Chapter 2

Juvenile Salmon Predation

Exxon Valdez Oil Spill
Restoration Project Annual Report

Sound Ecosystem Assessment: Juvenile Salmon Predation

Restoration Project 97320E
Annual Report

This annual report has been prepared for peer review as part of the *Exxon Valdez* Oil spill Trustee Council Restoration program for the purpose of assessing project progress. Peer review comments have not been addressed in this annual report.

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Study History: This project was initiated under Restoration project 94320E. An annual report was issued in 1994 by Willette, M., E. Debevec, Jay Johnson under the title Sound Ecosystem Assessment: Salmon Predation. The project effort was continued under Restoration Projects 95320E and 96320E. The final year of field sampling for this project in FY97 is the subject of this annual report. A final report will be prepared for project 320E in FY99.

Abstract: This project is a component of the Sound Ecosystem Assessment (SEA) program. SEA is a multi-disciplinary effort designed to acquire an ecosystem-level understanding of the marine and freshwater processes that interact to constrain levels of 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. Our efforts in 1997 focused on estimation of predator abundance, as well as predator behavior and feeding rates in nearshore habitats. Otolith marked juvenile salmon were also recovered to estimate stock composition and test for differences in size and growth of wild and hatchery salmon fry. Predation on juvenile salmon in nearshore habitats appeared to be lower in 1997 compared to 1996. Mean catch per net set at four sites sampled during both years in western PWS was lower for gadids, herring, and dolly varden trout during 1997 compared with 1996. The percent of the diet comprised of juvenile salmon was also lower for all taxonomic groups of potential predators in 1997 compared with 1996. As in previous years, dolly varden trout, Pacific cod and tomcod appeared to be relatively important predators on juvenile salmon in 1997. Further analyses will be conducted over the next year to evaluate the possible causes for these changes. In 1997, the relative abundance of nearshore benthic fish and herring was greater in eastern than western PWS. The proportion of wild- and hatchery-origin juvenile pink salmon emigrating from PWS was estimated from seine sampling and recovery of otolith thermal marks in the southwest passages in late June, 1997. Thirty-two percent of the pink salmon recovered originated from wildstock streams and the remainder from PWS hatcheries. Pink salmon originating from the Armin F. Koernig hatchery comprised the greatest proportion (33%) and those from the Solomon Gulch hatchery the smallest proportion (7%) of the fish sampled. Estimated energy contents indicated that fish originating from the Solomon Gulch hatchery were in the poorest condition. In 1997, sonic tagging methods were used to study the feeding behavior of age 3+ pollock. Two fish were successfully tagged and tracked for three to four days each. Both fish generally remained in the upper 50 m of the water column throughout the period of tracking. Estimated swimming speeds ranged from 0.04 to 0.11 m sec^{-1}. The fish did not exhibit diel vertical migrations or movements inshore at night. Results from field studies conducted since 1994 will be used to construct the SEA pink salmon recruitment model and conduct tests of the SEA predator/prey hypotheses.

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

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Executive Summary

This project is a component of the Sound Ecosystem Assessment (SEA) program. SEA is a multidisciplinary effort designed to acquire an ecosystem-level understanding of the marine and freshwater processes that interact to constrain levels of 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. These hypotheses include the following: (1) predation on juvenile salmon and other age-0 fish is inversely related to the abundance of large calanoid copepods, (2) predation risk is related to the daily foraging times of juvenile salmon, and (3) predation on wild salmon fry is greater when wild fry are mixed with larger hatchery-reared fish. This project was designed to achieve the following objectives: (1) estimate the juvenile salmon consumption rate of fish predators in PWS, (2) estimate the species/size composition of fish predators, and (3) conduct preliminary tests of predator/prey hypotheses. This project also provided logistical support (personnel and equipment) to the SEA herring program.

Our efforts in 1997 focused on estimation of predator abundance, as well as predator behavior and feeding rates in nearshore habitats. Studies were conducted at eight nearshore sites during each of three date periods in PWS during May and June. Four of these sites were located in areas dominated by wild salmon in eastern PWS and four in areas dominated by hatchery salmon in western PWS. Each nearshore study site consisted of an approximately 3000 m long segment of shoreline. Potential predators on juvenile salmon were sampled using variable-mesh gillnets. Sampling was conducted at two stations every 3 hours throughout a 12-hour period spanning the night. Otolith marked juvenile salmon were also recovered at each site to estimate stock composition and test for differences in size and growth of wild and hatchery salmon fry. Laboratory analyses of these samples is still ongoing.

In general, predation on juvenile salmon in nearshore habitats appeared to be lower in 1997 compared to 1996. Mean catch per net set at four sites sampled during both years in western PWS was lower for gadids, herring, and dolly varden trout during 1997 compared with 1996. The percent of the diet comprised of juvenile salmon was also lower for all taxonomic groups of potential predators in 1997 compared with 1996. As in previous years, dolly varden trout, Pacific cod and tomcod appeared to be relatively important predators on juvenile salmon in 1997. But unlike previous years, age 1-2 pollock apparently consumed only small amounts of juvenile salmon. Further analyses will be conducted over the next year to evaluate the possible causes for these changes. In 1997, the relative abundance of nearshore benthic fish and herring was greater in eastern than western PWS. The relative abundance of adult salmon and dolly varden trout increased from May to June in both areas sampled. For tomcod, the proportion of the diet comprised of juvenile salmon was significantly greater in western than eastern PWS, but there was no difference in the proportion of the diet comprised of salmon between these two areas for the other taxonomic groups.

The proportion of wild- and hatchery-origin juvenile pink salmon emigrating from PWS was estimated from seine sampling and recovery of otolith thermal marks in the southwest passages in late June, 1997. Thirty-two percent of the pink salmon recovered originated from wildstock streams and the

remainder from PWS hatcheries. Pink salmon originating from the Armin F. Koernig hatchery comprised the greatest proportion (33%) and those from the Solomon Gulch hatchery the smallest proportion (7%) of the fish sampled. Estimated energy contents indicated that fish originating from the Solomon Gulch hatchery were in the poorest condition.

In 1997, sonic tagging methods were used to study the diel feeding behavior of age 3+ pollock. Two fish were successfully tagged and tracked for three to four days each. Both fish generally remained in the upper 50 m of the water column throughout the period of tracking. Estimated swimming speeds ranged from 0.04 to 0.11 m sec^{-1}. The fish did not exhibit diel vertical migrations or movements inshore at night. Results from field studies conducted since 1994 will be used to construct the SEA pink salmon recruitment model and conduct tests of the SEA predator/prey hypotheses.

Introduction:

This project is a component of the Sound Ecosystem Assessment (SEA) program. SEA is a multidisciplinary effort to acquire an ecosystem-level understanding of the marine and freshwater processes that interact to constrain levels of pink salmon and herring production in Prince William Sound (PWS). Pink salmon runs to PWS failed in 1992 and 1993, and herring biomass dropped sharply in 1993. These run failures have drastically affected the economy of the PWS region which is largely based on the salmon and herring resources. In 1992, pink salmon returns were low in Kodiak, Lower Cook Inlet, and PWS, but pink salmon returns in 1993 were low only in PWS. Low returns of hatchery-produced salmon in both years indicates that the failures were likely caused by processes occurring during the juvenile lifestage. Damage assessment studies on juvenile pink salmon in PWS have demonstrated that growth during the juvenile lifestage is related to survival to adult (Willette et al. 1994). Growth rates of juvenile salmon were estimated in 1991 and 1992 after the fish were released from hatcheries. Juvenile growth and ocean temperatures were low in PWS during the early marine period in 1991. However, in 1992 juvenile growth and ocean temperatures were near average; although, zooplankton abundance was very low. The growth of juvenile fishes is believed to be related to survival, because slow-growing individuals are vulnerable to predators for a longer time (Parker 1971; Healey 1982; West and Larkin 1987). The growth and mortality rates of juvenile salmon released into PWS in 1992 suggests that a change in predation rate may have contributed to the observed run failures.

During phase I of SEA, pink salmon research focused on identification of the principal species preying on pink salmon and the processes affecting rates of predation. Phase I results indicate that predation by pelagic pollock (age 3+) and seabirds may account for only 15-25% of probable losses of juvenile salmon (Willette et al. 1995b). However, results from an experimental release of large juvenile pink salmon from Wally H. Noerenberg Hatchery suggests that high mortality likely occurred among an early release of small juvenile pink salmon during May, 1994 (Willette et al. 1995a). Age 3+ pollock and squid were the most abundant species in net catches during May, 1994 (Willette et al. 1994b). The following three hypotheses have been developed from our phase I results: (1) predation by age 3+ pollock in offshore habitats was underestimated in 1994, (2) age 3+ pollock that target juvenile salmon in nearshore habitats account for the majority of the predation losses and these predators were not sampled adequately in 1994, (3) other nearshore fish predators not sampled in 1994 account for the majority of the predation losses, and (4) high condition of the late release group resulted in differential mortality between early and late releases after early June.

Several factors may have resulted in underestimation of juvenile salmon consumption by pelagic age 3+ pollock. Pollock biomass may have been underestimated due to vessel avoidance, occurrence of pollock in the surface layer (0-5m) that was not surveyed, and occurrence of pollock below 125 m depth that was not surveyed. These questions are being addressed by project (97320N). In addition, pollock food consumption may have been underestimated if the fish are glut feeding in the surface layer then migrating to depth to rest. This project conducted sonic tagging studies in FY97 to evaluate the migratory behavior of age 3+ pollock. Sonic telemetry has been used successfully to investigate the daily activity and movement patterns of juvenile Atlantic cod (Clark and Green 1990). During summer, these fish migrated between a warm surface layer to feed at night and a deep cold layer to rest during the day. Much of our effort in FY97 focused on sampling predators in nearshore habitats that may not have been adequately sampled in previous years. This involved sampling with variable mesh gillnets to obtain samples for stomach contents analysis and estimate the species\size composition of potential predators on juvenile salmon.

This project also collected samples to evaluate whether condition-dependent predation may lead to differential mortality of juveniles rearing in nearshore habitats. If condition-dependent predation occurs the presence of large numbers of enhanced salmon may adversely affect wild salmon during the early marine period. An inverse relationship between whole body energy content and fry density at three sites sampled in 1995 suggests that growth may be density-dependent (Paul and Willette 1996). All juvenile pink salmon released from PWS hatcheries will be otolith thermal marked in FY97 providing an essential tool for these investigations. Seine sampling of juveniles emigrating from PWS was also initiated in FY97. It is anticipated that this effort will provide estimates of the proportions of wild- and hatchery-origin juveniles as well as the relative abundance of juveniles emigrating from the Sound (Karpenko 1998). This data will be used to validate the SEA pink salmon recruitment model.

Objectives:

1. Refine estimates of juvenile salmon consumption by pelagic pollock.

2. Estimate the species/size and diet composition of potential predators on juvenile salmon in nearshore habitats.

3. Evaluate condition-dependent predation among wild and hatchery salmon, and estimate the proportions of wild- and hatchery-origin juvenile salmon emigrating from PWS.

4. Use field data to evaluate SEA predator-prey hypotheses.

Methods:

Objective 1:

A sonic tagging study was conducted to examine the diel behavior of pelagic age 3+ pollock during the spring bloom period. Two pollock were tagged and tracked continuously for a total of eight days in June 1997. Fish were collected using a small-mesh purse seine (250 m x 30 m, 1.5 cm stretch mesh web) deployed from a commercial seine vessel. Fish were placed in a 30-gal. container and anesthetized with MS-222. A Vemco™ V16 depth sensitive sonic tag was attached to the fish between the second and third dorsal fin segment using Kevlar line and suture needles. Each fish was held until recovered (less than 3 minutes) prior to release. A global positioning system (GPS) was used to determine position. Tracking of position and depth of the fish commenced immediately upon release, using the Vemco™ V60 directional receiver operated from a 7 m vessel. Depth and position readings were recorded at least every 15 minutes and whenever any detectable rapid movements occurred. CTD casts were made frequently to determine the temperature gradient in the water column occupied by the tagged fish.

The swimming speed of each fish was estimated from movements of the fish relative to measured current velocities. A drogue and a GPS were employed to calculate current velocity. The drogue, which was connected by a thin Kevlar line to a small lighted buoy, was periodically placed in the water column at the approximate depth of the tagged fish. Initial positions of both the drogue and the fish were simultaneously recorded. After a period of at least 30 minutes, the positions of both the fish and the drogue were again recorded as well as elapsed time. These data were used to calculate the vector of the current at the depth of the tagged fish and the vector of the fish. These vectors were used to calculate the swimming speed of the fish.

Objective 2:

Investigations of predator/prey coupling in the nearshore zone were continued in FY97. Eight sites were sampled during three 9-day sampling trips in May and June (Figure 1, Table 1). Acoustic and net sampling were conducted every three hours from approximately 9 pm to 9 am each day. Project 97320N conducted acoustic surveys utilizing side-looking (420kHz) and downlooking echosounders (120kHz). Acoustic data was collected on one alongshore transect on each three hour cycle to estimate the abundance of predators and juvenile salmon in the nearshore zone. Acoustic data was also collected along five transects perpendicular to shore to relate nearshore and offshore predator abundances. A purse seine vessel sampled fish in the upper 20 m of the water column in nearshore areas with bottom depths greater than 20 m. The seine vessel deployed a small-mesh purse seine (250 m x 30 m, 1.5 cm stretch mesh web) holding a hook with the seine open in the direction of the prevailing current for 20 minutes. In nearshore areas shallower than 20 m, variable mesh sinking and floating gill nets (150 m, 1.5 cm to 10 cm stretch mesh) were used to sample fish predators. These gear were deployed from an approximately 6 m aluminum skiff. Each gill net was attached to the beach and set perpendicular to shore. A hotel boat provided room and board for field sampling crews. All sample processing was conducted on board the hotel boat by a single processing crew.

Processing of fish samples from each net set occurred in two stages following procedures outlined by Livingston (1989) and Dwyer et al. (1987). If less than 300 fish were captured, all fish in the catch were enumerated by species. If a large number of fish were caught, species composition was estimated from a random sample of 300 individuals. Fish greater than 150 mm FL were processed differently than those less than 150 mm FL. Fish less than 150 mm FL were identified to the lowest possible taxonomic level. A sample of 30 individuals from each species was preserved in 10% buffered formaldehyde for later analysis of stomach contents under project 97163 (Forage

Fish Influence on Recovery of Injured Species). The purpose of these studies is to examine diet overlap among forage fish.

For large fish (greater than 150 mm FL), a randomly selected sample (n=60) from each net set and each species was taken. The stomach was excised, placed in a cloth bag, and preserved in 10% buffered formaldehyde for later analysis of stomach contents. Fish showing evidence of regurgitation were not included in the sample. Fork length was measured to the nearest millimeter. Weight was measured to the nearest gram when conditions permitted. Sex and sexual maturity was recorded. Later in the laboratory, total stomach contents wet weight was measured to the nearest .01 gram. Invertebrate prey in the gut were generally identified to the family level. Fish in the gut were identified to the lowest possible taxonomic level, enumerated, and measured to the nearest millimeter. The proportion of total stomach contents in each taxonomic group was visually estimated. Stomach fullness was expressed as a proportion of fish body weight. In cases where distinct size classes occurred within species, stomach contents analysis was conducted for each size class as described above. Size related shifts in diet toward piscivory have been noted in several species of gadoid fishes, including Pacific cod (*Gadus macrocephalus*) (Livingston 1989), walleye pollock (*Theragra chalgogramma*) (Dwyer et al. 1987), Atlantic cod (*Gadus morhua*) (Daan 1973), Pacific whiting (*Merluccius productus*) (Livingston 1983), and silver hake (*Merluccius bilinearis*) (Langton 1982).

An analysis of variance was conducted to test for differences in the natural-logarithm transformed mean catch per net set of potential predators on juvenile salmon by date period (5/13-5/21, 5/26-6/3, and 6/10-6/18) as well as between the four sites in western and eastern PWS, respectively. An analysis of variance was also conducted to test for differences in the natural-logarithm transformed mean catch per net set of potential predators between 1996 and 1997. Only four sites in western PWS which were sampled in both years using the same gear type were included in the analysis.

An analysis of variance was conducted to test for differences in the mean percent of predator diets comprised of juvenile salmon among three date periods in May and June. Data were arcsin square root transformed prior to conducting the test (Zar 1984). Several species of nearshore benthic fish (*Hemilepidotus hemilepidotus, Myxocephalus verrucosus, Hexagrammos decagrammus, Hexagrammos octogrammus, Blepsias bilobus*) were pooled in the analysis All specimens were included in the analysis to examine changes in diet for the population within each taxonomic group as a whole.

Objective 3:

At each site, two samples (n=20) of juvenile salmon were obtained with a small mesh purse seine (10 m x 40 m, 2 mm mesh) deployed from an approximately 4 m skiff every three hours. All samples were frozen as soon as possible after collection. At each site, CTD and zooplankton samples (20m vertical tow, 243 um mesh) were also collected in association with each fry sample to evaluate environmental conditions. In the laboratory, the otolith was extracted from each juvenile pink salmon, length was measured to the nearest millimeter, wet weight to the nearest .01 g and stomach contents weight to the nearest milligram. The proportion of total stomach contents weight in three taxonomic groups (large calanoid copepod (>2.5 mm), small calanoid copepod (<2.5 mm), and 'other' prey was visually estimated.Otolith thermal marks were used to determine the wild or hatchery-origin of the fish. Zooplankton samples were subsampled with a stimpel pipette and zooplankton enumerated into the following groups: large calanoid copepod (>2.5 mm), small calanoid copepod (<2.5 mm), and 'other' zooplankters.

The proportion of wild- and hatchery-origin juvenile pink salmon emigrating from PWS was estimated from seine sampling at seven sites in the southwest passages of PWS during late June. A purse seine vessel sampled fish in the upper 20 m of the water column in nearshore areas with bottom depths greater than 20 m. The seine vessel deployed a small-mesh purse seine (250 m x 30 m, 1.5 cm stretch mesh web) holding a hook with the seine open in the direction of the prevailing current for 20 minutes. A sample (n=100) of juvenile salmon was taken from each net set and immediately frozen for later laboratory analysis. In the laboratory, the otolith was extracted from each juvenile pink salmon, length was measured to the nearest millimeter, headless stomachless wet weight to the nearest 0.01 mg and stomach contents weight to the nearest 0.01 mg . Each headless stomachless fish was dried to a constant weight at 80° C and then weighed to the nearest 0.01 mg. Energy content was estimated from moisture content using data provided by Parker and Vanstone (1966).

Objective 4:

See appendix I.

Results:

Objective 1:

The first fish was tagged at Unakwik Inlet at 0230 on May 31, 1997 and was tracked until 0225 on June 4, 1997. After release the fish immediately swam to a depth of 14 m and remained within a few meters of this depth for several hours. After this time any changes in depth were generally gradual. The fish ranged from 3 to 19 m in depth over the 4-day tracking period, averaging 8.67 m (sd = 3.05 m). The fish covered 14.5 km of horizontal distance over the tracking period but never moved more than 3.5 km from the original point of capture. The fish generally remained within the thermocline at temperatures ranging from 6-10 °C, in waters where the bottom depth exceeded 100 m. The results from two drogue-swimming speed trials indicated that the tagged fish was actively swimming at 0.08 and 0.09 m s^{-1}. No diel patterns of vertical migration or movements inshore at night were observed.

A second fish was tagged at Sheep Bay on June 12, 1997 at 0100 and was tracked until 0030 on June 16, 1997. After release the fish swam to a depth of about 35 m and then quickly moved to a depth of 13 m. The fish then began a gradual descent reaching about 68 m at 2300 hrs on June 16. By 0030 on June 17, the fish had ascended to around 45 m in 60 m of water. It remained approximately at this depth throughout June 17. On June 18 the fish made two rapid descents and ascents in 60 and 70 m of water. Both of these descents took the fish very near to the bottom, and both ascents took the fish back to around 50 m depth. On the last full day of tracking the fish made multiple descents and ascents that were 5-10 m in magnitude. The mean depth of the fish for the duration of the tracking period was 43.6 m (sd = 11.41 m) with a range from 13 to 72 m. It was generally below the thermocline in water approximately 5 °C. No diel patterns of vertical migration or movements inshore at night were observed.

The horizontal movements of the fish tagged at Sheep Bay were similar to those of the fish tracked at Unakwik Inlet. Both fish remained within 5 km of the release point and moved a total of less than 20 km. Multiple drogue-swimming speed trials indicated that swimming speeds averaged 0.067 m s^{-1} (sd = 0.028 m s^{-1}) with a range from 0.040 to 0.110 m s^{-1}. No trends between proximity to shore and time of day were observed and no trends between pollock position and temperature were observed.

Objective 2:

Nearshore benthic fishes (rockfish, sculpins, greenlings, etc.), gadids (Pacific cod, tomcod, and black cod) and herring were the most abundant taxonomic groups in nearshore gill net catches in 1997 (Table 2). The relative abundances of nearshore benthic fishes, gadids and herring were significantly greater ($P<0.01$) in eastern than western PWS in 1997 (Figure 2). In addition, the relative abundance of gadids increased from May to June in eastern PWS but not in western PWS (Figure 2). The relative abundance of adult salmon and dolly varden trout increased significantly ($P<0.01$) from May to June in both areas sampled. Comparison of relative abundances of fishes between 1996 and 1997 at four western PWS sites indicated significantly greater ($P<0.01$) abundances of gadids, herring and dolly varden trout in 1996 (Figure 3).

Approximately 3,400 stomach samples from potential predators on juvenile salmon were examined in 1997. The mean proportion of the diet comprised of juvenile salmon was substantially lower in 1997 than in 1996 for all taxonomic groups of potential predators (Table 3). The mean proportion of tomcod diets comprised of juvenile salmon decreased significantly ($P=0.001$) from May to June, 1997 (Table 3). The mean proportion of benthic fishes diets comprised of juvenile salmon was greatest during late May, 1997 (Table 3). For the other taxonomic groups included in the analysis, there were no significant differences in the mean proportion of the diet comprised of juvenile salmon between the three date periods (Table 3). For tomcod, the mean proportion of the diet comprised of juvenile salmon was significantly greater ($P<0.01$) in western (13.5 %) than eastern PWS (1.3 %) but there was no difference ($P>0.05$) in the proportion of the diet comprised of salmon between these two areas for the other taxonomic groups.

Objective 3:

Laboratory analyses of juvenile pink salmon samples collected at each nearshore study sites in 1997 are ongoing. Therefore, a complete dataset from 1997 is not currently available for evaluation of condition-dependent predation on juvenile salmon. In 1997, total zooplankton biomass in the passages adjacent to each study site peaked in mid-May and thereafter ranged from approximately 0.1-0.3 g m^{-3} (Figure 4a). The abundance of large calanoid copepods ranged from 0-100 m^{-3} and did not exhibit a clear seasonal decline (Figure 4b). The abundance of small copepods and 'other' zooplankters exhibited a peak in mid-May followed by a general decline (Figures 4c and 4d).

Thirty-two percent of the juvenile pink salmon sampled in the southwest passages of PWS during late June, 1997 originated from wildstock streams and the remainder from PWS hatcheries. Pink salmon originating from the Armin F. Koernig hatchery comprised the greatest proportion (33%) and those from the Solomon Gulch hatchery the smallest proportion (7%) of the fish sampled (Figure 5). Estimated energy content (derived from moisture content) ranged from approximately 4.6-5.0 KJ g^{-1} (Figure 5). Estimated energy content was generally greater in 1996 than in 1997, and the fish originating from the Solomon Gulch hatchery appeared to be in the poorest condition during both years (Figure 5).

Objective 4:

See appendix I.

Discussion:

Sampling with fixed gear in nearshore habitats revealed an assemblage of fish species that may be important predators on juvenile salmon. The species composition of this assemblage was generally similar between 1996 and 1997 (Table 2). Fixed gear sampling in 1997 consisted of sinking and floating variable-mesh gillnets deployed from the shore in nearshore habitats. These gear appeared to be very efficient for capturing potential predators in shallow nearshore habitats.

In general, predation on juvenile salmon in nearshore habitats appeared to be lower in 1997 compared with 1996. Mean catch per net set at four sites sampled during both years in western PWS was lower for gadids, herring, and dolly varden trout during 1997 compared with 1996 (Figure 3). The percent of the diet comprised of juvenile salmon was also lower for all taxonomic groups of potential predators in 1997 compared with 1996 (Table 3). The cause of these changes is unclear at this time.

As in previous years, dolly varden trout (*Salvelinus malma*), age 1-2 Pacific cod (*Gadus macrocephalus*) and Pacific tomcod (*Microgadus proximus*) appeared to be relatively important predators on juvenile salmon (Willette et al. 1995b, 1996b, 1997). However, unlike previous years age 1-2 pollock apparently only consumed small amounts of juvenile salmon (Table 3). Bakshtanskiy (1964) concluded that juvenile pollack (*Pollachius virens*) and cod (*Melanogrammus morhua morhua*) were important predators on juvenile pink and chum salmon in the White Sea. He observed that juvenile pink and chum salmon were at times driven from nearshore nursery habitats by large schools of juvenile pollack and cod. Consumption of juvenile salmon by nearshore benthic fish and herring appeared to increase in early June, 1996, but this pattern was not apparent in 1997 (Table 3). Bakshtanskiy (1964, 1965) concluded that predation by herring largely determined survival of juvenile pink and chum salmon in the Barents Sea and White Sea. Predation by herring and pollock on juvenile salmon has also been observed in Alaska (Thorsteinson 1962, Armstrong and Winslow 1968).

Mean catch per net set of herring and age 1-2 pollock tended to increase from May to June in 1996 (Willette et al. 1997). A similar seasonal increase in net catches was observed for all gadids in eastern PWS in 1997, but no seasonal increase in relative abundance was observed for herring or gadids in western PWS in 1997 (Figure 2). Rogers et al. (1986) noted a substantial seasonal increase in fish species diversity and density in PWS. In winter, fish distributions shifted further offshore and deeper in the water column (Rogers et al. 1986). Seasonal migrations of fish into deeper water in winter and shallow water in summer are well known (Trout 1957, Alverson 1960, Jean 1964, Heeseen 1983). These seasonal shifts in distribution may be related to temperature, light or food abundance (Laevastu and Hela 1970). Seasonal changes in the vertical distribution and activity patterns of cod have been related to seasonal stratification of the water column (Clark and Green 1990).

Sonic tagging studies of age 3+ pollock behavior suggest that this technique may be used effectively on this species. These studies were initiated to determine whether age 3+ pollock were glut feeding on large calanoid copepods in the surface layer or on juvenile salmon in nearshore habitats and then descending to depth for gastric evacuation. The results from our limited studies in 1997 indicated that adult pollock were not vertically migrating or moving inshore at night. The fish generally remained in the surface layer near the bottom of the thermocline. However, acoustic data collected by project 97320N and our net catch data indicated relatively low abundances of adult pollock in the surface layer during May-June 1997. Results from previous years indicated that adult pollock only remained in the surface layer when the abundance of macrozooplankton was relatively high during May and early June (Willette et al. 1995b, 1996b, 1997). In 1997, adult pollock were in relatively low abundance in the surface layer suggesting that macrozooplankton may not have been present at sufficient densities for profitable feeding. The first fish was not tagged until June 12, because of low pollock abundances and the resulting difficulties catching fish for the study. Therefore, the results from the present study may not be representative of the feeding and migratory behavior exhibited by adult pollock feeding on macrozooplankton during the peak of the bloom.

Conclusions:

1. Predation on juvenile salmon appeared to be lower in 1997 compared with 1996.

2. Dolly varden trout, Pacific cod, and tomcod appeared to be relatively important predators on juvenile salmon in nearshore habitats in 1997.

3. Catches of juvenile pink salmon emigrating from PWS appeared to be dominated by hatchery-origin fish. Estimated energy content indicated that fish originating from the Solomon Gulch hatchery were in the poorest condition.

4. Sonic tagging of age 3+ pollock appears to be an effective method for studying the behavior of these fish. The fish tagged in 1997 did not exhibit diel vertical migrations or movements inshore at night.

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Table 1: Dates and sites where sampling was conducted in nearshore habitats in Prince William Sound during May-June 1996-1997. See figure 1 for locations of sampling areas.

Year	Area	Dates Sampled
1996	501	May 3, May 6, June 5
	502	May 4, May 7, May 24, June 1
	525	May 5, May 8, May 19, May 23, June 2, June 8
	504	May 25, June 6
	506	May 20, June 7
	586	May 21, June 3
	587	May 22, June 4
1997	502	May 19, June 1
	505	June 16
	525	May 20, June 2, June 17
	585	May 15, May 28, June 12
	586	May 17, May 30, June 14
	587	May 18, May 31, June 15
	588	May 13, May 26, June 10
	589	May 14, May 27, June 11
	590	May 16, May 29, June 13

Table 2: Mean catch per net set for various fish taxonomic groups in nearshore habitats in Prince William Sound during May and June, 1996-1997 .

	1996			1997		
Species	n	Mean	SE	n	Mean	SE
Sculpins, gunnels, etc.	86	1.6	0.11	107	0.5	0.98
Pacific cod, tomcod	122	3.4	0.35	142	1.9	4.51
Flatfish	8	1.0	0.00	40	0.2	0.60
Greenlings	155	2.6	0.17	187	1.0	1.29
Rockfish	149	6.3	0.83	212	3.7	6.58
Herring	130	87.8	36.90	113	111.5	1256.52
Pollock	63	5.7	1.44	63	0.7	2.89
Adult Salmon	30	2.5	0.58	24	0.1	0.71
Sandlance, capelin	1	1.0	-	0	0	0
Dolly Varden	48	4.2	0.76	49	0.4	2.04
Squid	15	1.6	0.36	13	0.1	0.25

Table 3: Mean percent of diet comprised of juvenile salmon for several fish taxonomic groups during three time periods in northwest Prince William Sound during 1996 and 1997. Benthic fishes include various species of sculpin and greenlings. Statistical test for changes in the mean diet percentage comprised of juvenile salmon among time periods. All specimens included in the analysis.

Date	Pacific Herring	Pacific Cod	Pacific Tomcod	Pollock (age 1-2)	Pollock (age 3+)	Dolly Varden	Benthic Fishes
1996							
5/3 - 5/9	.19	14.68	25.00	20.33	1.21	-	.39
5/19-5/26	.60	15.16	25.54	11.56	1.61	65.69	0
6/1 - 6/9	8.31	24.12	14.52	9.42	1.50	28.59	5.70
P-value	0.043	0.634	0.638	0.556	0.937	0.027	0.057
1997							
5/13 - 5/21	0.00	0.00	15.75	0.27	0.00	0.00	0.06
5/26- 6/3	1.01	10.29	6.51	0.00	0.00	25.67	1.35
6/10 - 6/18	0.00	0.00	0.00	0.00	0.00	26.63	0.57
P-value	0.156	0.425	0.001	0.750	1.000	0.373	0.024

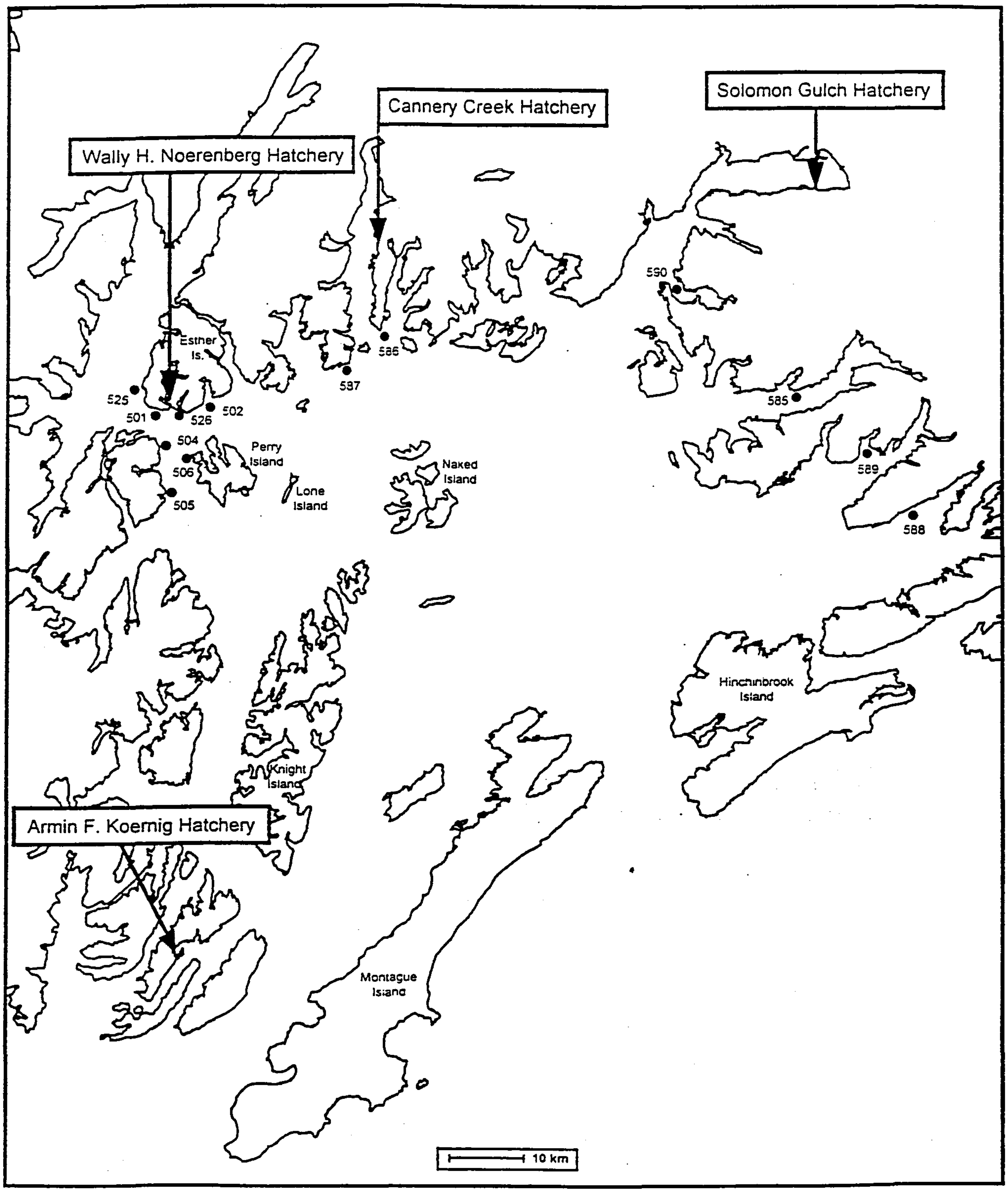


Figure 1: Study sites sampled in Prince William Sound during May-June, 1996-1997.

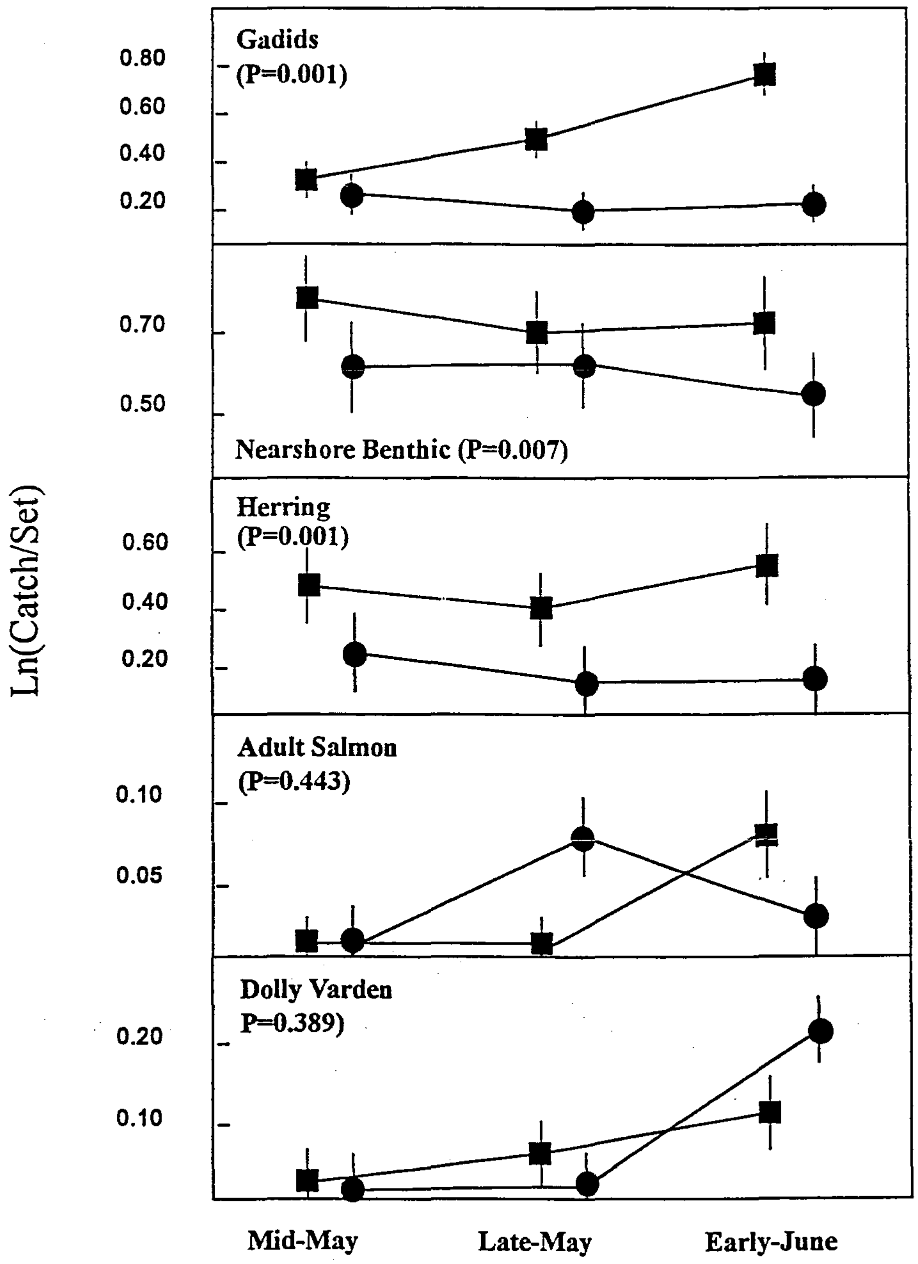


Figure 2: Mean catch per net set for five taxonomic groups of potential predators on juvenile pink salmon in eastern (solid squares) and western Prince (solid circles) William Sound during May-June 1997. Results from analysis of variance tests for a difference in mean catch per net set between eastern and western Prince William Sound are indicated.

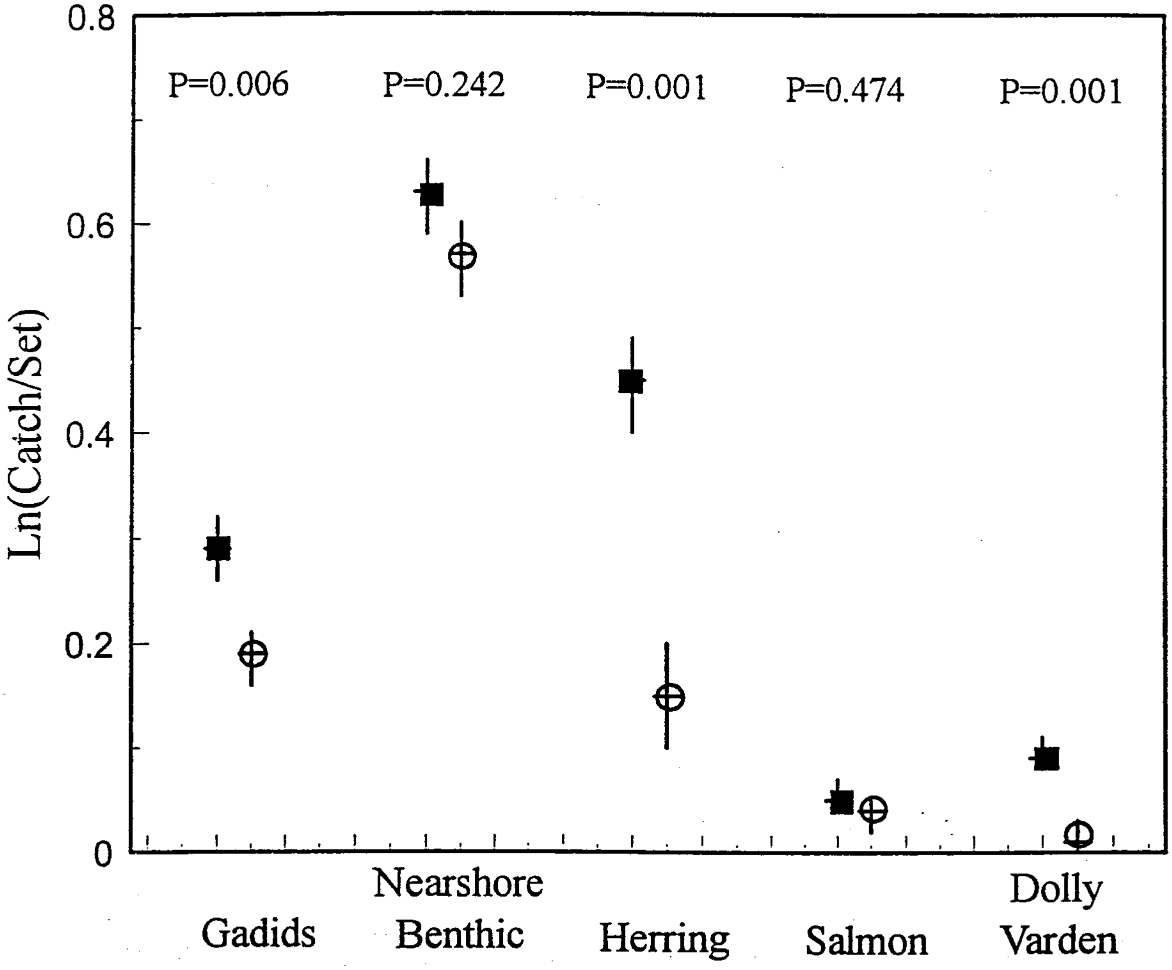


Figure 3: Mean catch per net set for three taxonomic groups of potential predators on juvenile pink salmon in western Prince William Sound during May-June1996 (solid squares) and 1997 (open circles). Results from analysis of variance tests for a difference in mean catch per net set between years are indicated above each group.

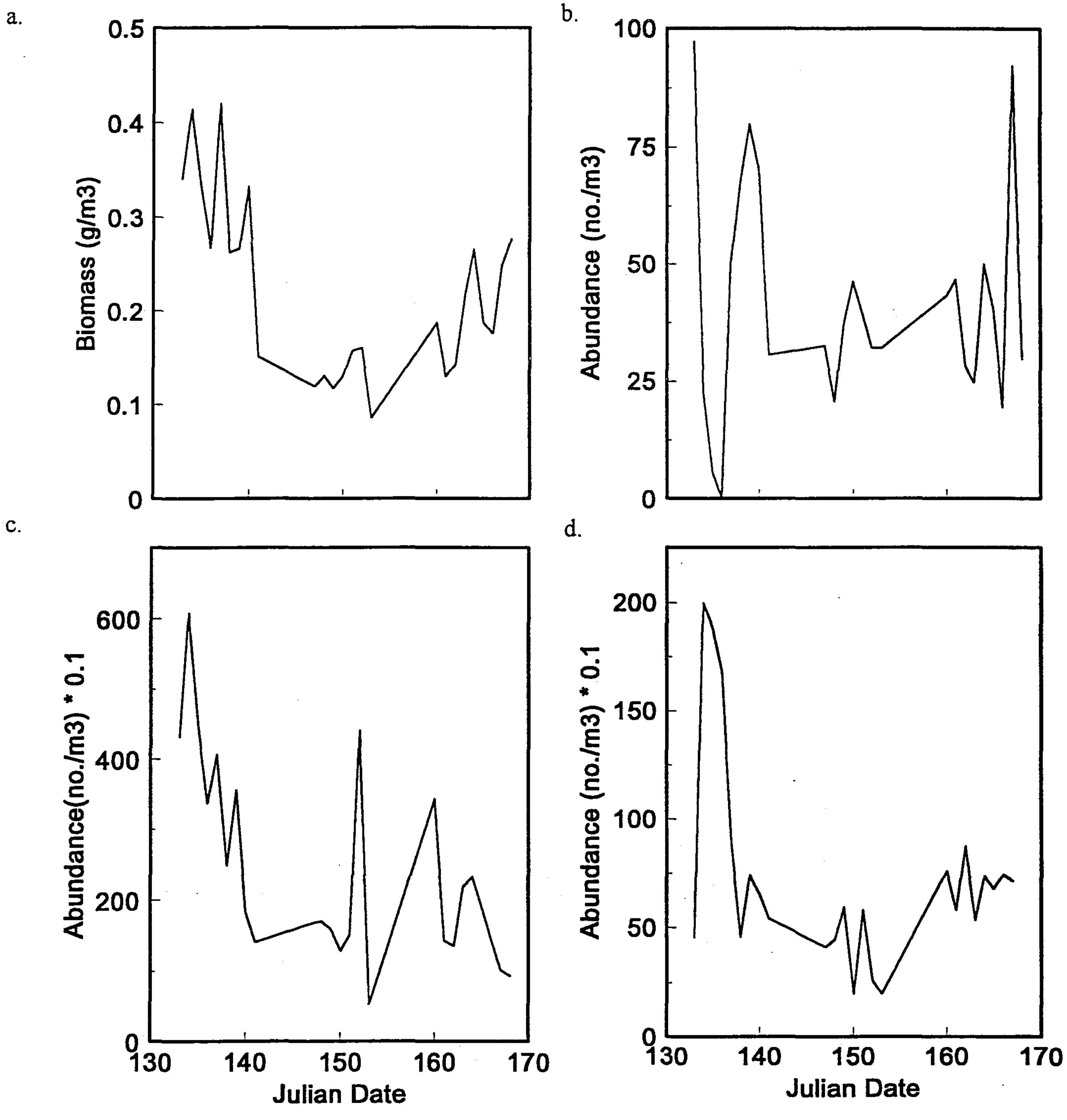
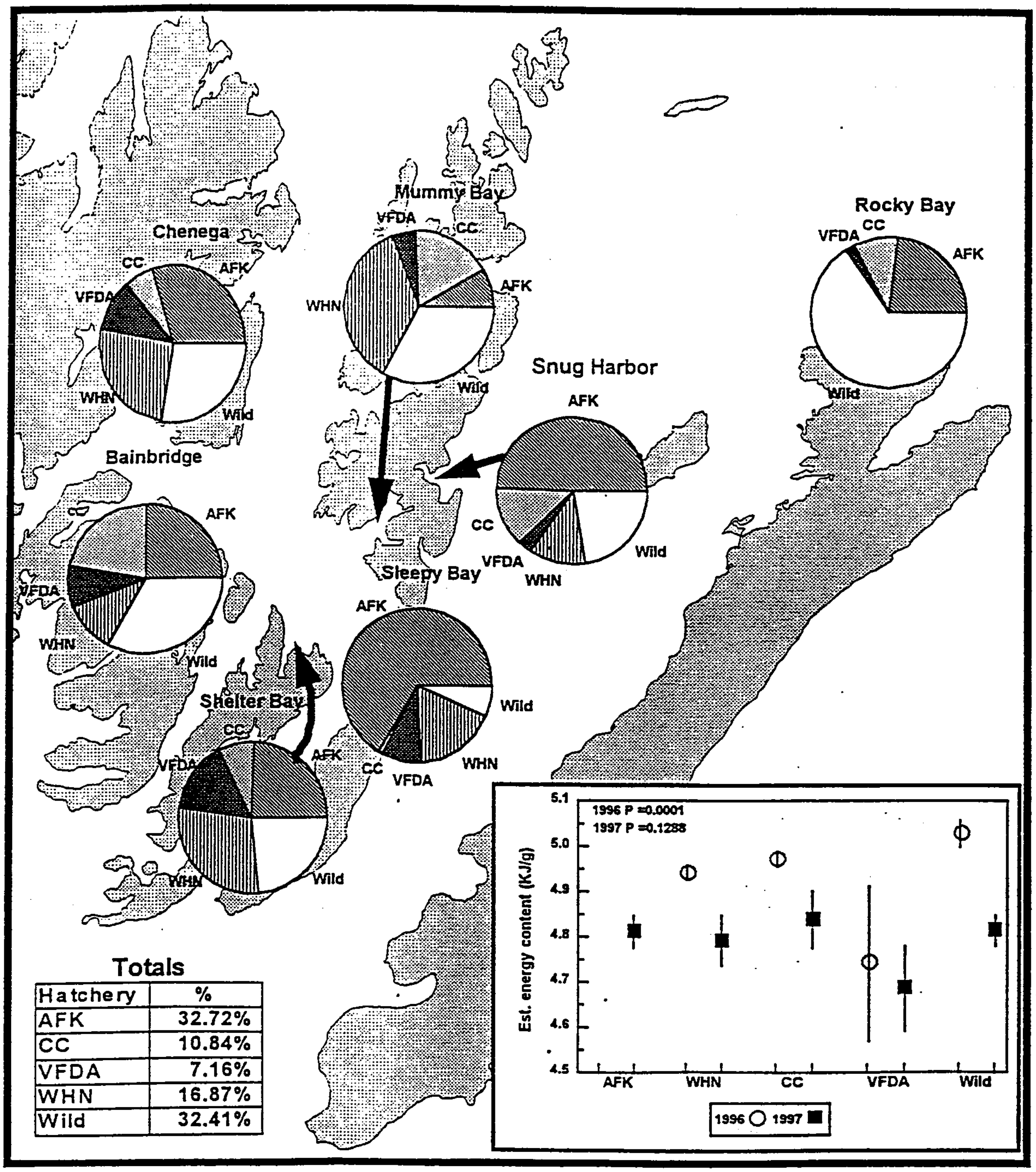


Figure 4: (a) Total zooplankton biomass and abundance (no./m3) of (b) large calanoid copepods, (c) small calanoid copepods, and (c) other zooplankters in offshore habitats in Prince William Sound, May-June 1997.



Totals

Hatchery	%
AFK	32.72%
CC	10.84%
VFDA	7.16%
WHN	16.87%
Wild	32.41%

Figure 5: Origins of juvenile pink salmon sampled during late June in southwest Prince William Sound based on recovery of otolith thermal marks. Estimated energy content (derived from moisture content) of wild- and hatchery-origin juvenile pink salmon during 1996 and 1997. Results from analysis of variance tests for a differences in estimated mean energy content between hatcheries within years are indicated. The following codes are used: Armin F. Koernig Hatchery (AFK), Cannery Creek Hatchery (CC), Solomon Gulch Hatchery (VFDA), Wally H. Noerenberg Hatchery (WHN).

Appendix I:

An evaluation of some factors affecting piscivory among pelagic fish during the spring bloom in a subarctic embayment

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Abstract

Factors affecting piscivory among herring (*Clupea pallasi*) and walleye pollock (*Theragra chalcogramma*) during the spring bloom in Prince William Sound, Alaska were examined using field data. Analyses of predator stomach contents indicated that predation by herring and pollock on larval and juvenile fishes was reduced during the spring bloom of large calanoid copepods, principally *Neocalanus spp.* Functional response models developed for herring and adult pollock feeding on large calanoid copepods (>2.5 mm) indicated that each predator began to switch to alternative prey when copepod biomass declined below 0.2 g m^{-3} and 1.0 g m^{-3}, respectively. The parameters of the functional response models for herring and adult pollock were consistent with particulate and filter feeding modes, respectively. Large calanoid copepod biomass was negatively correlated with the proportion of the diet comprised of fish for herring (P=0.083) and immature pollock (P=0.150), but not for adult pollock (P=0.564). Juvenile gadids and salmonids (*Oncorhynchus spp.*) less than 50-70 mm in length were the most common fish prey taken by herring and immature pollock; whereas, squid (<150 mm) were the most common fish prey taken by adult pollock. Thus, mortality among juvenile gadids and salmonids is likely affected by the timing of the seasonal decline of the *Neocalanus spp.* bloom relative to the prey fishes' growth rate. Analyses of seven years of data from hatchery-reared coded-wire tagged pink salmon (*O. gorbuscha*) support conclusions drawn from stomach content analyses. Mortality of pink salmon was negatively correlated with the duration of the copepod bloom during the juvenile lifestage (P=0.013), as well as juvenile growth rate (P<0.001), juvenile body weight at release (P<0.001), and the number of juveniles released (P<0.001). The duration of the spring bloom of *Neocalanus spp.* appeared to be more abbreviated in years when the water column (0-100 m) was more highly stratified. Thus, bottom-up processes affecting secondary production and juvenile growth rate appear to also modify top-down processes involving predator switching behavior and thus mortality of juvenile fishes.

Introduction

Trophic interactions during the spring bloom period are critical to the successful reproduction of many fish species that release larvae at this time. Mortality during these early lifestages is typically very high and may determine recruitment to adult populations (Hjort 1914). Year-class success may be determined by the match or mismatch between the release of larvae and the production of their food (Cushing 1967). This concept is based on the notion that recruitment success is driven by production from lower trophic levels (bottom up). However, these processes may be modified by interactions with animals at higher trophic levels (top down). The spring bloom is also an important period in the seasonal energy cycle for the later lifestages of subarctic fishes (Smith and Paul 1986, Paul et al. 1993). Movements of these larger animals into the surface layer during this season leads to an overlap in distributions of larvae or juveniles with potential predators. Feeding mode shifts toward piscivory among these larger individuals may modify the mortality rates of larval or juvenile lifestages predicted by bottom up processes.

This paper examines some processes affecting feeding mode shifts toward piscivory among the later lifestages of Pacific herring (*Clupea pallasi*) and walleye pollock (*Theragra chalcogramma*) during the spring bloom period in coastal waters of the northern Gulf of Alaska. These species are relatively abundant pelagic fishes in this region (Rogers et al. 1986). The early life stages of herring, pollock, pink salmon (*Oncorhynchus gorbuscha*), chum salmon (*O. keta*), capelin (*Mallotus villosus*), Pacific sandlance (*Ammodytes hexapterus*) and others enter the coastal ocean as larvae or juveniles during spring (Rogers et al. 1986). Older lifestages of herring and pollock are also distributed in the surface layers at this time feeding heavily on calanoid copepods (Okada 1986, Rogers et al. 1986, Coyle and Paul 1992). The copepods *Neocalanus plumchrus* and *N. flemingeri* (Miller 1988) comprise the majority of the zooplankton biomass in the region during the spring bloom (Cooney 1986). *N. plumchrus* and *N. flemingeri* reproduce at depth in late winter. Their progeny migrate to the surface layer to graze during the phytoplankton bloom for a brief period in late April and early May (Fulton 1973, Cooney 1986, Miller and Clemons 1988). During this period, these large copepods build a substantial high-energy lipid reserve which is utilized during the subsequent winter for egg development (Cooney 1986). The relatively high energy content of these copepods (Platt et al. 1969) makes them an attractive food source for many fishes. Large calanoid copepods comprise a major part of the diet of herring and pollock during this season (Okada 1986, Dwyer et al. 1987, Coyle and Paul 1992, Yoshida 1994), but both species are also piscivorous (Thorsteinson 1962, Bakshtansky 1965, Armstrong and Winslow 1968, Dwyer et al. 1987).

Particulate and filter feeding are two common foraging strategies employed by fish. Most optimal foraging models (based on particulate feeding behavior) predict prey selection from the relative profitabilities of potential prey (Charnov 1976, Mittelbach 1981, Osenberg and Mittelbach 1989) which are a function of the energy content of prey and the time (energy) required to capture and ingest prey. Shifts between particulate and filter feeding modes are likely related to the relative profitability of each feeding strategy, which is largely determined by prey size and density (Crowder 1985). Two types of filter feeding have been observed among fish. Ram filtering involves continuous swimming with the mouth agape and opercles flared. Pump filtering (or gulping) involves a series of nondirected suctions while the fish is stationary (Gerking 1994). Pump filtering appears to be a relatively rare behavior (Gibson and Ezzi 1992). It likely involves sighting of prey patches, and it tends to be employed at lower prey densities than those required for ram filtering (Gibson and Ezzi 1992, Gerking 1994). Durbin (1979) postulated that particulate feeders consume relatively large prey (prey-predator size ratio 0.5 to 5%); whereas, filter feeders consumer smaller prey (prey-predator size ratio 0.01 to 0.7%). Piscivory is a special case of particulate feeding. Prey-predator size ratios typically range from 20 to 30% for piscivores but ratios as high as 50% sometimes occur at ontogenetic transitions to piscivory (Popova 1978, Juanes 1994). Herring exhibit particulate and filter feeding modes which appear to be determined by prey density and light level (Gibson and Ezzi 1985, 1992). Adult pollock in the Bering Sea consume macrozooplankton greater than 4 mm in length; although, based on gill raker spacing they have the ability to feed on prey greater than 2 mm (Yoshida 1994). These prey sizes are near the threshold for filter feeding suggested by Durbin (1979). Adult pollock are also known to prey heavily on juvenile pollock when conditions lead to an overlap in their distributions (Dwyer et al. 1987). Walline (1983) concluded that predation on juvenile pollock likely determined year-class strength rather than the match or mismatch of pollock larvae with their food.

In the analysis that follows, we will first present data indicating seasonal changes in ocean conditions, calanoid copepod biomass, the relative abundance of herring and pollock, and the relative abundance and size of various juvenile fishes in Prince William Sound (PWS), Alaska. An analysis of the functional responses of herring, immature pollock and adult pollock feeding on large calanoid copepods will be conducted to determine the biomass of large calanoid copepods at which these predators begin to feed on alternative prey. This analysis will also examine the probable feeding modes employed by herring and pollock feeding on large calanoid copepods, because this may affect the timing of shifts to other strategies such as piscivory. We will then examine whether piscivory in these predators is a function of prey-predator size ratio, the relative abundance of prey fish, or the biomass of large calanoid copepods. Finally, we will evaluate the effect of size-selective predation and copepod biomass on the mortality of juvenile coded-wire tagged pink salmon released from four hatcheries in PWS.

Methods

Prince William Sound is an approximately 8500 km^2 basin surrounded by numerous deepwater fjords and islands. Herring, pollock and their prey were sampled in the passages of western PWS in 1994, 1995, and 1996. Seven areas were sampled from late April through mid-July in 1994 (Table 1, Figure 1). In 1995 and 1996, several sites in northwest PWS were sampled from early May through mid-June (Table 1, Figure 1). Sampling was conducted from approximately 6 pm to 6 am each day. The sampling area\dates indicated in Table 1 were generally used as sample units in the following analyses.

Adult pollock (>30 cm) were collected in deepwater passages with a mid-water wing trawl (40 m x 28 m) equipped with a net sounder. The net was towed at about 1.5 m sec^{-1} for approximately 30 minutes in the 0-60 m layer of the water column. At least two zooplankton samples were taken at stations located near the center of the passages to estimate the mean density of large calanoid copepods available to adult pollock at each location. Zooplankton samples in the passages were collected with a 0.5 m diameter ring net (335 um mesh) towed vertically from 50 m depth to the surface. Herring and immature pollock (<30 cm) and various juvenile fishes were collected with small-mesh purse seines (250 m x 20 m, 1.5 cm stretch mesh). Seines were set in an approximate semi-circle with the net open in the direction of the prevailing current for approximately 20 minutes (Hartt (1980). Seine sampling was conducted within 1 km of the shore up to the 20 m isobath. Samples of herring and immature pollock were also obtained with variable-mesh gill nets set out from the shore at two locations within each study site. At least four zooplankton samples were taken at stations located near the 20 m isobath to estimate the mean density of large calanoid copepods available to herring and immature pollock in nearshore habitats. These samples were collected with a 0.5 m ring net (243 um mesh) towed vertically from 20 m depth to the surface. At each study site, temperature and salinity was measured to a depth of 100 m with a conductivity-temperature-depth profiler (CTD).

Over 15,000 specimens were analyzed to determine the diet compostion of herring and pollock during the spring bloom period from 1994 through 1996 (Table 2). At least thirty specimens from each fish species were randomly selected from each net set for length-weight measurements and analysis of stomach contents. Fork length was measured to the nearest millimeter and wet weight to the nearest gram. Stomachs were excised and preserved in formalin for later analysis. In the laboratory, total stomach contents wet weight was measured to the nearest 0.01g, and the proportion of total stomach contents weight in several taxonomic groups (large calanoid copepod, small calanoid copepod, euphausiid, amphipod, etc.) was visually estimated. Fish found in the stomachs were measured to the nearest millimeter. The weighted mean proportion of the diet comprised of various prey taxa was estimated for herring, immature pollock and adult pollock within each sample unit. The catch of each respective predator in each net set was used as the weighing variable.

Over 300 samples were analyzed to estimate the species composition and biomass of zooplankton available to herring and pollock. In the field, zooplankton samples were preserved in formalin. In the laboratory, zooplankters collected with the 335-um mesh net were identified to the lowest possible taxonomic level and enumerated using standard subsampling techniques (Coyle et al. 1990). Zooplankters collected with the 243 um mesh net were enumerated into three taxonomic groups (large calanoid copepods (>2.5 mm), small calanoid copepods (<2.5 mm), and 'other' zooplankton) using standard subsampling techniques. Zooplankton biomass was calculated as the product of abundance and the mean individual wet weight for each taxonomic group (Coyle et al. 1990).

Changes in the relative abundance of herring, immature pollock, adult pollock and various juvenile fishes was examined through analyses of net catch data. Mean catch per hour in mid-water trawls was used as a measure of relative abundance of adult pollock in the surface layer of the passages within each sample unit. Mean catch per net set in small-mesh purse seines and variable-mesh gillnets was used as a measure of relative abundance of herring and immature pollock, respectively within each sample unit. Catch data were natural logarithm transformed prior to calculating the mean catch for each of the sample units indicated in Table 1.

Functional responses of herring, immature pollock and adult pollock

The functional responses of herring, immature pollock and adult pollock feeding on large calanoid copepods were evaluated using non-linear regression analyses of field data. Type II and III functional response curves were fit to field estimates of total daily consumption of large calanoid copepods in relation to measured copepod densities. The type II functional response rises at a decelerating rate to an asymptote and generally applies to particulate feeders (Hassel 1978), i.e.

$$I = \frac{\gamma p U}{1 + \gamma p U h} \qquad 1$$

where I is the daily food consumption (g day^{-1}), γ is the cross-sectional area of the reactive field (m^2), p is the prey density (g m^{-3}), U is the swimming speed (m day^{-1}) and h is the prey handling time (day g^{-1}). The type III functional response is a sigmoid. It often best describes situations where alternative prey are available, and the predator switches from feeding on one prey type to another (Lawton et al. 1974, Akre and Johnson 1979), i.e.

$$I = \frac{\gamma p^2 U}{1 \div \gamma p^2 U h} \quad . \qquad 2$$

Because our analysis utilizes field estimates of daily food consumption, swimming speed represents the total distance traversed while feeding throughout the entire day, and handling time includes the time required to capture and ingest prey as well as any time during which the fish is not searching for prey due to satiation or low light level.

Daily consumption of large calanoid copepods (I) was estimated from

$$I = 24 \overline{S} \alpha \qquad 3$$

where $\overline{S}$ is the mean wet weight of large calanoid copepods in the stomach over a twenty-four hour period and α is the gastric evacuation rate (Eggers 1977). In the present study, the daily consumption of copepods was estimated using diet data for the period from 6 pm to 6 am. This was done because data was available from this time period for each of our sample units. Analysis of variance was conducted to test for a difference in the mean wet weight of large calanoid copepods in the stomachs of herring, immature pollock and adult pollock between the 6 pm to 6 am period and the full 24 hour day using data from sixteen diel studies conducted in 1995. Results indicated that the mean weight of copepods in the stomachs was not significantly different ($P>0.350$) between this 12 hour period and the full 24 hour day for any of these three predators. Temperature-specific gastric evacuation rates were estimated for herring using an equation for juvenile menhaden provided by Peters and Kjelson (1975), i.e. $\alpha = -0.0132+0.0316 \log T - 0.0403 (\log T)^2$, where T is temperature (°C). Data provided by Smith et al. (1989) were used to estimate a relationship between temperature and gastric evacuation rate for adult pollock ($\alpha = -0.0235 e^{.168T}$) and immature pollock ($\alpha = -0.0217 e^{.168T}$). Mean 0-15 m ocean temperatures were used to estimate gastric evacuation rates of herring and immature pollock which were sampled in this layer. Mean 0-50 m temperatures were used to estimate gastric evacuation rates of adult pollock which were sampled in this layer.

Two values were used for γ to evaluate whether the fish were likely particulate or filter feeding. For particulate feeders, γ is the cross-sectional area of the reactive field, i.e. πd^2_r where d_r is the reactive distance (Ware 1972). Reactive distance is a function of fish size (Ware 1978) and prey size (Ware 1972). Data provided by Ware (1972) were used to estimate a regression equation relating reactive distance to fish length and prey length, i.e.,

$$d_r = 0.29 L_f^{1.1} + 3.3 L_p \qquad \mathbf{4}$$

($R^2=0.960$, $P=0.005$) where d_r is the reactive distance (cm), L_f is total fish length (cm) and L_p is prey length (mm). For ram filter feeders, γ is simply the cross-sectional area of the mouth gape, because individual prey are not sighted and attacked.

Ware's (1978) analysis of the bioenergetics of foraging pelagic fishes was used to determine an appropriate range of swimming speeds for evaluation of functional response models. Ware (1978) found that the optimal foraging speed of pelagic fishes likely ranged between 1 and 3 L sec^{-1}. Three body lengths per second is likely an appropriate upper range for swimming speeds of foraging pelagic fishes. Brett and Glass (1973) found that maximum sustained swimming speeds of sockeye salmon (>150 mm) range between 3 and 4.5 L sec^{-1} depending on temperature. In the present study, swimming speeds were varied between 1 and 3 L sec^{-1}. However, we also evaluated a swimming speed of 15 km day^{-1} (0.3 L sec^{-1}) which was estimated for adult pollock schools feeding in the Bering Sea (Radchenko and Sobolevskiy 1993).

Densities of large calanoid copepods in layers found within the upper 50 m of the water column were estimated in 1996 using a MOCNESS sampler. Samples were collected from eight discrete layers (0-5 m, 5-10 m, 10-15 m, 15-20 m, 20-25 m, 25-30 m, 30-40 m, 40-50 m) at 24 stations in PWS. The weighted mean biomass of large calanoid copepods across all layers within the upper 50 m was regressed against the biomass of large calanoid copepods for samples collected within high density layers. Samples having a copepod biomass greater than the mean for the upper 50 m as a whole were considered to have come from high density layers. The results from this analysis indicated that probable mean biomass of large calanoid copepods in layers was about 2.25 times the biomass estimated from 0-50 m vertical net tows ($R^2 = 0.451$, $P<0.001$). The probable mean copepod biomass in layers was used in the evaluation of functional responses of adult pollock, because adult pollock were likely feeding in these high density layers. For herring and immature pollock feeding nearshore, we assumed that 0-20 m vertical net tows adequately estimated the mean biomass of copepods available in these relatively shallow habitats which are likely vertically mixed by tidal currents (Simpson and Hunter 1974).

Non-linear regression analysis was used to fittype II and III functional response models to field estimates of daily consumption of large calanoid copepods in relation to copepod density. Each analysis was conducted for an average size herring ($\overline{L}$ =195 mm), immature pollock ($\overline{L}$ = 195) or adult pollock ($\overline{L}$ =501). The mean length for each predator was used to estimate the cross-sectional area of the mouth gape, swimming speed and reactive distance for an average individual fish. The cross-sectional area of the mouth gape was estimated for an average-size herring and pollock using measurements from samples obtained during this study. The analysis of functional response models was conducted in two stages. In the first stage, non-linear regression analyses were conducted using several possible combinations of the values of γ and U as constants to estimate handling time (h). Studentized deleted residuals were calculated to identify and exclude outliers in the data at this stage (Neter et al. 1989). The combinations of γ and U that resulted in the smallest mean square error were considered to provide the best fit of the functional response model to the data. In the second stage, the handling times (h) estimated from the two 'best fit' models obtained in the first stage were used as constants to estimate U using the two values of γ associated with ram filter and particulate feeding. The value of γ that resulted in the best fit of the data was considered to indicate the probable feeding mode of the predator.

Piscivory in herring, immature and adult pollock

The mean percent of the diet comprised of fish was estimated for herring, immature pollock and adult pollock for several prey taxonomic groups (herring, gadids, salmonids, capelin, sandlance, squid, 'other fish', unidentified fish). Diet proportions were weighted by the catch of each respective predator in each net set. The ratio of the length of prey fish to predator length was calculated for herring, immature pollock and adult pollock as predators with all prey species pooled and by prey taxonomic group. Analyses of variance were conducted to test for a difference in the prey-predator length ratio (arcsin square root transformed) among predator species and among prey species. Mean catch per net set in purse seines and mean length was also estimated for each of the prey fish taxonomic groups consumed by herring and pollock.

Multiple regression analyses were conducted to test the hypothesis that piscivory in herring and pollock is reduced when the biomass of large calanoid copepods is high. The percent of the diet comprised of fish (arcsin square root transformed) was the dependent variable in the analysis and the relative abundance of prey fish and the mean biomass of large calanoid copepods were the independent variables. The mean catch per net set of juvenile fish in purse seines was used as a measure of the relative abundance of prey fish (Hartt 1980). Catch data were natural logarithm transformed prior to calculating the mean catch for each of the sample units indicated in Table 1. The mean biomass of large calanoid copepods in nearshore habitats was used as an independent variable in the analyses for herring and immature pollock. For adult pollock, the mean biomass of large calanoid copepods in offshore habitats was used as an independent variable.

Effect of size-selective predation and copepod biomass on mortality of juvenile salmonids

The effect of copepod biomass and size-selective predation on mortality of juvenile salmonids was evaluated using estimates of survival from fry release to adult for 147 coded-wire tag groups of pink salmon released from the Armin F. Koernig, Wally H. Noerenberg, Cannery Creek and Solomon Gulch hatcheries from 1989 through 1995 (Figure 1). An analysis of covariance was conducted to test the following null hypothesis: mortality of juvenile pink salmon is not related to the duration of the bloom of large calanoid copepods from ocean entry to the time the fish reach 60 mm in length, or the body weight of juveniles at release, or juvenile growth rate, or number of juveniles released at each hatchery each day.

Instantaneous natural mortality from ocean entry to adult return was the dependent variable in this analysis of covariance while mean body weight at release, mean juvenile growth rate, mean zooplankton settled volume and number of juveniles in each tag group were the independent variables. The survival of pink salmon in each tag group from ocean entry to adult was estimated from recovery of tagged adults at the hatcheries as well as in gill net and purse seine fisheries in PWS. A tag group was comprised of one or more net pens of juveniles released from the same hatchery on the same day. The methods used to estimate survival are described by Peltz and Miller (1990) and Geiger (1990). Instantaneous natural mortality was estimated on a daily basis assuming a total of 470 days at sea. Mean body weight at release was estimated from three samples collected from each net pen immediately prior to the release of each tag group. The three samples were composited and a random subsample of approximately

100 individuals was weighed to the nearest 0.01 g. The mean growth rate of juveniles belonging to each tag group was estimated from an equation developed from an analysis of covariance involving juvenile growth as the dependent variable and number of juveniles in each tag group as well as environmental data as independent variables. The methods used in this analysis will be described later in detail. Mean zooplankton settled volume weighted by the number of days elapsed between each measurement was estimated for the 30 days immediately following release of each tag group. This was done because sampling of tagged juveniles indicated that 98.5% of these fish did not reach 60 mm in length within 30 days after release. A threshold zooplankton volume was set at 2.0 ml m^{-3}, i.e. zooplankton volumes greater than 2.0 ml m^{-3} were set equal to 2.0 ml m^{-3}. This was done because analyses of predator stomach contents indicated that consumption of fish was greater when the biomass of large calanoid copepods declined below about 0.2 g m^{-3} (Figure 13). Also, data provided by Willette et al. (1994) as well as data obtained in the present study indicated that this threshold biomass corresponded to a settled volume equal to about 2.0 ml m^{-3}, and that total zooplankton biomass in May was correlated (R^2=0.658) with the biomass of large calanoid copepods. A class variable was established based upon the value of the mean zooplankton settled volume that divided the data into three groups with roughly equal numbers of observations. The mean zooplankton settled volume (ml m^{-3}) for the low, moderate, and high classes was 1.3 (n=50), 1.9 (n=56), and 2.0 (n=48), respectively. The data used to estimate zooplankton settled volume was obtained from samples collected twice each week (late April-early June) using a 0.5 m ring net (243 um mesh) towed vertically from 20 m depth to the surface in the passages adjacent to each hatchery. Generally, one to three samples were composited to obtain sufficient material to estimate the settled volume of zooplankton in the samples collected each day. Tag groups with mean body weights at release greater than 0.35 g were not included in the analysis. This was done because groups comprised of larger fish (up to 1.3 g) were relatively rare (<9% of the data), and they occurred more frequently in association with moderate and high zooplankton volumes. Each of the continuous independent variables in the analysis was natural logarithm transformed. A stepwise analysis of covariance procedure was used to develop the most parsimonious model of mortality, and the least-squares mean mortality was estimated for the low, moderate and high zooplankton classes.

As previously indicated, mean growth rate was estimated from an analysis of covariance function of growth data on juvenile release and environmental data. Growth rate estimates were available for 2,637 individual coded-wire tagged juvenile pink salmon collected during May and early June in PWS (1989-1994). The methods used to recover tagged juveniles and estimate growth are described by Willette (1996). Mean growth was estimated for 108 groups of juveniles which exhibited a common release site, release date and recapture date. Mean zooplankton settled volume and ocean temperature weighted by the number of days between each measurement was estimated from the date of release of each tag group to the date of recapture. The ocean temperature data was obtained from measurements taken at 1 m depth when each zooplankton sample was collected. These environmental variables (natural logarithm transformed) were used as independent variables in the analysis. A class variable was established based upon the number of juvenile pink salmon released each day from each hatchery that divided the data into two groups with approximately equal numbers of observations. Groups with less than and greater than 20 million juveniles were designated as small and large releases, respectively. A stepwise analysis of covariance procedure was used to develop the most parsimonious model of juvenile growth.

Results

Ocean conditions in May 1994 were characterized by relatively frequent storms (Figure 2), weak surface layer stratification (Figure 3), cooler surface layer temperatures (Figure 3), and a prolonged bloom of large calanoid copepods (Figure 4). In May 1995, storms were again frequent in the area (Figure 2), but the water column was more strongly stratified (Figure 3), and surface temperatures were warmer than in 1994 (Figure 3). The bloom of large calanoid copepods in May 1995 was also more abbreviated than in 1994 (Figure 4). In May 1996, storms were less frequent (Figure 2), the water column was again strongly stratified (Figure 3), surface layer temperatures were relatively warm (Figure 3), and the bloom of large calanoid copepods was very abbreviated (Figure 4). In each of the three years of this study, the surface layer became strongly stratified in June and the bloom of large calanoid copepods declined. *Neocalanus spp.* comprised the majority of the biomass of large calanoid copepods during the spring bloom in both 1994 and 1995 (Figure 4).

Herring and pollock were the most abundant pelagic fishes during each of the three years of this study; although, adult salmonids (*Oncorhynchus spp.*) and squid (mostly *Berryteuthis spp.*) were commonly encountered (Table 3). The mean catch of herring in purse seines tended to increase from May through June in each of the three years of the study (Figure 5). In 1994, total catch of immature pollock in all gear types increased in late July. A similar increase in mean catch per set of immature pollock in variable-mesh gillnets was seen in June 1996 but not in 1995 (Figure 5). Mean catch per hour of tow of adult pollock in the upper 50 m of the water column declined from June through July in 1994 (Figure 5). However, in 1995 adult pollock catches declined in mid May but increased again in early June. In 1996, adult pollock catches were lower than in the previous two years and no seasonal changes in abundance were evident (Figure 5).

Large calanoid copepods tended to dominate herring diets during the calanoid copepod bloom in early May (Figures 4 and 6). In 1995 and 1996, herring continued to feed predominately on large calanoid copepods several weeks after copepod densities declined. In all three years of the study, herring eventually switched to feeding on other prey by mid-June. In 1994, herring switched to feeding primarily on euphausiids and amphipods; in 1995 to euphausiids, amphipods, pteropods and fish; and in 1996 to euphausiids, amphipods and fish (Figure 6). Large calanoid copepods also dominated the diets of immature pollock in May 1995 (Figure 7). However, in 1994 and 1996 diets of immature pollock were more varied. In 1994, immature pollock fed primarily on euphausiids and amphipods, although few samples were obtained during May. In both 1995 and 1996, immature pollock tended to feed more heavily on fish during June. Adult pollock diets were dominated by large calanoid copepods during May, 1994-1995 (Figure 8). After the seasonal decline in copepod density, adult pollock switched to feeding primarily on euphausiids, amphipods and fish in 1994 and 1996; whereas, pteropods comprised the majority of adult pollock diets after the bloom in 1995. Large copepods did not dominate adult pollock diets during the bloom in May 1996.

Functional responses of herring, immature pollock and adult pollock

The functional response for herring feeding on large calanoid copepods was best described by a type III model (Table 4). The Studentized deleted residuals identified two outliers in the data that were excluded from the analysis of functional reponses of herring. The value of γ consistent with a particulate feeding mode provided the best fit of the herring data at all values of U used with the type III model (Appendix I, Table 1). When a value for γ consistent with a ram filter feeding mode was used, handling time estimates were negative in four of the six parameter combinations used in the analysis (Appendix I, Table 1). The best fit functional response model for herring resulted in a swimming speed estimate of 10.0 km day^{-1} (Table 4) and a daily food consumption of 0.8 g day $^{-1}$ at the asymptote (Figure 9). Herring began to feed on alternative prey as the mean biomass of large calanoid copepods in the upper 20 m of the water column declined below about 0.2 g m^{-3} (Figure 9). The functional response for immature pollock feeding on large calanoid copepods was not adequately described by the type II or III models regardless of the values of the parameters used (Table 4 and Appendix I, Table 2). The response function for immature pollock did not reach an asymptote within the range of the data used in the analysis (Figure 9). The functional response for adult pollock feeding on large calanoid copepods was best described by a type III model (Table 4 and Appendix I, Table 3). A value of γ consistent with a ram filter feeding mode provided the best fit of the adult pollock data at all values of U used in the analysis. The best fit functional response model for adult pollock resulted in a swimming speed estimate of 16.7 km day^{-1} and a daily food consumption of 7.0 g day $^{-1}$ at the asymptote (Figure 9). Adult pollock began to feed on alternative prey as the mean biomass of large calanoid copepods in high density layers declined below about 1.0 g m^{-3} (Figure 9).

Piscivory in herring, immature pollock and adult pollock

Immature pollock generally exhibited a greater degree of piscivory than either herring or adult pollock. The overall mean percent of the diet comprised of fish ranged from 13.9 to 26.2 for immature pollock, 4.2-11.4 for herring, and 6.7-17.1 for adult pollock (Table 5). Juvenile gadids (mostly age-0 pollock) and salmonids (mostly pink and chum salmon) were the most commonly encountered fish in the diets of herring and immature pollock, but squid was the most important fish species in the diets of adult pollock (Table 5). Herring and immature pollock generally consumed fish less than 50-70 mm in length; whereas, adult pollock generally consumed fish less than 150 mm (Figure 10). Mean lengths of fish prey consumed by immature and adult pollock did not differ substantially, but adult pollock occasionally consumed larger fish that were not taken by immature pollock. Mean prey-predator length ratios differed significantly between herring, immature pollock and adult pollock ($P<0.001$). Herring generally consumed fish ranging from 5-25% of their length, immature pollock 5-35%, and adult pollock 3-40% (Figure 10). Mean prey-predator length ratios also differed significantly ($P<0.001$) among prey species (Table 6). The smaller prey fish consumed by adult pollock were generally juvenile gadids, juvenile salmonids and 'other fish'; whereas, the larger prey were herring, capelin, sandlance and squid (Table 6).

In 1994, the mean catch per net set of juvenile fishes (<150 mm) increased considerably from May through June (Figure 11). In 1995 and 1996, juvenile fish catches were much higher in May than in 1994. Juvenile fish catches increased in June of 1996, but no appreciable increase in catches was observed from May to June in 1995. In 1994, juvenile fish catches were dominated by gadids and salmonids; whereas, in 1995 and 1996 salmonids and capelin were most numerous (Table 7). Squid were more abundant in 1996 than in the previous two years. Mean lengths of the fish species consumed by herring and pollock did not appear to differ substantially from year to year (Figure 12). Juvenile gadids grew from about 40 to 60 mm from late May to July; whereas, juvenile salmonids were somewhat larger throughout this period. Mean lengths of herring and capelin increased slightly from May through July (Figure 12).

Sequential sums of squares (Type I) and partial sums of squares (Type III) indicated that the proportion of herring diets comprised of fish was marginally significantly related to the biomass of large calanoid copepods but the relative abundance of prey fish was not related to consumption of fish (Table 8). For immature pollock, the relative abundance of prey fish was significantly related ($P=0.044$) to the proportion of the diet comprised of fish. Sequential sums of squares indicated that the biomass of large copepods was significantly related to consumption of fish by immature pollock, but partial sums of squares indicated that this variable was only marginally significant in the model (Table 8). Neither independent variable was significantly related to the proportion of adult pollock diets comprised of fish (Table 8). The variance inflation factor was calculated to assess whether multicollinearity may have affected estimation of the regression coefficients and their statistical significance (Neter et al. 1989). The variance inflation factors were 1.07 for herring, 1.17 for immature pollock, and 1.11 for adult pollock. Graphical evaluation of the original data indicated that the proportion of the diet comprised of fish tended to be greater for all three predators when the biomass of large copepods was less than about 0.2 g m^{-3} (Figure 13).

Effect of size-selective predation and copepod biomass on mortality of juvenile salmonids

Analysis of covariance indicated that the growth rate of coded-wire tagged juvenile pink salmon was positively correlated to mean ocean temperature ($P<0.001$) and mean zooplankton settled volume ($P=0.002$) during the period from juvenile release to recapture (Table 9). The intercepts and slopes of the relationship between growth and zooplankton settled volume were also significantly different between small and large release groups from each hatchery (Table 9, Figure 14). The variance inflation factor for this analysis was 4.60.

Analysis of covariance further indicated that the instantaneous natural mortality of pink salmon was significantly correlated to zooplankton settled volume, mean juvenile growth rate, mean body weight of juveniles at release and number of juveniles released ($R^2=0.350$, $P<0.001$). Mortality was significantly greater when zooplankton settled volume during the initial 30 days of marine residence was relatively low (Tables 10 and 11). Mortality was also greater when mean growth rate, mean body weight at release, or the number of juveniles released was relatively low (Table 10). The variance inflation factor for this analysis was 6.54.

Discussion

The environmental conditions observed during the three years of this study provide for a useful comparison of the effect of physical conditions on secondary production in the PWS ecosystem. The duration of the bloom of large calanoid copepods in May appeared to be associated with the degree of stratification of the surface layer. In 1994, the surface layer was weakly stratified, and the bloom of large copepods extended to the end of May. In May 1995 and 1996, the surface layer was more highly stratified, and the bloom of large copepods was more abbreviated (Figures 3-4). These associations are likely related to the frequency of storms with winds sufficiently strong to breakdown surface stratification, resupply nutrients to the surface mixed layer, and thus prolong the phytoplankton bloom (Iverson et al. 1974, Walsh et al. 1978, Sambrotto and Goering 1983, Sambrotto 1985, Ziemann et al. 1991). In years when storms are more frequent and the phytoplankton bloom is prolonged, the mean (April-June) abundance and growth of *Neocalanus plumchrus* is greater (Smith and Vidal 1982, Sambrotto and Goering 1983). The frequency of wind events was similar during May in 1994 and 1995 (Figure 2), yet the surface layer remained more highly stratified in 1995 (Figure 3). This indicates that the effect of intense storms on primary and secondary production at this time of year is likely modified by other physical processes that affect development of surface stratification during the spring bloom period. The stronger surface layer stratification observed in May 1995 and 1996 was associated with higher salinities and lower temperatures below 50 m depth compared to 1994 (Figure 3). The strength of surface stratification during this season is largely determined by the vertical salinity gradient because seawater density is primarily a function of salinity at low temperatures (Royer 1979). In years when the 0-100 m salinity is relatively high at the onset of the spring bloom, the seasonal decrease in surface salinity due to increased freshwater discharge (Xiong and Royer 1984) results in a greater vertical salinity (density) gradient compared to years when the 0-100 m salinity is relatively low at the onset of the spring bloom. Higher wind speeds are required to breakdown the stronger surface stratification that occurs under these conditions. Thus, in 1995 although wind speeds were relatively high, the surface stratification was not broken down and the spring bloom of large calanoid copepods was relatively abbreviated.

Large scale oceanographic processes occurring the previous winter may determine the 0-100 m temperature-salinity conditions present at the onset of the spring bloom period. Lower ocean temperatures and sea levels in the northeast Pacific are associated with a weaker winter Aleutian low (Emery and Hamilton 1985). Higher salinities in this region are associated with reduced freshwater discharge (Xiong and Royer 1984), and lower sea levels are associated with reduced precipitation and dynamic height of the upper layers of the ocean (Royer 1979). Thus, a weak (strong) Aleutian low during the previous winter may result in relatively high (low) 0-100 m salinities and low (high) 0-100 m temperatures at the onset of the spring bloom. Niebauer et al. (1994) concluded that 200% of the volume of PWS was flushed during winter (October-April), and that flushing of the surface layer (0-100 m) was most rapid during winter. Thus, large-scale oceanographic processes in the Gulf of Alaska may be expected to affect conditions in the surface layer of PWS during winter.

Herring and pollock were the most commonly encountered and abundant species in surface layer net catches during each of the three years of this study (Table 3). These two species have been found to dominate the pelagic fish community in other areas of the northern Gulf of Alaska (Rogers et al. 1986). In the present study, the relative abundance of herring, immature pollock, and various species of juvenile fishes tended to increase from May through June (Figures 5 and 11). A similar seasonal increase in the abundance of nearshore fishes has been observed in other areas of the North Pacific (Miller et al. 1976, Moulton 1977, Cross et al. 1978, Rosenthal 1983).

Size-related shifts in amounts of copepods and fish consumed by pollock have been reported in other areas but were not consistently observed in the present study. Dwyer et al. (1987) found that the proportion of the diet comprised of copepods declined from about 75-100 % in small pollock (< 30 cm) to less than 50% among large pollock (>30 cm) during spring and summer in the Bering Sea. In the present study, a similar pattern was observed in 1995 but not in 1996 (Figures 7-8). In other regions, the proportion of pollock diets comprised of age-0 pollock (Dwyer et al. 1987) and fish (Clausen 1983) have been found to increase with pollock size. However, in the present study, the overall mean proportion of the diet comprised of juvenile gadids and all fish combined was greater for immature pollock than for adult pollock in two out of three years (Table 5). In the present study, pteropods also dominated the diet of adult pollock in June 1995 (Figure 8), but in previous studies pteropods have been absent from or comprised only a minor portion of pollock diets (Clausen 1983, Dwyer et al. 1987, Maeda 1986, Okada 1986, Gorbatenko and Dolganova 1989, Yoshida 1994).

Determining the appropriate functional response model for specific predator-prey interactions has often proved difficult. Most often prey density is manipulated under controlled laboratory conditions and feeding rates of predators are estimated (Ware 1972, Ranta and Nuutinen 1985, Gulbrandsen 1991, Winkler and Orellana 1992). This approach can minimize ambiguities caused by predator satiation, prey patchiness, and variable light level and swimming speeds that can complicate interpretation of results from field studies. However, results from laboratory experiments may be difficult to extrapolate to nature, because many laboratory studies do not adequately account for variables known to affect prey encounter rates and selection (MacKenzie et al. 1990). This may be especially true for relatively large predators such as adult pollock. In the present study, least-squares non-linear regression analysis was used to estimate the functional responses of herring and pollock feeding on large calanoid copepods using field data. Visual examination of the relation between predator consumption and prey density has commonly been employed to determine functional responses of fish predators using field data (Peterman and Gatto 1978, Ruggerone and Rogers 1984, Fresh and Schroder 1987), but this approach has often proved difficult due to the highly variable predation rates observed in nature. Non-linear regression analysis provides a more quantitative procedure for determining the underlying functional response when using field data.

We recognize that herring and pollock probably feed in high density patches or layers of copepods, because relatively mobile predators often aggregate in areas where relatively immobile invertebrate prey occur at high densities (Goss-Custard 1970, Krebs et al. 1974, Smith and Sweatman 1974, Zach and Falls 1976a, 1976b, Cowie 1977, Cook and Hubbard 1977, Waage 1979). Our analysis is based on the assumption that relatively large-scale seasonal changes in mean surface layer copepod densities are correlated with densities in patches exploited by herring and pollock. An analysis of plankton patchiness off California provides some insight into the validity of this assumption. Studies employing a Longhurst plankton recorder (Longhurst et al. 1966) indicated that the ratio of copepod densities in patches varied horizontally by a mean factor of 2.6 above background densities, and the patch-to-background density ratio did not differ significantly among 11 tow lines (Wiebe 1970). Owen's (1989) results were similar, i.e. the median prey density within a patch was approximately 2 times the density that would be obtained with an integrative sampler. However, the validity of this assumption to our analysis may not be critical, because our method of estimating daily consumption of copepods integrates amounts taken from many patches by many individuals over a 12 hour period.

A sigmoid type III functional response model provided the best fit of the data for both herring and adult pollock. This function typically fits a predator's response to the principal prey when alternative prey are available and prey switching occurs (Lawton et al. 1974, Akre and Johnson 1979). In a system involving two prey types (A and B), Murdoch (1969) defined switching as A/B in the diet = c(A/B available), i.e. for prey type A, fewer prey than expected are taken a low density and more prey than expected are taken a high density. Switching behavior is often associated with predator preferences for particular prey resulting in differential rejection of encountered prey (Holling 1965, Murdoch 1969, Oaten and Murdoch 1975). In vertebrate predators, prey preferences and switching behavior may result from learning (Holling 1965, Krebs 1973, Murdoch and Oaten 1975, Curio 1976). Predators may learn the shape (Jacobs 1965), visibility (Mellors 1975, Zaret and Kerfoot 1975), or movement patterns (Zaret 1980, Wright and O'Brien 1982) of a particular prey type. Prey capture success rate may also increase as predators learn successful techniques for capturing prey, thus increasing the profitability associated with preferred prey (Vinyard 1982). Hassell (1978) indicated that the shape of the type III response model may arise from an underlying relationship between attack rate and prey density. Such a relationship may result from predator preferences, but a relationship between prey density and swimming speed (Ware 1978) affecting encounter rate ($\gamma \cdot U$) may also result in a type III functional response. Several authors have also indicated that predators capable of concentrating their search efforts in high density prey patches may exhibit type III functional responses if different prey types dominate different patches (Hassell and May 1974, Murdoch et al. 1975, Murdoch and Oaten 1975). In the present study, numerous alternative prey types were available at varying (unknown) densities, so application of Murdoch's (1969) test for switching behavior is not possible and the mechanisms underlying our type III response models are unknown. We will use the term 'switching' in this paper to describe cases when the dominant prey type in the diet changes abruptly.

Our analysis indicated that herring may begin to switch to alternative prey as the mean biomass of large calanoid copepods in the upper 20 m of the water column declines below about 0.2 g m^{-3}. Similarly, adult pollock may begin to switch to alternative prey as the mean biomass of large calanoid copepods in high density layers declines below about 1.0 g m^{-3}. There was considerable variability about the functional response near this threshold as each predator began to switch to alternative prey. This variability may result from the presence of different alternative prey at varying densities at each location or individual or group variation in prey preferences. In an experiment conducted by Olmsted et al. (1979), one group of mimic shiners (*Notropis volucellus*) developed a strong preference for a particular prey type and another group a weak preference. When an alternative prey was offered, the strong preference group did not switch to the alternative prey even when it was presented at a much higher density than the preferred prey. Olmsted et al. (1979) also found a high degree of individual variability in prey preferences. A high degree of individual variation in prey preferences has also been documented from field studies of fishes (Bryan and Larkin 1972, Ehlinger 1990). In the present study, the percent of herring and immature pollock diets comprised of large calanoid copepods remained relatively high in late May 1995 (Figures 6-7), well after copepod densities in the surface layer had declined (Figure 4). This may be an indication of a preference for large calanoid copepods among herring and immature pollock for a period of time after the bloom.

The parameters of our best fit functional response model for herring were consistent with a particulate feeding mode. Values for γ (0.0791 m^2) and U (10.0 km day^{-1}) consistent with particulate feeding provided the best fit to the data. An identical fit could be obtained with values for γ and U of 0.0001 m^2 (consistent with ram filter feeding) and 7900 km day^{-1} (469 L sec^{-1}), respectively. However, burst swimming speeds of fish typically range between 10-20 L sec^{-1} (Brett and Groves 1979), so the swimming speed required to obtain a similar fit of our herring data using a value of γ consistent with ram filter feeding is not physiologically possible. Filter feeding is energetically more profitable than particulate feeding for herring (13-20 cm) feeding on *Calanus finmarchichus* (2.8 mm) at prey densities exceeding about 13,000 ind. m^{-3} (Gibson and Ezzi 1992). In the present study, densities of large calanoid copepods were only 80 ind. m^{-3} at the asymptote of our functional response model for herring. It is likely that herring were feeding in high density patches of copepods, but it seems unlikely that copepod densities in patches were high enough for profitable filter feeding by herring. Copepod densities have been found to vary horizontally by a factor of 7.0 off British Columbia (Parsons and LeBrasseur 1973) and 2.5-6.0 off California

(Huntley et al. 1995), but densities more than two orders of magnitude greater than densities measured in the present study would be required for profitable filter feeding by herring.

The parameters of our best fit functional response model for adult pollock were consistent with a ram filter feeding mode with limitation of daily food consumption by gastric evacuation. As previously indicated, our handling time estimate includes time spent capturing and ingesting prey, as well as, any time spent not searching for prey due to satiation or low light level. Our functional response model for adult pollock reached an asymptote at a mean surface layer prey density of 1.0 g m^{-3} (385 ind. m^{-3}), and the daily food consumption at the asymptote was about 7.0 g day^{-1} (0.8% BW day^{-1}) or 0.08 mg sec^{-1}. If we assume continuous feeding throughout the day and no limitation due to gastric evacuation rate, an adult pollock swimming at 0.2 m sec^{-1} , filter feeding on copepods at a density of 1.0 g m^{-3} should consume prey at a rate of about 0.4 mg sec^{-1}. This rate is about 5 times greater than the daily food consumption at the asymptote of our functional response model indicating some portion of the day is likely spent not feeding due to satiation or low light level. If adult pollock are filter feeding, low light level will likely not limit the time spent feeding, indicating that gastric evacuation rate may limit daily food consumption. Our best fit of the functional response model for adult pollock was obtained with values for γ and U of 0.0022 m^2 (consistent with ram filter feeding) and 16.7 km day^{-1} (0.4 L sec^{-1}), respectively. This swimming speed estimate is very similar to that estimated from field measurements (15 km day^{-1}) for foraging schools of adult pollock in the Bering Sea (Radchenko and Sobolevskiy 1993). However, an identical fit of the functional response for adult pollock could be obtained with values for γ and U of 0.2778 m^2 (consistent with particulate feeding) and 0.13 km day^{-1} (3.0×10^{-6} L sec^{-1}), respectively. Further direct measurements of swimming speeds of individual adult pollock foraging on large calanoid copepods are needed to resolve this question. Feeding mode is likely determined by the relative profitability of each strategy (Crowder 1985) which is a function of fish size, prey size, and prey density (Durbin 1979, Gerking 1994). Studies involving herring and alewifes and Pacific mackerel have shown that ram filter feeding generally occurs at prey densities greater than 10,000 ind. m^{-3} (Janssen 1976, Gibson and Ezzi 1985, 1992). In the present study, the mean copepod density in layers was about 385 ind. m^3 at the asymptote of our best fit functional response model for adult pollock. Thus, laboratory studies suggest that copepod densities more than an order of magnitude greater would be required for profitable filter feeding by adult pollock. However, no laboratory data is available regarding the densities required for fish the size of adult pollock to profitably filter feed on prey the size of large calanoid copepods. The prey-predator size ratio estimated in the present study for adult pollock feeding on large calanoid copepods is about 0.5%. This ratio is at the lower end of the range for particulate feeding and the upper end of the range for filter feeding as estimated by Durbin (1979). Yoshida (1994) predicted from gill raker spacings that adult pollock would likely consume prey greater than 2 mm, but zooplankton greater than 4 mm were generally taken. Yoshida (1994) suggested that sight was involved in selecting larger prey. However, retention probabilities calculated from gill raker spacing have been found to underestimate the size of prey actually retained by a factor of two (Wright et al. 1983). Further studies focused on plankton densities actually utilized by foraging adult pollock, swimming speeds while foraging, and the relationship between prey size, predator size and gill raker spacing (Lammens 1985) will help determine the feeding mode utilized by adult pollock feeding on large calanoid copepods.

In the present study, mean prey-predator length ratios estimated for herring and adult pollock were below the range for mean prey-predator length ratios (20-30%) typically observed among piscivorous fish. The mean prey-predator length ratio for adult pollock was 8.4%, minimum and modal prey lengths were similar for both immature and adult pollock, but adult pollock consumed prey up to 15 cm which were not taken by immature pollock (Figure 10). In a review of piscivory in freshwater systems, Popova (1978) showed that maximum prey size increases as predaceous fish grow whereas minimum prey size remains constant. Thus, mean prey-predator length ratios tend to stabilize around 10% for larger predators. The results from the present study are generally consistent with Popova's (1978) conclusions suggesting that similar generalizations may apply in marine systems. Mean prey-predator length ratios were smallest for juvenile gadids and salmonids as prey (Table 6). This was likely due simply to the smaller lengths of these prey fish in the environment (Figure 12) rather than any difference in escape response between these species and the others. The relationship between burst swimming speeds of potential prey and optimal foraging speeds of predaceous fish may largely determine mean prey-predator length ratios. Burst swimming speeds typically range from 10-20 L sec^{-1} (Brett and Groves 1979, Puckett and Dill 1984); whereas, optimal foraging speeds range from 1-3 L sec^{-1} (Ware 1978). Thus, a mean prey-predator length ratio of 10% roughly equalizes the burst swimming speed of potential prey and the optimal foraging speeds of predators. Thus, generally a predator may prey on fish up to 10% of its length and still maximize its production (Ware 1978).

Multiple regression analysis indicated that herring and immature pollock tend to switch from large calanoid copepods to fish after the decline of the copepod bloom, but adult pollock do not switch to fish after the bloom. Much of the variance in copepod biomass and relative abundances of prey fish was associated with a seasonal decrease (increase) of each variable, respectively (Figures 4 and 11), suggesting that multicollinearity may have affected our results. But, the variance inflation factors for these analyses were substantially less than the threshold above which multicollinearity is generally considered to adversely affect parameter estimates (Neter et al. 1989). Our regression results indicate that consumption of fish by herring and immature pollock was associated copepod biomass, but consumption of fish by adult pollock was not (Table 8). Herring, immature pollock and adult pollock diets were generally dominated by large calanoid copepods during the bloom in May (Figures 6-8). Consumption of alternative prey including fish by these predators was generally reduced at this time. After the copepod bloom, herring and immature pollock tended to consume more fish (Table 8), but other alternative prey were also taken (Figures 6-7). Consumption of fish by immature pollock was also associated with the relative abundance of prey fish, but this was not the case for the other two predators (Table 8). Immature pollock also exhibited the greatest degree of piscivory overall (Table 5) suggesting a preference for fish as prey. Juvenile gadids and salmonids were the most commonly encountered fish in the diets of herring and immature pollock (Table 5). Thus, as herring and immature pollock switch to feeding on fish after the copepod bloom, mortality among juvenile gadids and salmonids will likely increase.

Coded-wire tag data allowed us to further examine whether mortality among juvenile pink salmon was related to copepod biomass. The analysis was structured to enable examination of the simultaneous effects of zooplankton density on juvenile growth rate and predator switching behavior. The results from this analysis support the hypothesis that a prolonged spring bloom of large calanoid copepods generally results in reduced mortality among juvenile pelagic fishes (Tables 10 and 11). This result is also generally consistent with our results from analyses of predator stomach contents (Table 8, Figure 13) suggesting that predator switching behavior is the cause. The range of juvenile body weights (0.20-0.35 g) in our data corresponds roughly to lengths ranging from 30-36 mm. The apparent decrease in mortality with size among juvenile pink salmon over this relatively narrow size range indicates that predation is highly size-selective. Sizes of prey fish in stomachs of herring and adult pollock are generally consistent with this conclusion, but sizes of prey fish in immature pollock stomachs are not (Figure 10). Size-selective predation by other fish species/sizes not included in this analysis may have also caused the observed relationship. Differences in mortality over similar narrow size ranges have been observed among juvenile sockeye (West and Larkin 1987) and chum salmon (Healey 1982).

In the present study, mortality of hatchery-reared pink salmon during the marine lifestage appeared to be depensatory. Several studies have documented density-dependent mortality during the marine lifestage of salmonids without identifying the processes causing the observed relationships (Peterman 1980, Kaeriyama 1983, Elmen et al. 1990). In the present study, we also cannot conclusively determine the processes causing the observed depensation. Our estimates of natural mortality of pink salmon include effects over a 470 day period during which these fishes range throughout the Gulf of Alaska (Heard 1991). However, saturation of predator populations feeding on juvenile pink salmon is a possible cause of the observed relationship. Data presented by Dobrynina et al. (1989) indicates that several marine fish species feeding on juvenile pink salmon emigrating from the Utka River were likely operating near the lower end of their functional response curves. But, the densities of juveniles in this natural setting were likely much lower than those resulting from large-scale releases of hatchery-reared fish.

Further study is needed to determine whether predator saturation is the cause of the apparent depensatory mortality among juvenile pink salmon released from hatcheries in PWS.

Our results also indicate that growth of juvenile pink salmon is reduced when zooplankton densities are low and juvenile salmonid densities are high (Figure 14). This suggests that competition for food among juvenile pink salmon is likely under these conditions. Walters et al. (1978) concluded that competition for food among juvenile salmonids is unlikely in the coastal ocean; whereas, Bailey et al. (1975) estimated that enhancement programs may lead to food limitation among juvenile salmonids in nearshore habitats. Walters and Juanes (1993) suggest that consumption per time spent feeding and foraging times should be density dependent when juveniles occupy restricted feeding habitats to avoid predation. This is likely the case with juvenile pink salmon which often occupy nearshore habitats before reaching a length of about 60 mm (Heard 1991).

The results from these analyses indicate that mortality among juvenile gadids and salmonids is likely affected by the timing of the seasonal decline of the *Neocalanus spp.* bloom relative to the prey fishes' growth rate. Mortality among other larval or relatively small juvenile fishes (e.g. sandlance, capelin, herring etc.) that occur in pelagic habitats during the spring bloom period is also likely affected by these processes. Juvenile gadids and salmonids are growing rapidly at this time of year (Figure 12). Individuals that reach a length exceeding 50-70 mm are probably less vulnerable to predation by herring and immature pollock (Figure 10). Predation by herring and immature pollock may be relatively high in early June in some years (Figures 6 and 7), because copepod densities have generally declined by that time (Figure 4), yet a substantial portion of the juvenile gadid and salmonid population is still vulnerable to predation due to their small size (range approximately 40-65 mm, Figure 12). These results are consistent with Healey (1982) who concluded that mortality was probably high and strongly size selective among juvenile chum salmon over the length range 45-55 mm corresponding to the size of emigration from nearshore habitats. In the present study, the relative abundance of herring and immature pollock also increased in nearshore habitats during early June in some years (Figure 5). This may indicate a numerical response to the presence of juvenile salmonids (Holling 1959, Beddington et al. 1976, Hassel et al. 1976) after the decline of the copepod bloom.

Our analysis indicates that bottom-up processes affecting the duration of the spring copepod bloom also modify top-down processes involving the timing of feeding mode shifts toward piscivory among the later lifestages of herring and pollock. As previously indicated, the bloom of *Neocalanus spp.* may be prolonged during May when the surface layer is weakly stratified and cooler. At the present time, we are only beginning to understand how these conditions may affect predation on juvenile fishes. Lower temperatures will likely slow the growth of juvenile fishes (Brett and Groves 1979), yet a prolonged *Neocalanus spp.* bloom may accelerate juvenile growth and shelter juveniles from predation for a longer time. The converse may be true when the surface layer is more strongly stratified and warmer. Further study is needed to define the relationship between growth rates of juvenile fishes, the timing of the seasonal decline of the *Neocalanus spp.* bloom and mortality of juvenile fishes.

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Table 1: Dates and areas where sampling was conducted in western Prince William Sound, 1994-1996. See figure 1 for locations of sampling areas.

Year	Area	Dates Sampled
1994	60	April 27, May 7, May 22, June 5, July 8
	61	May 9, May 23, June 9, July 10
	62	May 12, May 26, June 8, July 18
	63	June 7, June 22, July 9
	64	June 21, July 13
	65	June 28, July 14
	66	May 13, June 23, July 12
1995	501	May 3, May 11, May 30
	502	May 17, June 5
	504	June 9
	505	June 11
	506	May 5, May 15, June 8
	509	June 13
	525	May 8, May 13, June 3
	526	May 9

Table 1: continued.

Year	Area	Dates Sampled
1996	501	May 3, May 6, June 5
	502	May 4, May 7, May 24, June 1
	525	May 5, May 8, May 19, May 23, June 2, June 8
	504	May 25, June 6
	506	May 20, June 7
	586	May 21, June 3
	587	May 22, June 4

Table 2: Number of specimens processed for stomach contents analysis in western Prince William Sound, 1994-1996.

Year	Herring	Immature Pollock	Adult Pollock
1994	1,594	280	2,232
1995	3,486	745	3,111
1996	2,659	398	901

Table 3: Geometric mean catch per net set for immature and adult fishes (>150 mm length) in purse seines in western Prince William Sound, 1994-1996. Catch per hour of tow in mid-water trawls is used for pollock.

Year	Taxonomic Group	% Frequency Occurrence	Geometric Mean Catch/Set
1994	Herring	43.6	5.4
	Pollock	66.8	18.3
	Salmonids	27.7	1.8
	Capelin	0.2	1.0
	Sandlance	0.2	1.0
	Squid	3.0	1.1
	Other Fish	10.7	1.1
1995	Herring	36.9	10.5
	Pollock	81.8	33.5
	Salmonids	18.6	1.6
	Capelin	1.3	1.0
	Sandlance	0.6	1.0
	Squid	4.0	1.1
	Other Fish	21.1	1.4

Table 3: continued.

Year	Taxonomic Group	% Frequency Occurrence	Geometric Mean Catch/Set
1996	Herring	33.0	3.1
	Pollock	80.9	13.6
	Salmonids	16.0	1.5
	Capelin	3.2	1.2
	Sandlance	0	0
	Squid	22.3	4.7
	Other Fish	16.0	1.1

Table 4: Summary of 'best fit' non-linear regression models for type II and III functional responses for herring, immature pollock and adult pollock feeding on large calanoid copepods. The best fit model for each species is indicated with an asterisk, and the standard error of the estimated swimming speed (U) is indicated in parentheses.

Predator Type		γ (m^2)	Estimated U (km day^{-1})	H (day g^{-1})	MS Regression	MS Error	
Herring	II	0.0001	43.0 (7.3)	.167	7.86	0.16	
		0.0791	0.6 (0.5)	1.930	7.91	0.16	
	III	0.0001	17.2 (2.0)	-1.913	2.99	0.33	
		0.0791	10.0 (5.3)	1.247	9.40	0.10	*
Immature	II	0.0003	16.7 (3.7)	.304	5.27	0.14	
Pollock		0.0791	0.3 (0.4)	2.813	3.29	0.22	
	III	0.0003	61.3 (18.4)	.319	4.59	0.16	
		0.0791	4.5 (5.6)	2.151	3.96	0.19	
Adult	II	0.0022	8.1 (3.8)	.248	208.02	5.52	
Pollock		0.2788	0.1 (0.2)	.524	156.47	6.96	
	III	0.0022	16.7 (5.0)	.142	243.46	4.54	*
		0.2788	0.4 (0.5)	.438	185.24	6.16	

Table 5: Mean percent of the diet for various prey fish consumed by herring, immature pollock and adult pollock in western Prince William Sound, 1994-1996. The standard error of the mean is indicated in parentheses.

Year	Prey	Herring	Immature Pollock	Adult Pollock
1994	Herring	0.12 (0.37)	0.01 (0.70)	0.91 (0.36)
	Gadids	0.39 (0.98)	3.42 (1.83)	2.16 (0.93)
	Salmonids	0.04 (0.23)	0.03 (0.43)	0.94 (0.22)
	Capelin	0	0	0
	Sandlance	0.11 (0.09)	0	0.16 (0.09)
	Squid	0	0	4.90 (0.93)
	Other Fish	0.14 (0.77)	0.22 (1.44)	2.22 (0.73)
	Uni. Fish	3.64 (1.53)	10.75 (2.86)	5.76 (1.45)
	All Fish	4.44 (2.14)	14.43 (4.01)	17.06 (2.04)
1995	Herring	0	0	0.11 (0.04)
	Gadids	1.13 (0.73)	2.03 (1.01)	0.30 (0.72)
	Salmonids	0.09 (0.66)	4.08 (0.91)	0.13 (0.65)
	Capelin	0	0	0
	Sandlance	0	0	0
	Squid	0.01 (0.44)	0	3.81 (0.44)
	Other Fish	0.31 (0.22)	0.67 (0.31)	0.14 (0.22)
	Uni. Fish	9.85 (1.49)	7.17 (2.06)	2.16 (1.46)
	All Fish	11.39 (1.91)	13.90 (2.64)	6.69 (1.88)

Table 5: continued.

Year	Prey	Herring	Immature Pollock	Adult Pollock
1996	Herring	0	0	1.69 (0.72)
	Gadids	0.05 (0.03)	0	0.01 (0.03)
	Salmonids	3.18 (1.81)	10.32 (2.43)	1.10 (1.84)
	Capelin	0	0	0.73 (0.45)
	Sandlance	0	7.23 (1.90)	0
	Squid	0	0	7.67 (1.39)
	Uni. Fish	0.35 (0.33)	1.38 (0.44)	0.27 (0.33)
	Other Fish	0.59 (1.40)	7.33 (1.87)	4.60 (1.42)
	Total Fish	4.18 (2.86)	26.25 (3.83)	16.02 (2.90)

Table 6: Mean length and prey-predator length ratios for various prey fish in the diets of herring, immature pollock, and adult pollock. Data from 1994-1996 combined.

	Herring		Immature Pollock		Adult Pollock	
Prey Species	Length	Ratio	Length	Ratio	Length	Ratio
Herring	-	-	-	-	115.5	20.9
Gadids	28.0	14.1	34.3	20.3	22.7	5.0
Salmonids	40.3	18.9	40.5	19.5	39.1	8.1
Capelin	-	-	-	-	92.5	19.1
Sandlance	-	-	57.4	22.9	98.8	17.6
Squid	-	-	-	-	68.9	13.1
Other Fish	19.3	10.4	24.5	12.5	47.9	8.6
Uni. Fish	21.7	11.4	23.7	9.6	42.2	8.2

Table 7: Geometric mean catch per net set for juvenile fishes (<150 mm length) in purse seines in western Prince William Sound, 1994-1996.

Year	Taxonomic Group	% Frequency Occurrence	Geometric Mean Catch/Set
1994	Herring	12.5	1.7
	Gadids	33.2	54.6
	Salmonids	30.0	5.4
	Capelin	3.7	1.2
	Sandlance	1.6	1.0
	Squid	0.7	1.0
	Other Fish	18.2	1.6
1995	Herring	15.5	1.6
	Gadids	5.5	1.3
	Salmonids	23.2	3.7
	Capelin	18.2	2.1
	Sandlance	2.7	1.0
	Squid	6.5	1.6
	Other Fish	28.4	3.1

Table 7: continued.

Year	Taxonomic Group	% Frequency Occurrence	Geometric Mean Catch/Set
1996	Herring	4.9	1.1
	Gadids	6.5	1.5
	Salmonids	32.4	27.5
	Capelin	20.0	2.4
	Sandlance	0	0
	Squid	13.0	3.5
	Other Fish	23.2	2.4

Table 8: Parameters estimated from a multiple regression analysis with the proportion of herring and pollock diets comprised of fish as the dependent variable and the relative abundance of prey fish and the biomass of large calanoid copepods as independent variables.

Fish Species	Independent Variable	Regression Parameter	Standard Error	Type I Test P-value	Type III Test P-value
Herring	Copepod biomass	-0.620	0.346	0.126	0.083
	Prey fish abundance	-0.028	0.026	0.298	0.298
Immature Pollock	Copepod biomass	-1.145	0.771	0.020	0.150
	Prey fish abundance	0.117	0.055	0.044	0.044
Adult Pollock	Copepod biomass	-0.194	0.332	0.646	0.564
	Prey fish abundance	0.005	0.019	0.748	0.709

Table 9: Parameters estimated from an analysis of covariance relating the growth rate of coded-wire tagged juvenile pink salmon to mean zooplankton settled volume, mean ocean temperature, and number of juveniles released from each hatchery each day.

Parameter		Estimate	Standard Error	Type III Test P-value
Intercept		-5.762	1.468	<0.001
Mean zooplankton volume		3.201	0.445	<0.001
Mean ocean temperature		2.421	0.780	0.002
Number juveniles released:	low	4.850	0.676	<0.001
	high	0.000	-	-
Zooplankton x release number:	low	-2.729	0.480	<0.001
	high	0.000	-	-

Table 10: Parameters estimated from an analysis of covariance relating the instantaneous natural mortality of coded-wire tagged pink salmon to zooplankton settled volume, mean juvenile growth rate, mean body weight at release, and number of juveniles released from each hatchery each day.

Parameter		Estimate	Standard Error	Type III Test P-value
Intercept		0.0774	0.0123	<0.001
Zooplankton volume:	low	0.0014	0.0006	0.013
	moderate	0.0002	0.0005	-
	high	0.0000	-	-
Mean juvenile growth rate		-0.0112	0.0024	<0.001
Body weight at release		-0.2419	0.0455	<0.001
Number juveniles released		-0.0077	0.0020	<0.001
Growth x release weight:		0.0391	0.0085	<0.001
Number released x release weight		0.0264	0.0075	<0.001

Table 11: Least-squares means estimated from an analysis of covariance relating the instantaneous natural mortality of coded-wire tagged pink salmon to zooplankton settled volume, mean juvenile growth rate, mean body weight at release, and number of juveniles released from each hatchery each day. P-values for pairwise comparisons of the means are indicated.

Zooplankton Volume	Least Squares Mean	Standard Error	Pairwise Comparisons Low	Pairwise Comparisons Mod.	Pairwise Comparisons High
low	0.0097	0.0003	-	0.008	0.013
moderate	0.0085	0.0003	-	-	0.644
high	0.0083	0.0004	-	-	-

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Appendix I: Summary of results of non-linear regression analysis of type II and III functional response models for herring, immature pollock and adult pollock feeding on large calanoid copepods using all possible parameter values.

Table 1: Summary of non-linear regression models for type II and III functional responses of herring feeding on large calanoid copepods. 'Best fit' type II and III models are indicated with an asterisk.

Type	γ (m^2)	U (km day^{-1})	Estimated H (day g^{-1})	MS Regression	MS Error
II	0.0001	16.8	-0.469	6.14	0.22
	0.0791	16.8	1.906	7.11	0.25
	0.0001	33.7	0.167	7.60	0.17 *
	0.0791	33.7	1.930	7.06	0.19 *
	0.0001	50.5	0.400	7.12	0.19
	0.0791	50.5	1.940	7.04	0.19
III	0.0001	16.8	-1.913	2.98	0.33 *
	0.0791	16.8	1.247	9.30	0.11 *
	0.0001	33.7	-.515	3.65	0.31
	0.0791	33.7	1.359	8.92	0.12
	0.0001	50.5	-.061	4.16	0.29
	0.0791	50.5	1.433	8.63	0.13

Table 2: Summary of non-linear regression models for type II and III functional responses of immature pollock feeding on large calanoid copepods. 'Best fit' type II and III models are indicated with an asterisk.

Type	γ (m^2)	U (m day^{-1})	Estimated H (day g^{-1})	MS Regression	MS Error
II	0.0003	16.8	0.304	5.27	0.14 *
	0.0791	16.8	2.679	2.81	0.24 *
	0.0003	33.7	0.726	4.99	0.15
	0.0791	33.7	2.770	2.79	0.24
	0.0003	50.5	0.978	4.64	0.16
	0.0791	50.5	2.808	2.78	0.24
III	0.0003	16.8	-0.355	3.66	0.20
	0.0791	16.8	1.304	3.88	0.19
	0.0003	33.7	0.137	4.26	0.18
	0.0791	33.7	1.567	3.55	0.21
	0.0003	50.5	0.319	4.53	0.17 *
	0.0791	50.5	1.719	3.38	0.21 *

Table 3: Summary of non-linear regression models for type II and III functional responses of adult pollock feeding on large calanoid copepods. 'Best fit' type II and III models are indicated with an asterisk.

Type	γ (m^2)	U (km day^{-1})	Estimated H (day g^{-1})	MS Regression	MS Error
II	0.0022	15.0	0.248	196.18	5.85 *
	0.2778	15.0	0.524	131.85	7.64 *
	0.0022	43.3	0.367	164.12	6.74
	0.2778	43.3	0.529	131.04	7.66
	0.0022	86.7	0.423	151.01	7.11
	0.2778	86.7	0.531	130.82	7.67
	0.0022	130.0	0.449	145.47	7.26
	0.2778	130.0	0.531	130.75	7.67
III	0.0022	15.0	0.142	242.91	4.55 *
	0.2778	15.0	0.438	152.64	7.06 *
	0.0022	43.3	0.217	229.88	4.92
	0.2778	43.3	0.468	144.27	7.29
	0.0022	86.7	0.268	209.98	5.47
	0.2778	86.7	0.486	139.63	7.42
	0.0022	130.0	0.296	198.46	5.79
	0.2778	130.0	0.496	137.35	7.49

List of Figures

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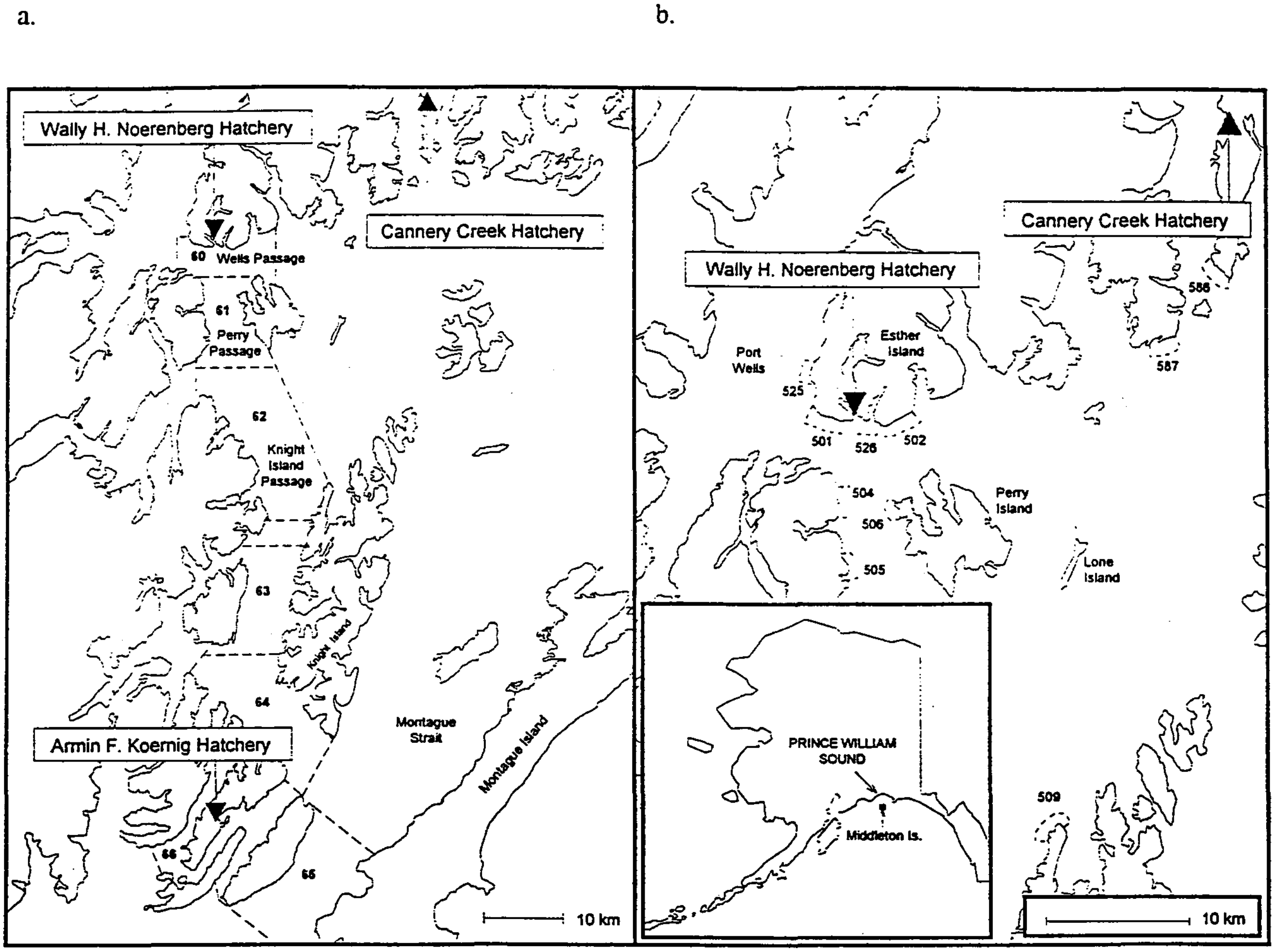

a.
b.
Wally H. Noerenberg Hatchery
Cannery Creek Hatchery
60
Wells Passage
61
Perry Passage
62
Knight Island Passage
63
Knight Island
64
Armin F. Koernig Hatchery
Montague Strait
Montague Island
65
66
10 km
Cannery Creek Hatchery
Wally H. Noerenberg Hatchery
586
587
Port Wells
Esther Island
525
501
526
502
504
506
505
Perry Island
Lone Island
PRINCE WILLIAM SOUND
Middleton Is.
509
10 km

Figure 1

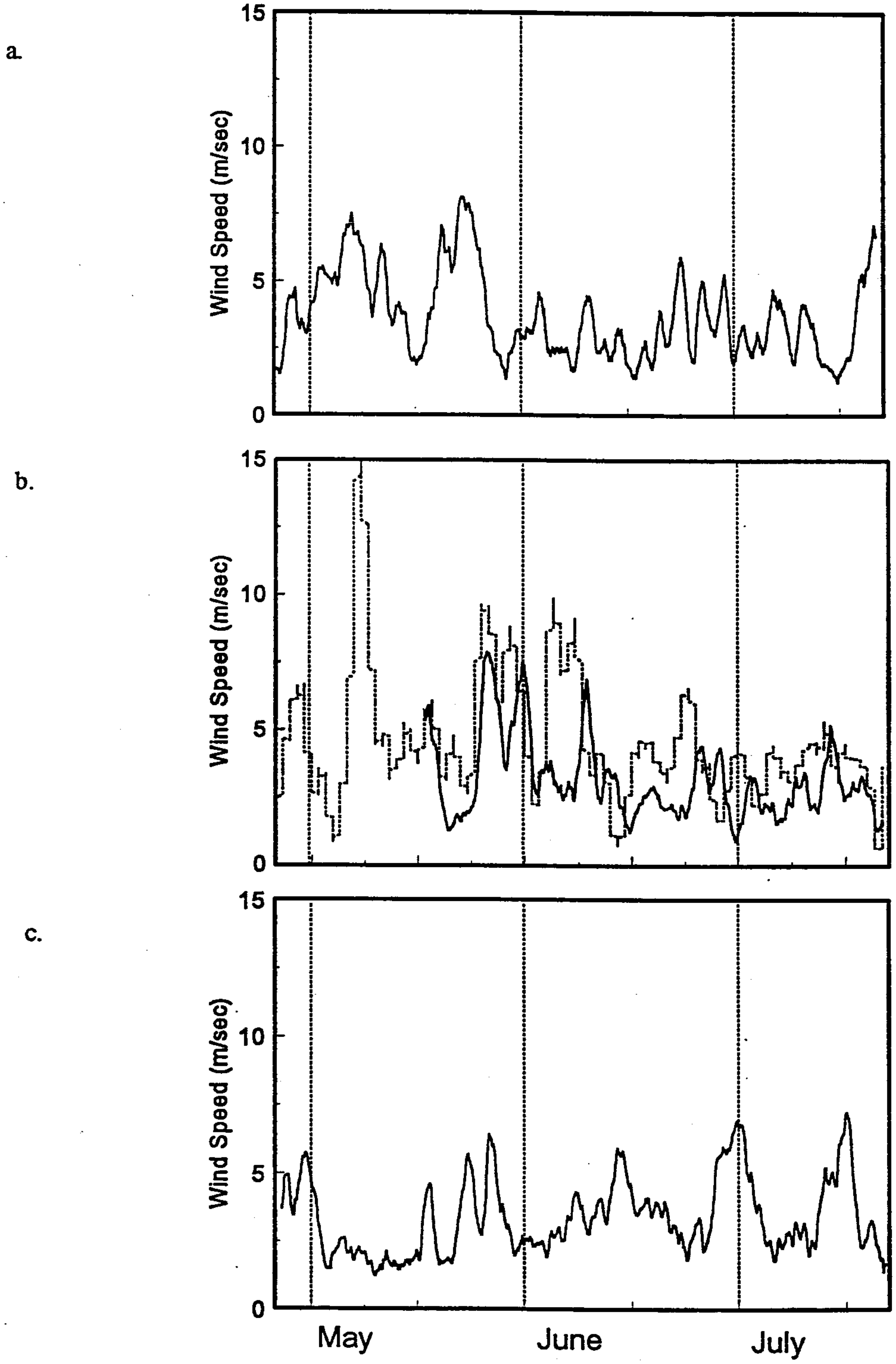
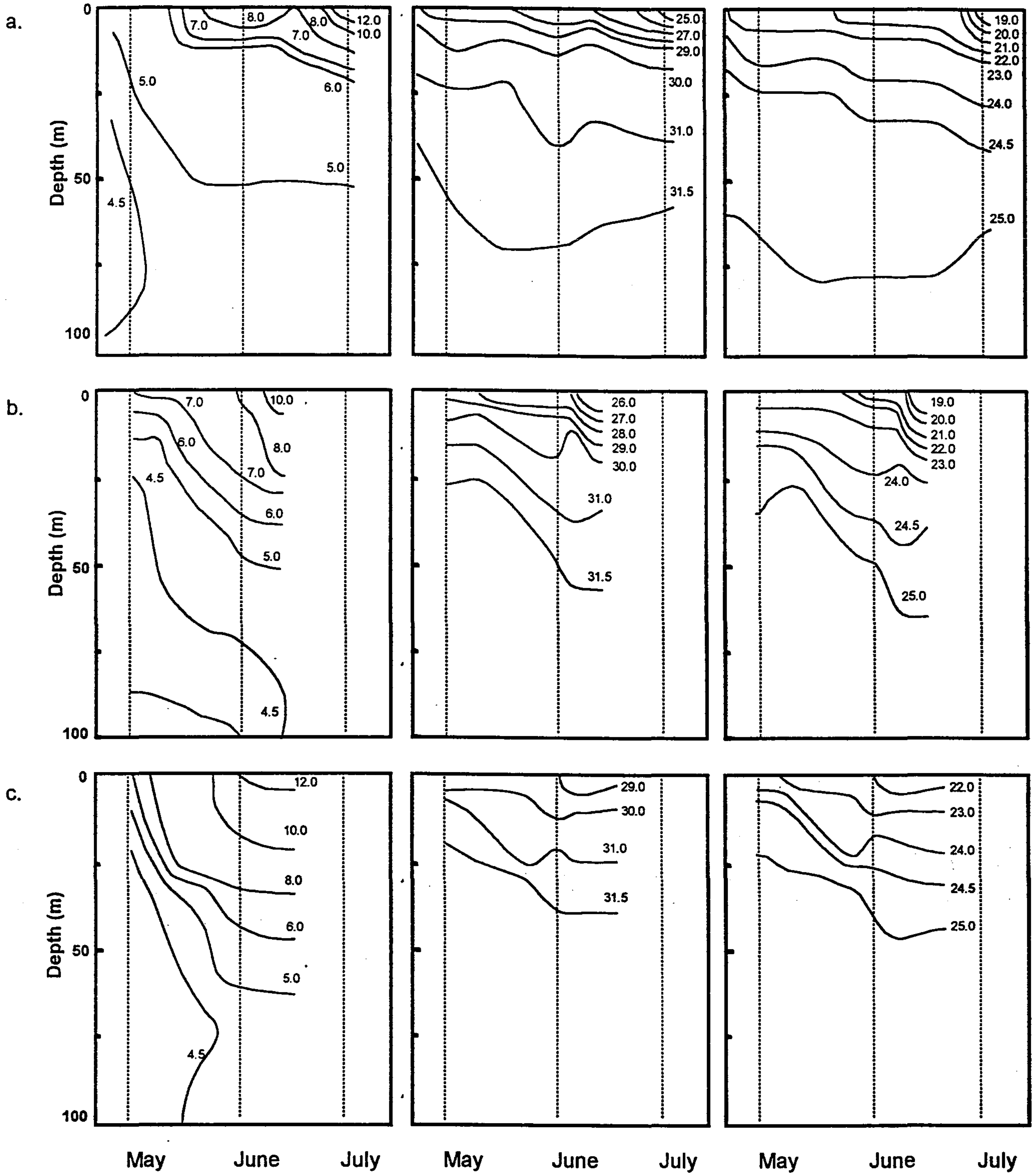


Figure 2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b.
c.
Depth (m)
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50
100
4.5
5.0
6.0
7.0
8.0
10.0
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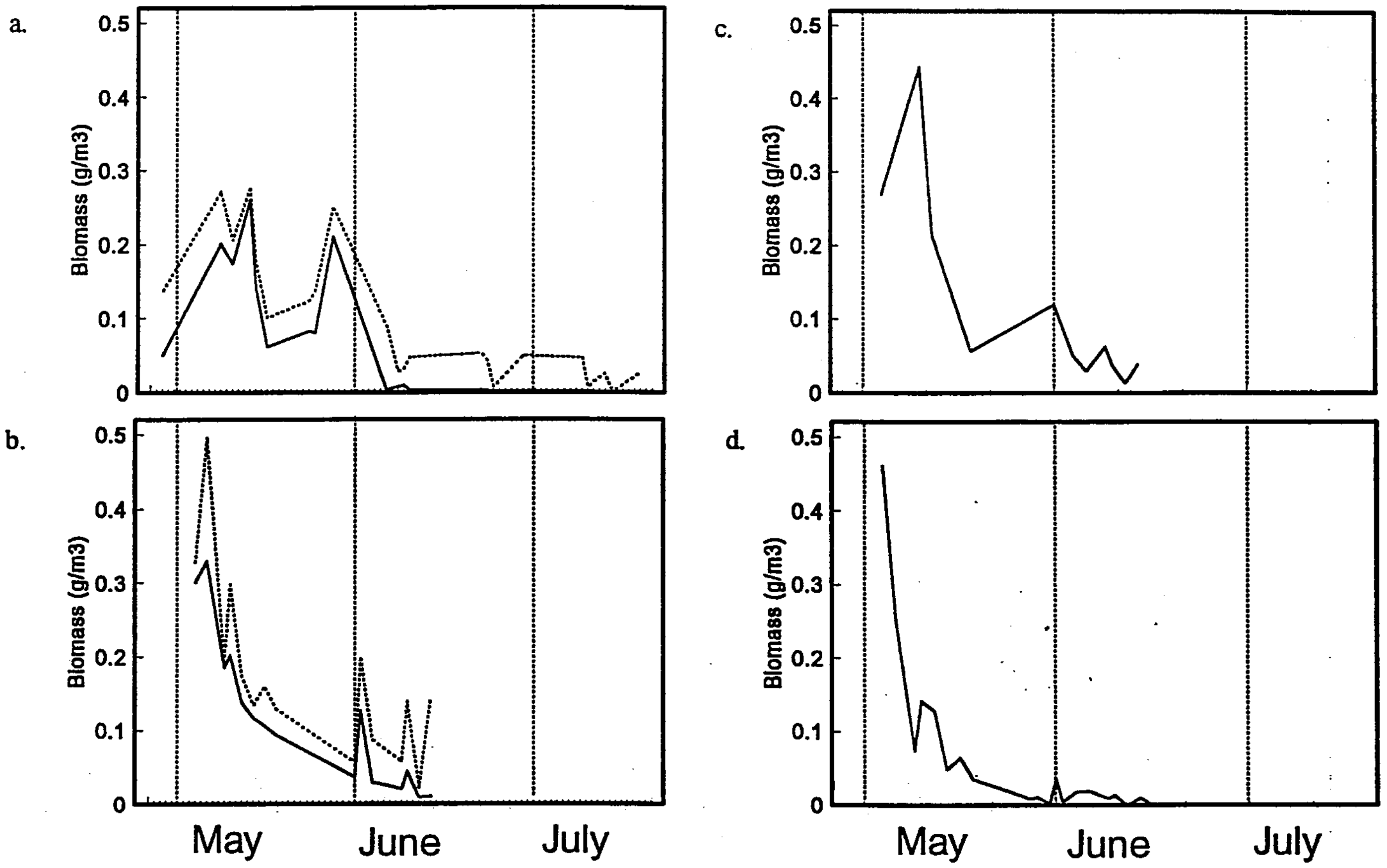
25.0
26.0
27.0
28.0
29.0
30.0
31.0
31.5
19.0
20.0
21.0
22.0
23.0
24.0
24.5
25.0
May
June
July

Figure 3


a.
b.
c.
d.
Biomass (g/m3)
Biomass (g/m3)
Biomass (g/m3)
Biomass (g/m3)
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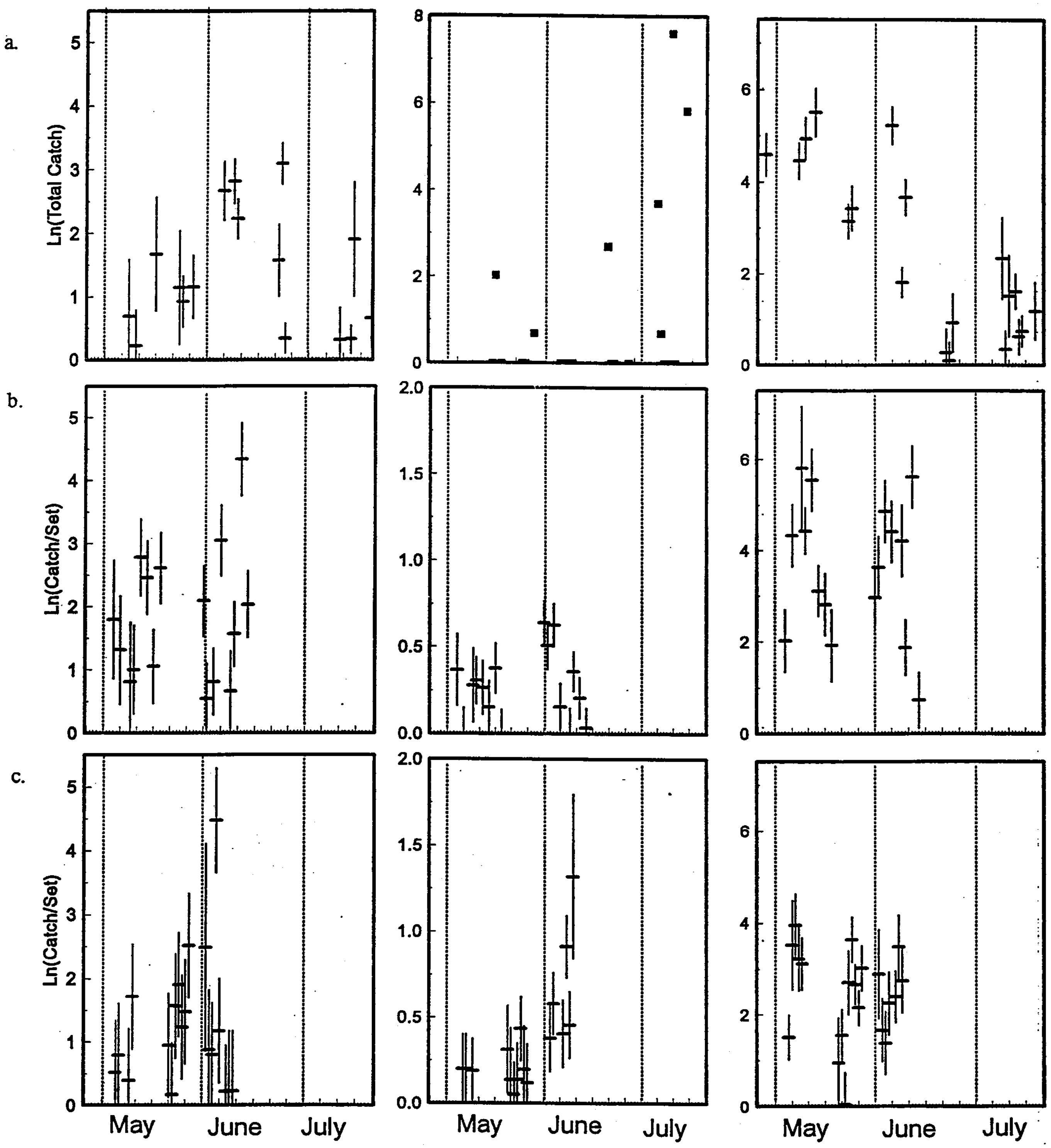
0.4
0.3
0.2
0.1
0
May
June
July
May
June
July

Figure 4


a.
b.
c.
Ln(Total Catch)
Ln(Catch/Set)
Ln(Catch/Set)
0
1
2
3
4
5
0
2
4
6
8
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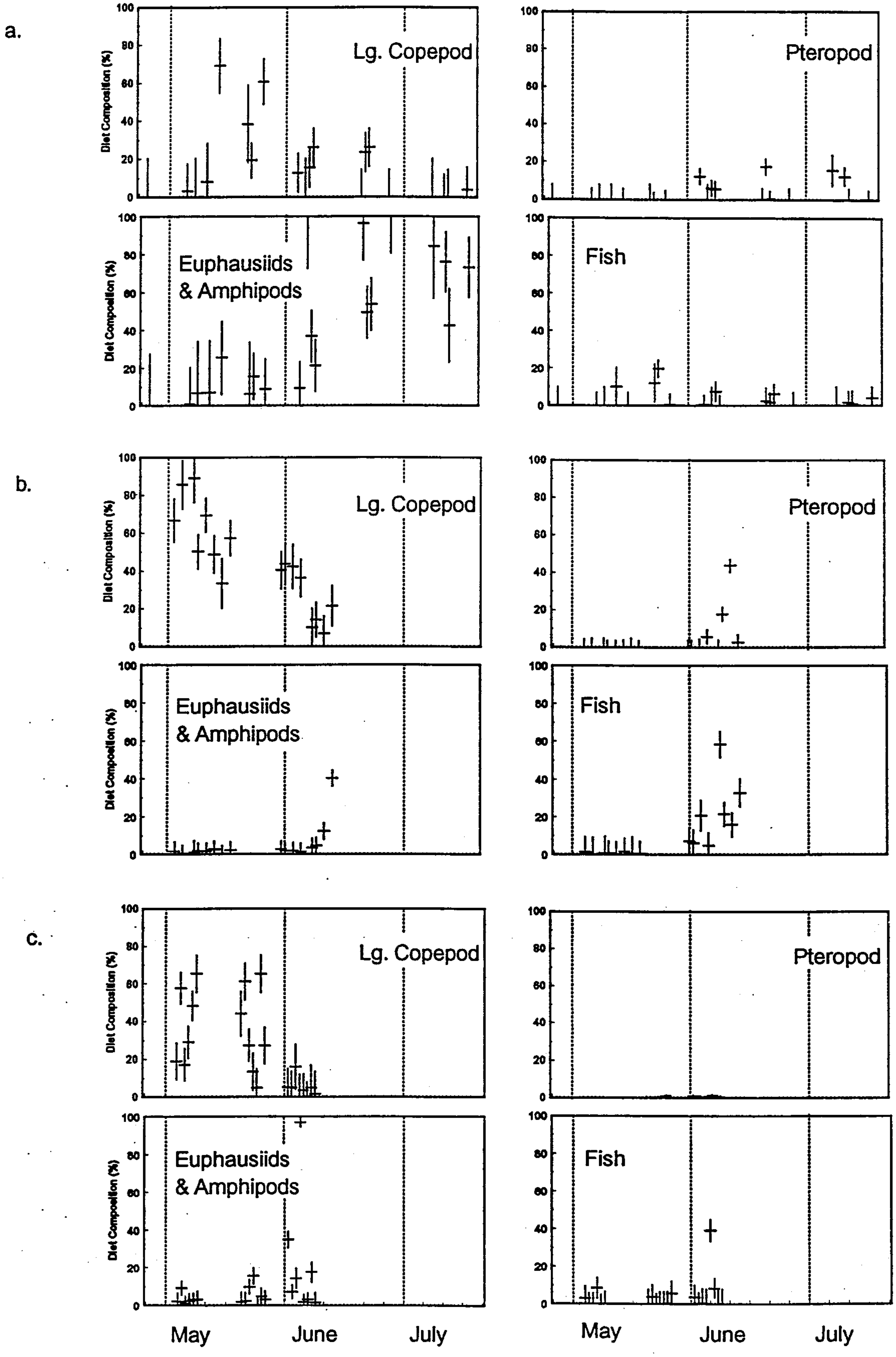
0.5
1.0
1.5
2.0
May
June
July
May
June
July
May
June
July

Figure 5


a.
b.
c.
Lg. Copepod
Pteropod
Euphausiids & Amphipods
Fish
Diet Composition (%)
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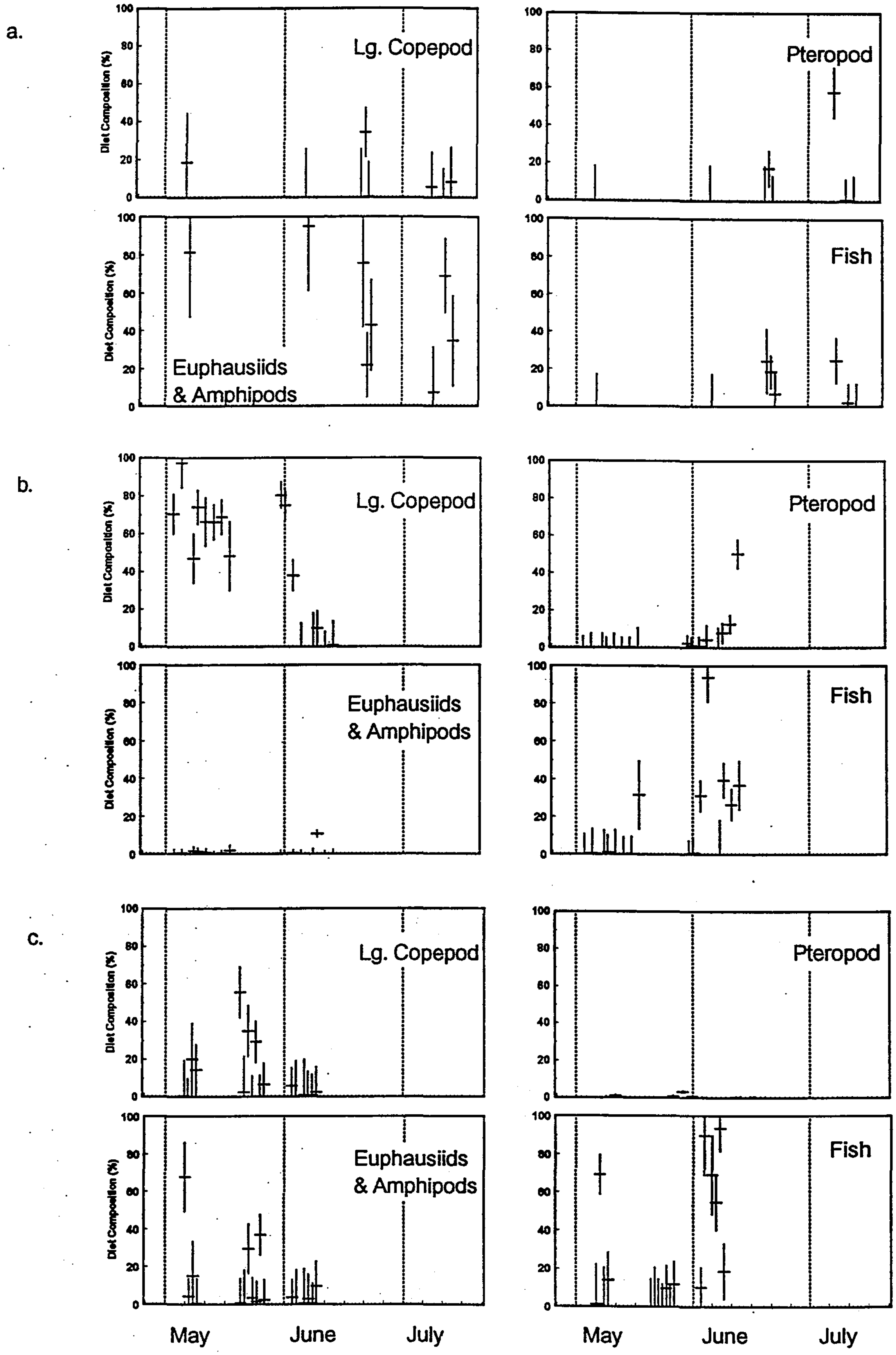
20
40
60
80
100
May
June
July

Figure 6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Lg. Copepod
Pteropod
Euphausiids & Amphipods
Fish
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Lg. Copepod
Pteropod
Euphausiids & Amphipods
Fish
c.
Lg. Copepod
Pteropod
Euphausiids & Amphipods
Fish
Diet Composition (%)
0
20
40
60
80
100
May
June
July

Figure 7

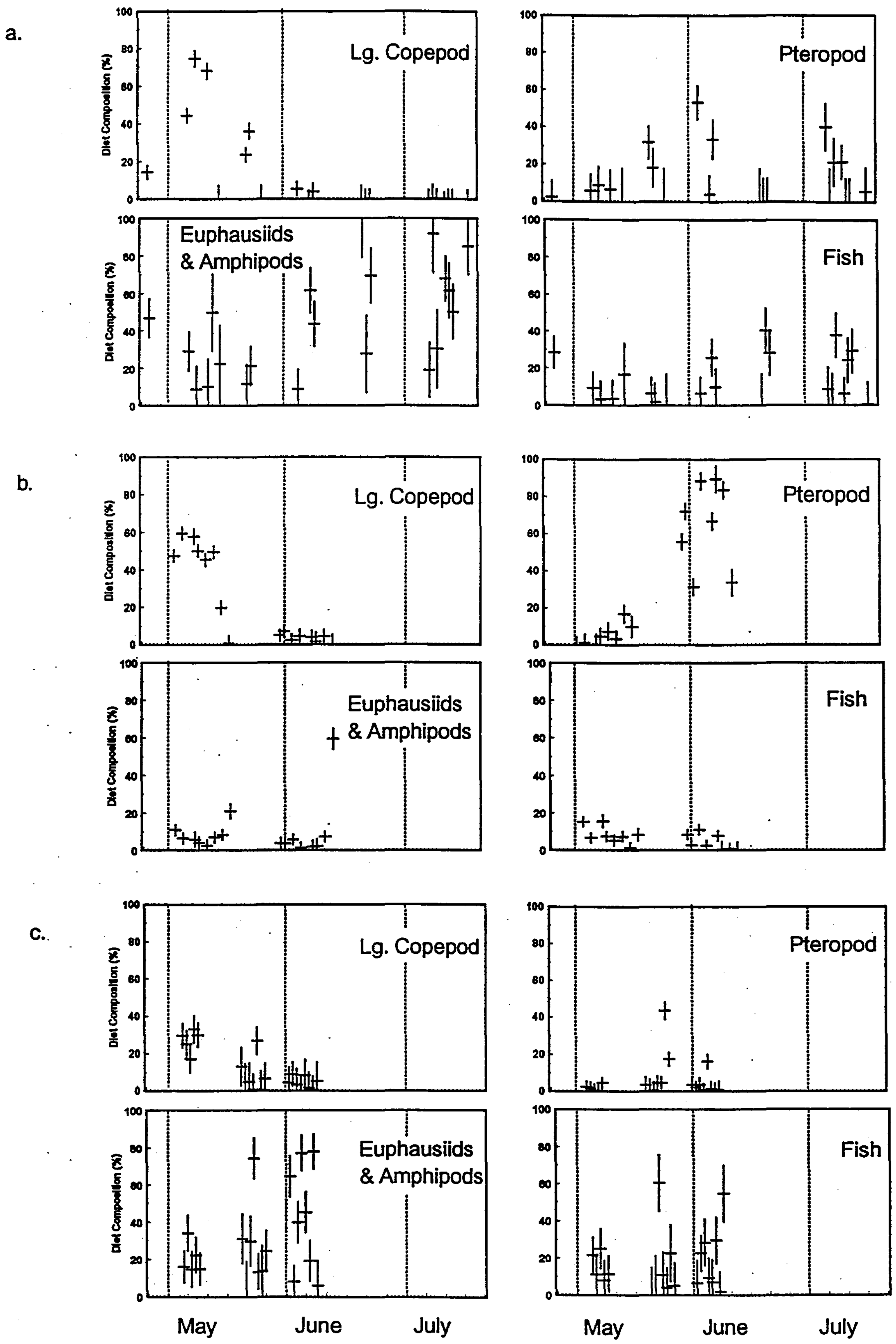
a.
Lg. Copepod
Pteropod
Euphausiids & Amphipods
Fish
b.
Lg. Copepod
Pteropod
Euphausiids & Amphipods
Fish
c.
Lg. Copepod
Pteropod
Euphausiids & Amphipods
Fish
Diet Composition (%)
0
20
40
60
80
100
May
June
July

Figure 8

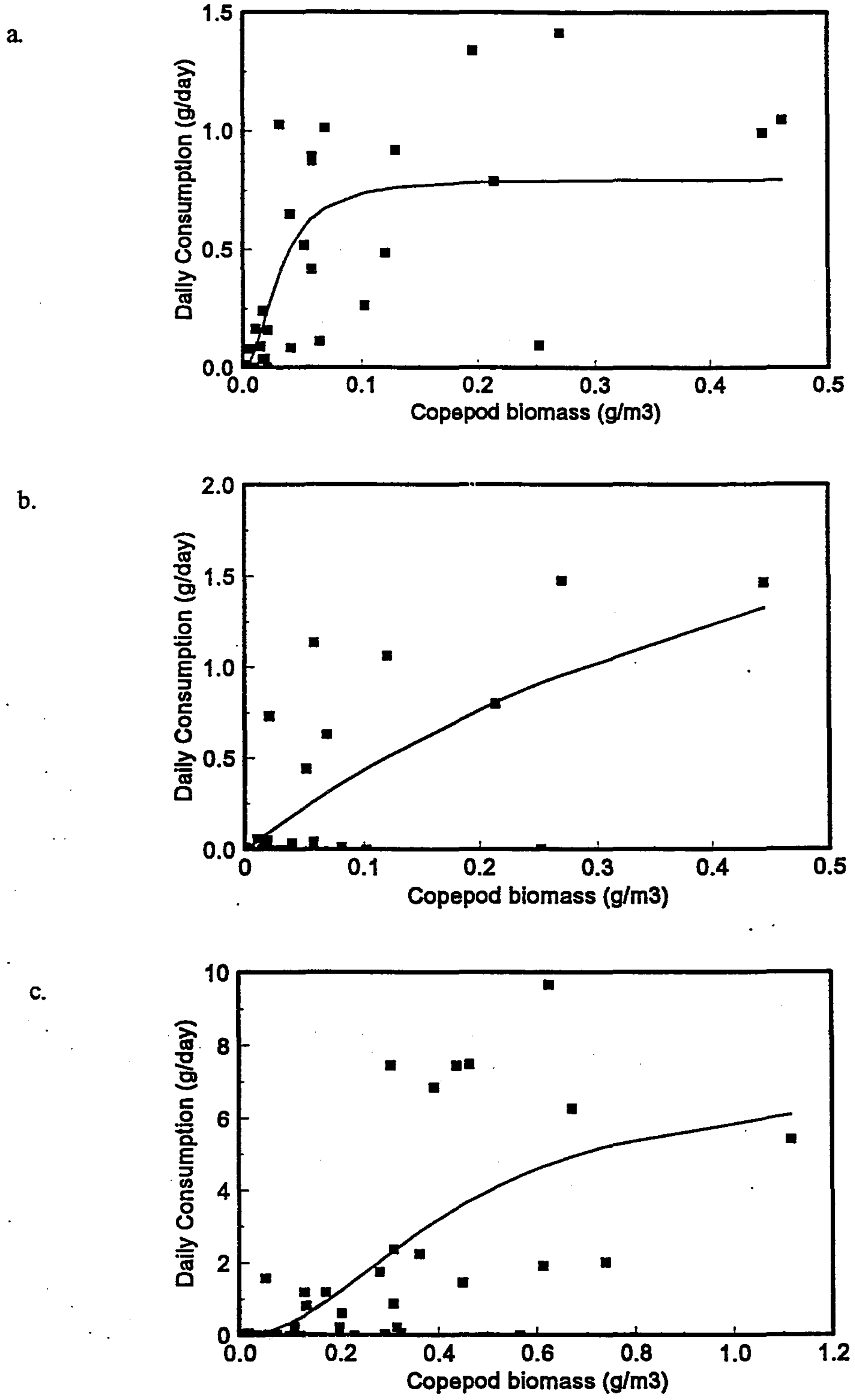
a.
Daily Consumption (g/day)
1.5
1.0
0.5
0.0
0.0
0.1
0.2
0.3
0.4
0.5
Copepod biomass (g/m3)
b.
Daily Consumption (g/day)
2.0
1.5
1.0
0.5
0.0
0
0.1
0.2
0.3
0.4
0.5
Copepod biomass (g/m3)
c.
Daily Consumption (g/day)
10
8
6
4
2
0
0.0
0.2
0.4
0.6
0.8
1.0
1.2
Copepod biomass (g/m3)

Figure 9

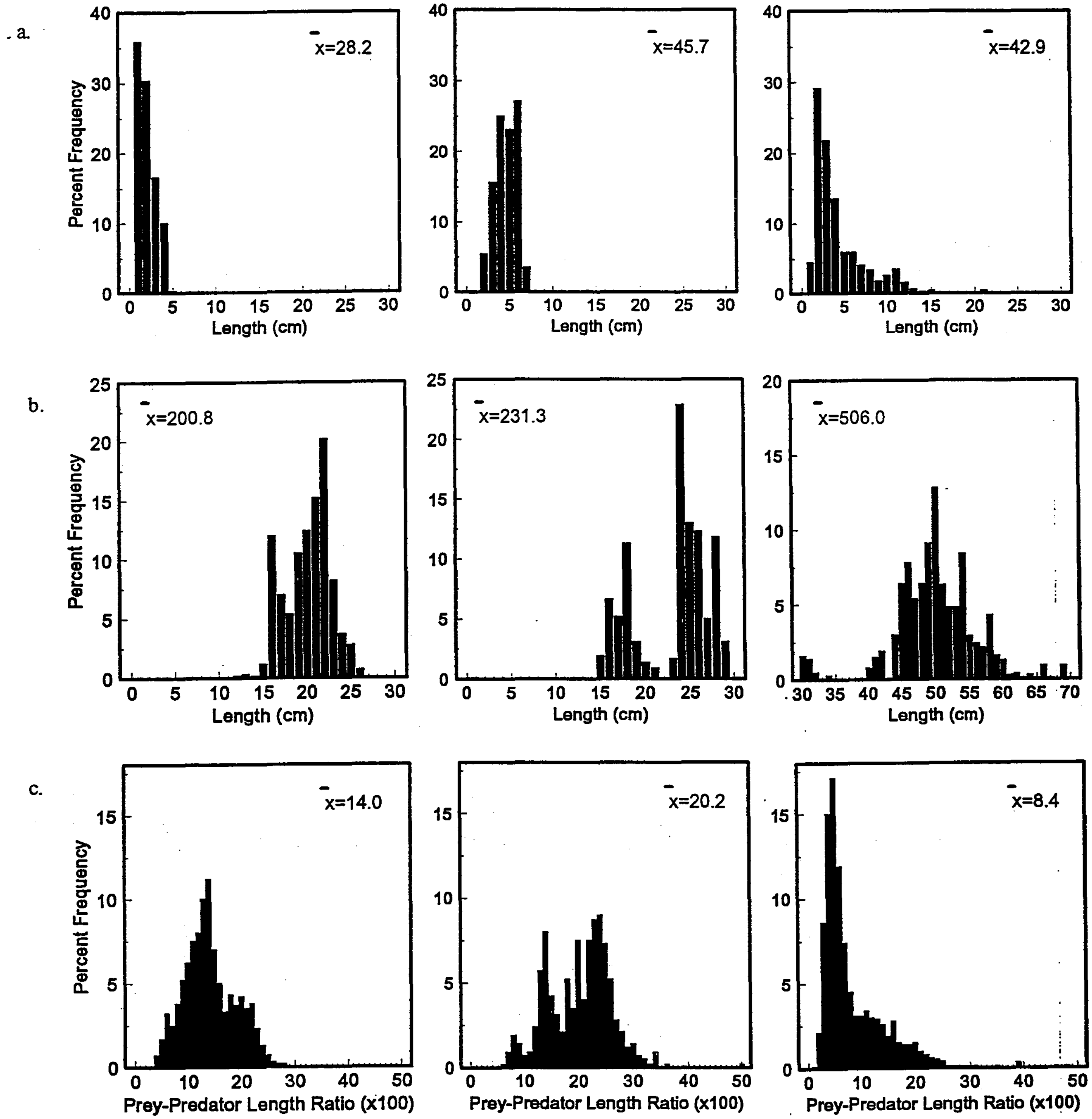
a.
Percent Frequency
Length (cm)
x̄=28.2
x̄=45.7
x̄=42.9
b.
Percent Frequency
Length (cm)
x̄=200.8
x̄=231.3
x̄=506.0
c.
Percent Frequency
Prey-Predator Length Ratio (x100)
x̄=14.0
x̄=20.2
x̄=8.4

Figure 10

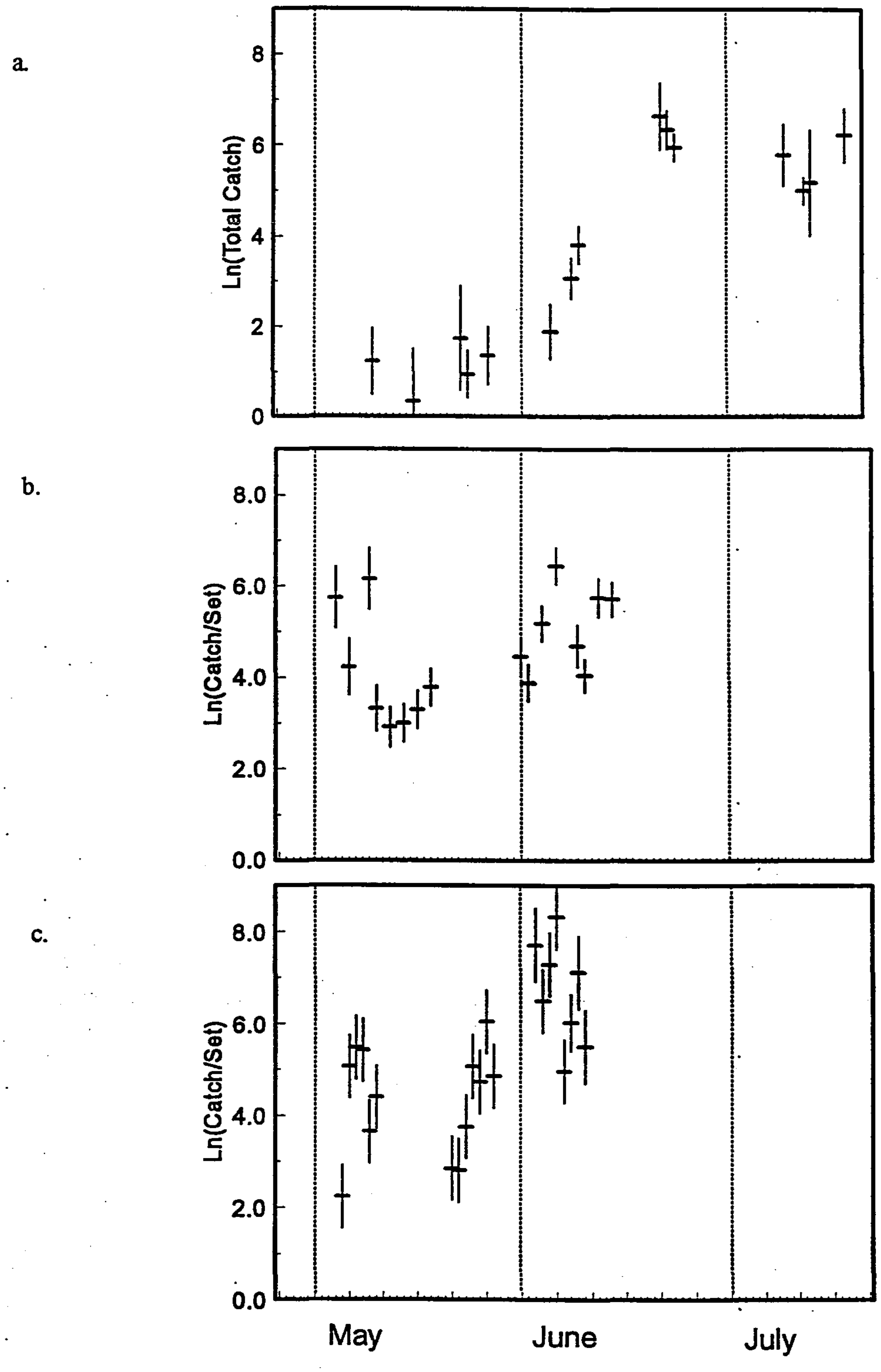
a.
8
6
4
2
0
Ln(Total Catch)
b.
8.0
6.0
4.0
2.0
0.0
Ln(Catch/Set)
c.
8.0
6.0
4.0
2.0
0.0
Ln(Catch/Set)
May
June
July

Figure 11

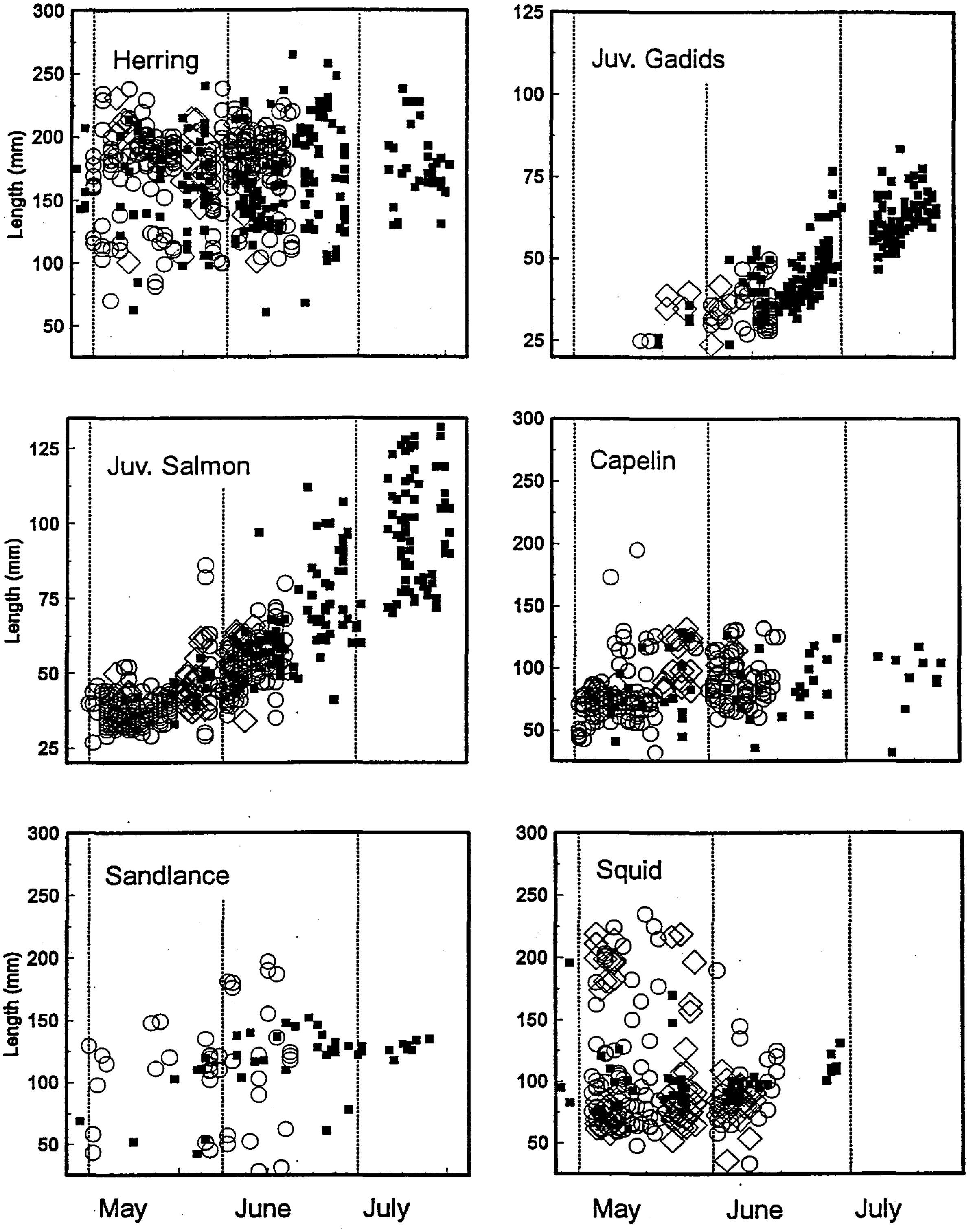
Herring
Juv. Gadids
Juv. Salmon
Capelin
Sandlance
Squid
Length (mm)
300
250
200
150
100
50
125
100
75
50
25
May
June
July

Figure 12

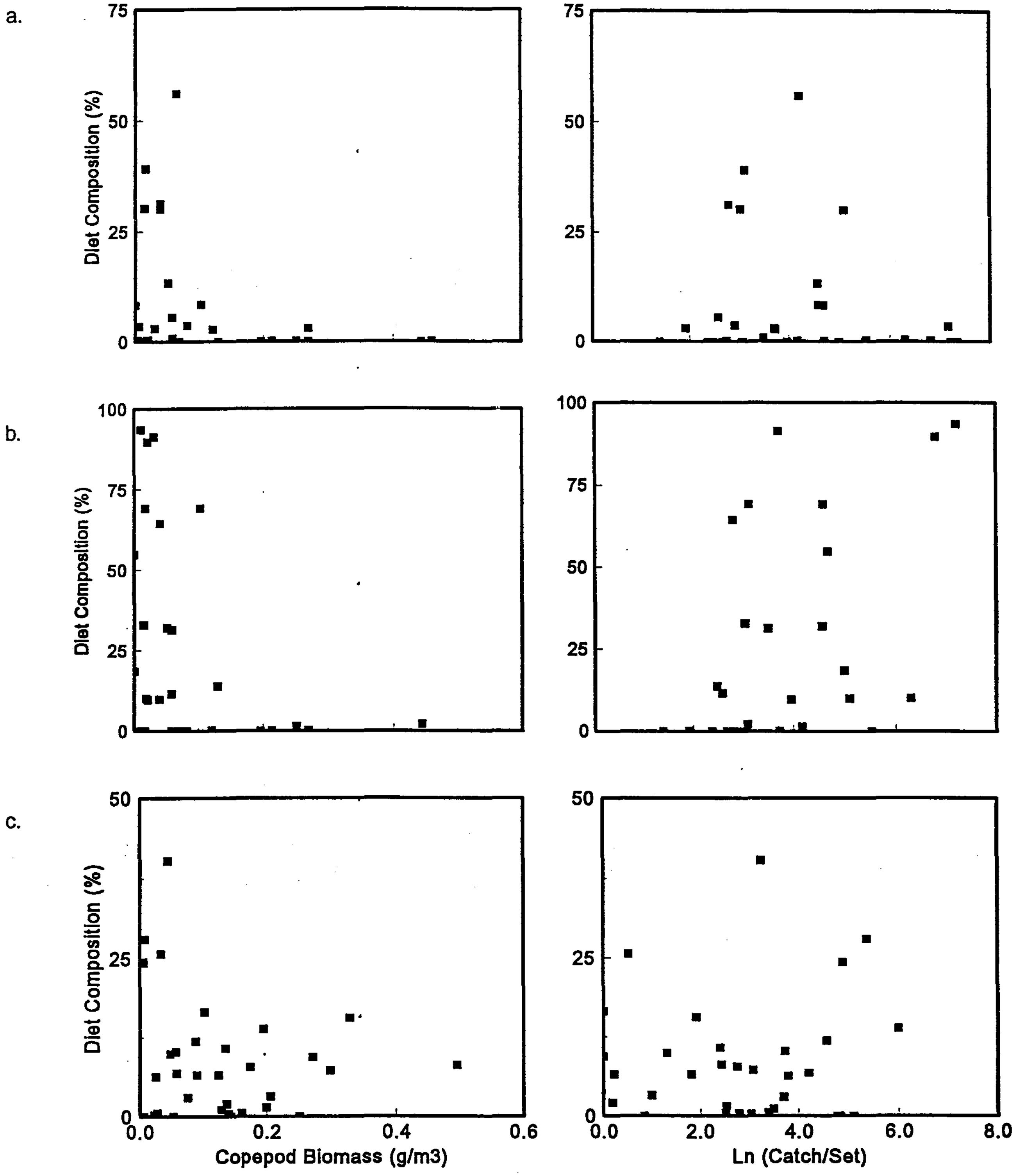
a.
b.
c.
Diet Composition (%)
75
50
25
0
100
Copepod Biomass (g/m3)
0.0
0.2
0.4
0.6
Ln (Catch/Set)
0.0
2.0
4.0
6.0
8.0

Figure 13

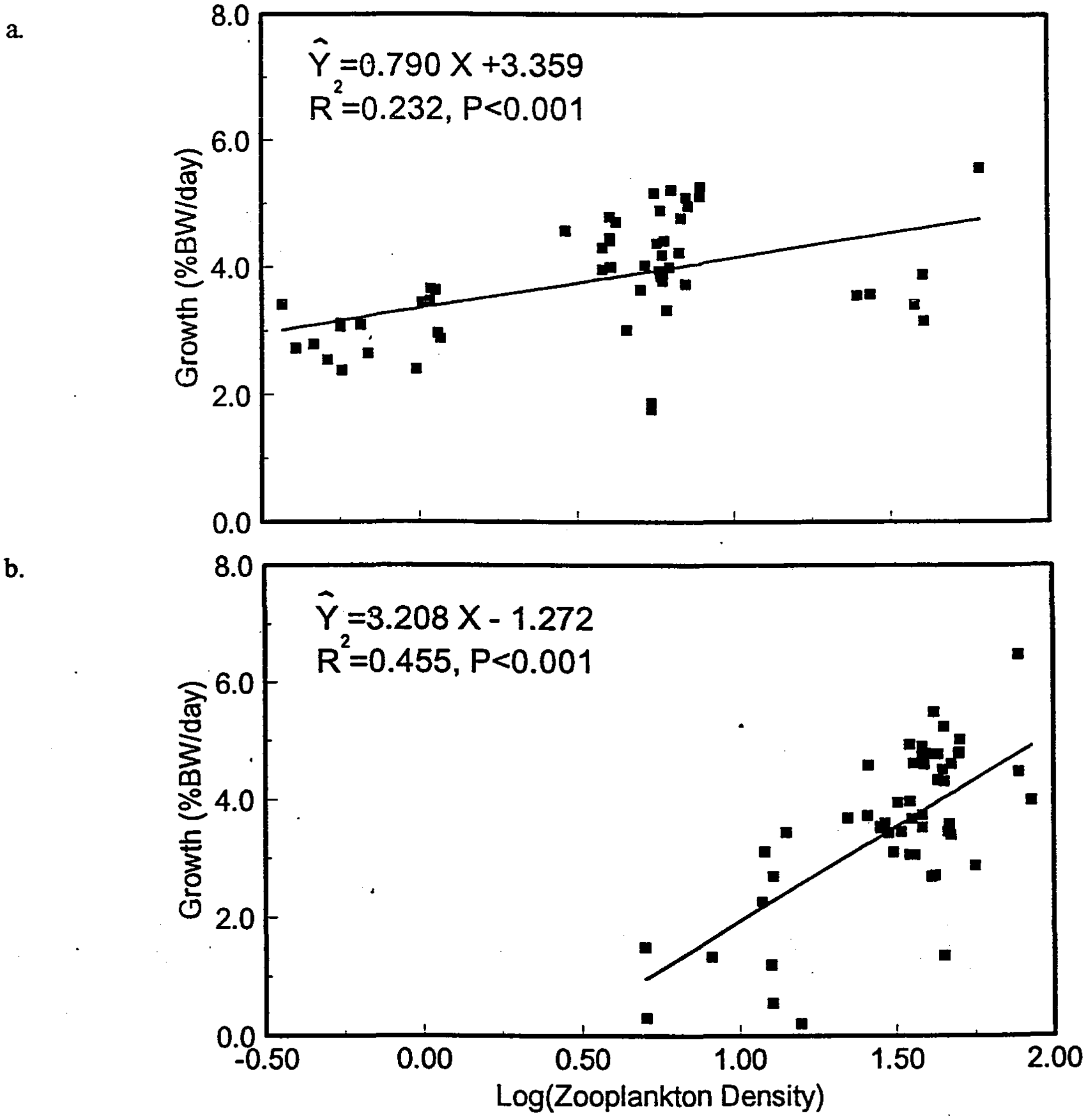
a.
$\hat{Y}$=0.790 X +3.359
R^2=0.232, P<0.001
Growth (%BW/day)
8.0
6.0
4.0
2.0
0.0
b.
$\hat{Y}$=3.208 X - 1.272
R^2=0.455, P<0.001
Growth (%BW/day)
8.0
6.0
4.0
2.0
0.0
-0.50
0.00
0.50
1.00
1.50
2.00
Log(Zooplankton Density)

Figure 14

Chapter 3

Phytoplankton and Nutrients