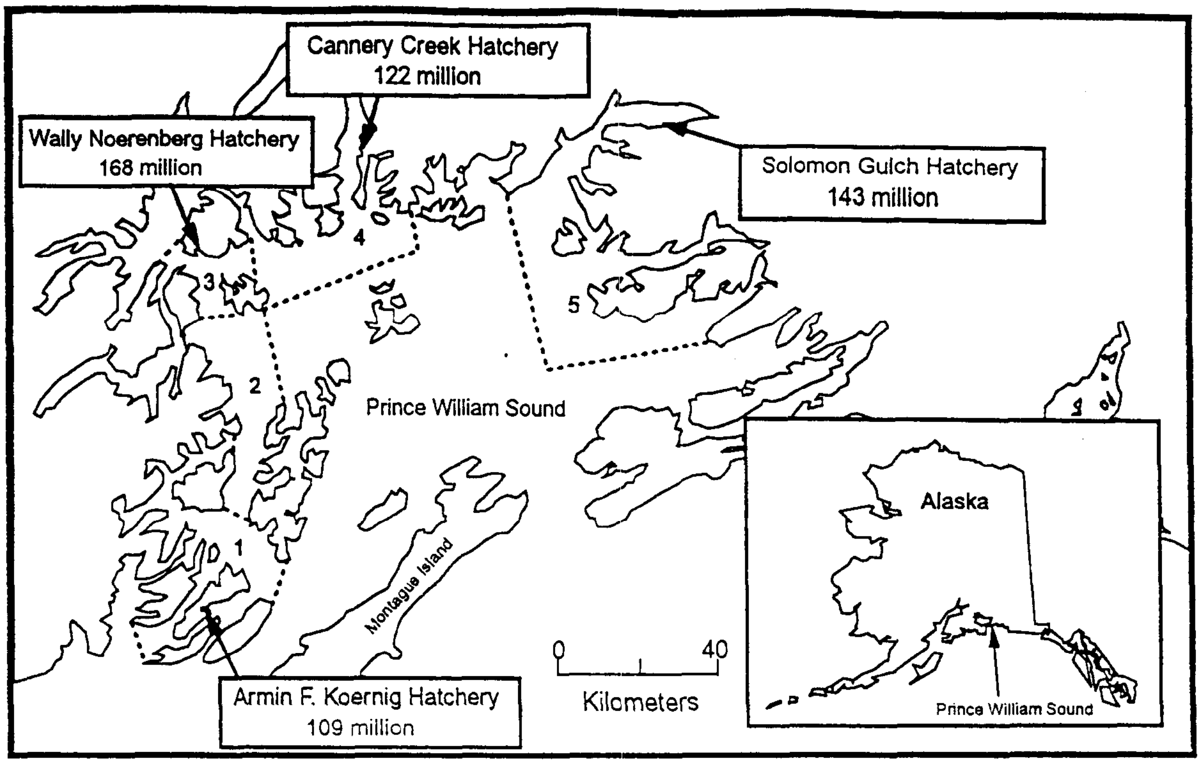
Fig. 3. Relationships between estimated energy content of juvenile pink salmon and the proportion of their diet composed of large copepods and small copepods.

Fig. 4. (a) Relationship between juvenile diet composition and juvenile density (low densities: solid circles; moderate densities: open circles; high densities: solid squares). (b) Mean energy content (and SE) of juvenile pink salmon in relation to juvenile density in 1996 (solid circles) and 1997 (solid squares).

Fig. 5. Length frequency distributions (solid lines) for wild- and hatchery-origin juvenile salmon during 2-week sampling periods, May-July 1996-1997. Dashed lines indicate the length-frequency distribution for each group predicted from the length distribution during the previous period assuming equal growth among groups.

Fig. 6. Length frequency distributions for juvenile salmon found in the stomachs of planktivores (solid line) and piscivores\demersal fish (dashed line) during 2-week sampling periods, May-June 1996-1997.

a.


Cannery Creek Hatchery
122 million
Wally Noerenberg Hatchery
168 million
Solomon Gulch Hatchery
143 million
4
3
5
2
Prince William Sound
1
Montague Island
0
40
Kilometers
Armin F. Koernig Hatchery
109 million
Alaska
Prince William Sound

b.

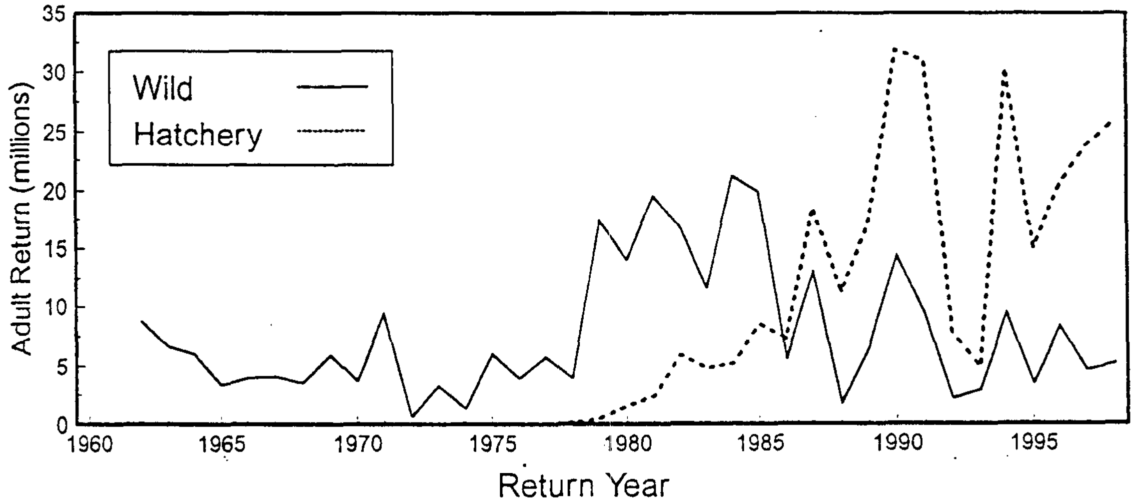

Wild
Hatchery
Adult Return (millions)
0
5
10
15
20
25
30
35
1960
1965
1970
1975
1980
1985
1990
1995
Return Year

Figure 1

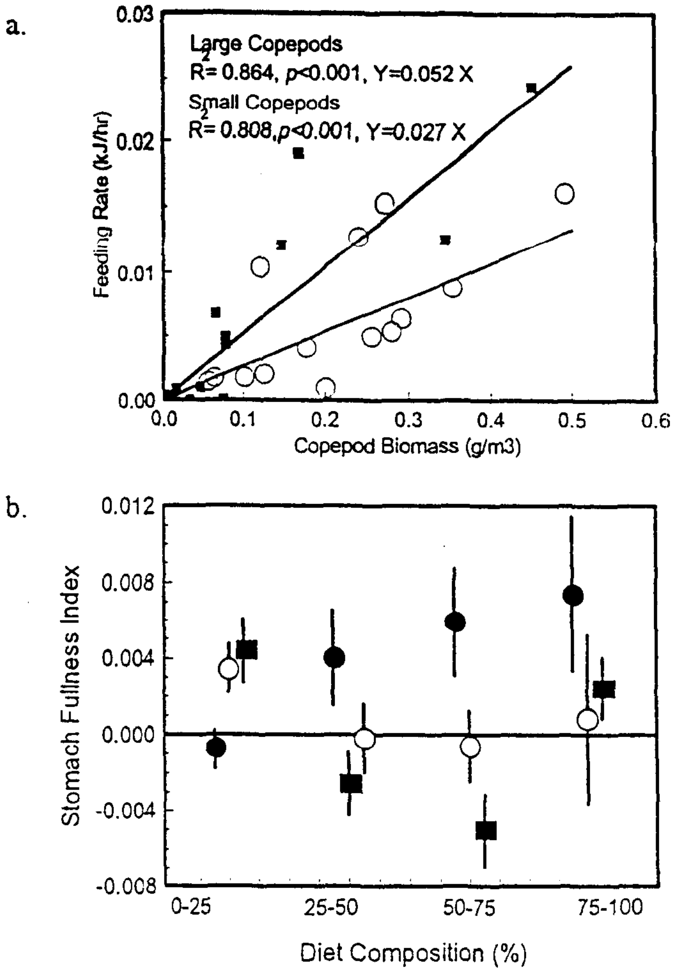

a.
Large Copepods
R^2= 0.864, p<0.001, Y=0.052 X
Small Copepods
R^2= 0.808, p<0.001, Y=0.027 X
Feeding Rate (kJ/hr)
0.03
0.02
0.01
0.00
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Copepod Biomass (g/m3)
b.
Stomach Fullness Index
0.012
0.008
0.004
0.000
-0.004
-0.008
0-25
25-50
50-75
75-100
Diet Composition (%)

Figure 2

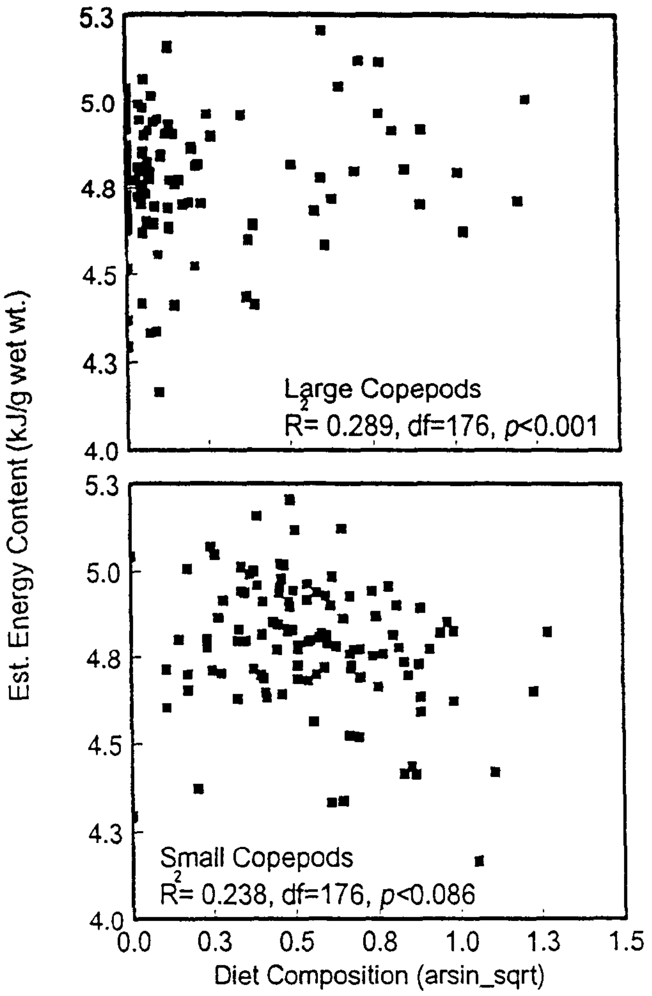

5.3
5.0
4.8
4.5
4.3
4.0
Est. Energy Content (kJ/g wet wt.)
Large Copepods
R^2= 0.289, df=176, p<0.001
Small Copepods
R^2= 0.238, df=176, p<0.086
0.0
0.3
0.5
0.8
1.0
1.3
1.5
Diet Composition (arsin_sqrt)

Figure 3

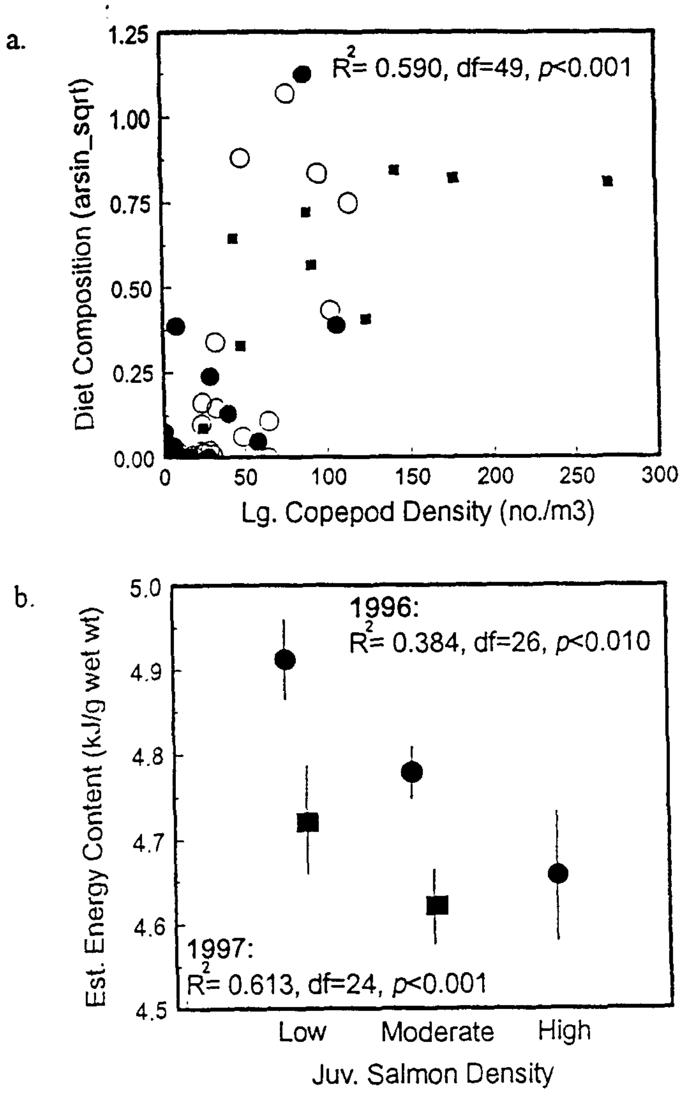

a.
1.25
1.00
0.75
0.50
0.25
0.00
Diet Composition (arsin_sqrt)
R^2= 0.590, df=49, p<0.001
0
50
100
150
200
250
300
Lg. Copepod Density (no./m3)
b.
5.0
4.9
4.8
4.7
4.6
4.5
Est. Energy Content (kJ/g wet wt)
1996:
R^2= 0.384, df=26, p<0.010
1997:
R^2= 0.613, df=24, p<0.001
Low
Moderate
High
Juv. Salmon Density

Figure 4

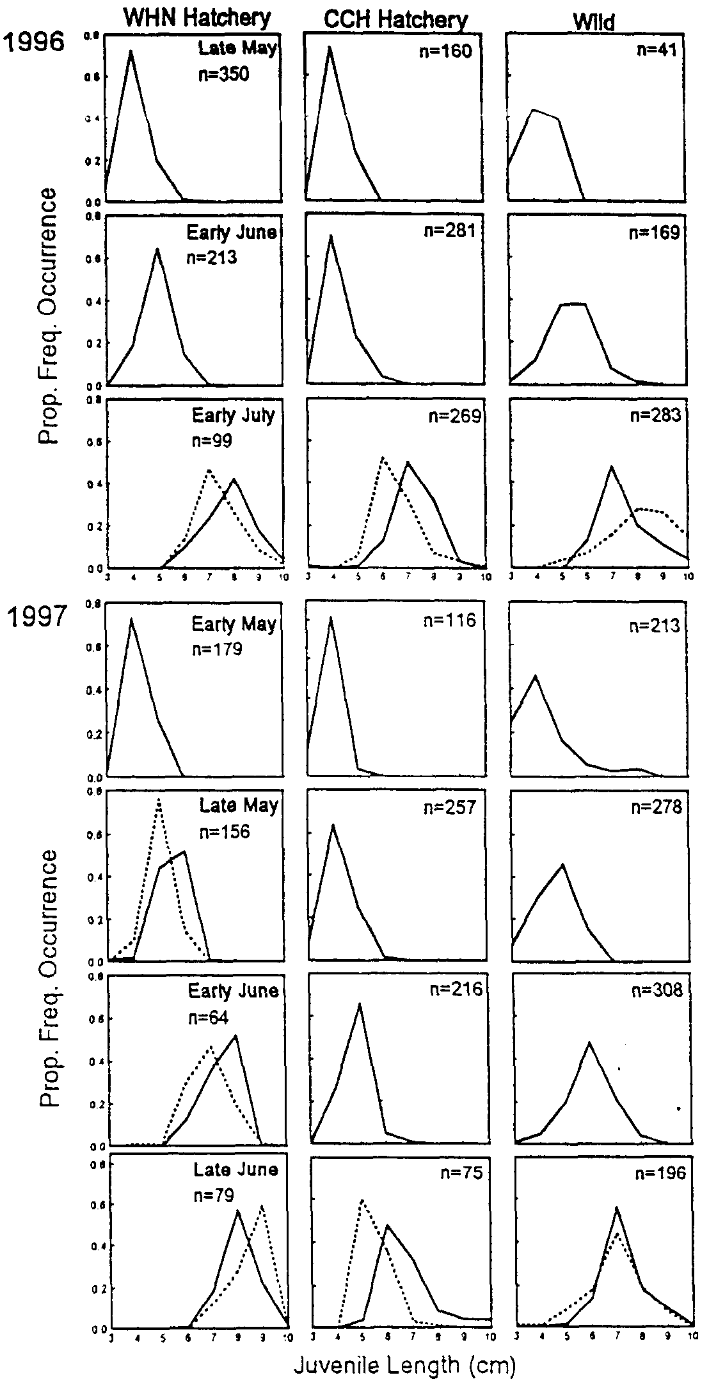

WHN Hatchery
CCH Hatchery
Wild
1996
Late May
n=350
n=160
n=41
Early June
n=213
n=281
n=169
Early July
n=99
n=269
n=283
1997
Early May
n=179
n=116
n=213
Late May
n=156
n=257
n=278
Early June
n=64
n=216
n=308
Late June
n=79
n=75
n=196
Prop. Freq. Occurrence
0.0
0.2
0.4
0.6
0.8
3
4
5
6
7
8
9
10
Juvenile Length (cm)

Figure 5

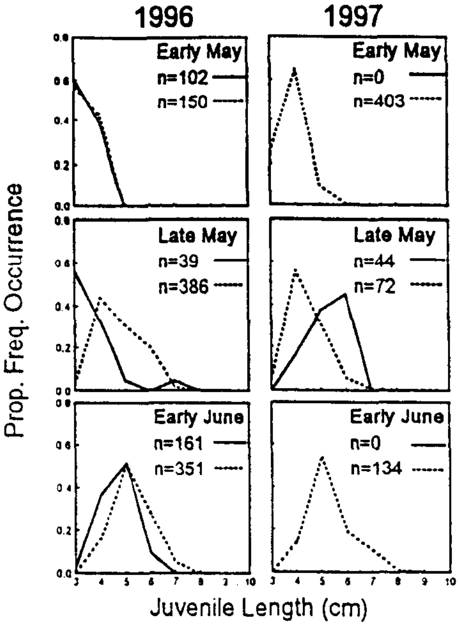

1996
1997
Early May
n=102
n=150
Early May
n=0
n=403
Late May
n=39
n=386
Late May
n=44
n=72
Early June
n=161
n=351
Early June
n=0
n=134
Prop. Freq. Occurrence
0.0
0.2
0.4
0.6
0.8
3
4
5
6
7
8
9
10
Juvenile Length (cm)

Figure 6