CHAPTER 2

94320-E Salmon Predation

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Exxon Valdez Oil Spill
Restoration Project Final Report

Sound Ecosystem Assessment: Salmon Predation

Restoration Project 94320E
Final Report

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Abstract

This project collected data needed to estimate the juvenile salmon consumption rate of fish predators in western Prince William Sound (PWS). Mid-water trawls and purse seines sampled fish in offshore and nearshore strata, respectively. Approximately, 6,800 stomach samples were collected from potential fish predators and all samples have been processed. Consumption rates have not yet been estimated pending availability of fish abundance and biomass estimates from the Nearshore Fish component (94320N) of the SEA program.

Walleye pollock (*Theragra chalcogramma*) and squid were the most abundant fish species captured in offshore strata in western PWS. Abundance of both species in offshore areas declined after June 1. After the beginning of June, adult chum and pink salmon (*Oncorhynchus spp.*) were common in offshore trawl catches. During late April and early May, total catch per net set was relatively consistent in offshore strata. Catch rates in offshore strata were more variable after the middle of May. In nearshore strata, total fish catch was low prior to the beginning of June. After June 1, Pacific herring (*Clupea harengus pallasi*), adult salmon, and juvenile walleye pollock were common in nearshore catches. Many of the fish species captured in nearshore areas were less than 150 mm FL. Samples of these small fish were preserved for later stomach contents analysis under the Salmon Growth and Mortality (94320A) and Forage Fish (94163) projects.

Walleye pollock appeared to be the most significant fish predator on juvenile salmon in western PWS in 1994. Apparent abundance and the overall proportion of the diet comprised of juvenile salmon was greatest for this species. However, adult pink salmon, herring, dolly varden trout (*Salvelinus malma*), Pacific tomcod (*Microgadus proximus*), and various greenlings (*Hexagrammidae*) and sculpins (*Cottidae*) also preyed upon juvenile salmon. The juvenile salmon consumption rate of each potential predator must be estimated to determine the relative importance of each species. In 1994, it appeared that the greatest predation on juvenile salmon occurred during the first week after the fry were released. Walleye pollock (age 3+) captured in offshore areas appeared to be the principal predator during this time period. Age composition of walleye pollock indicated that the 1988 year class was dominant. This year class would have recruited to the offshore population (comprised of age 3+ fish) in 1991. Juvenile pink salmon that reared in PWS during 1991 and 1992 exhibited poor survival resulting in salmon run failures in 1992 and 1993. The age composition and length-at-age of walleye pollock in northern Gulf of Alaska commercial catches was similar to that observed in PWS.

The results from the present study support the hypothesis that predation on age 0 fish is greater when macrozooplankton abundance is low. During the bloom, predator diets were comprised largely of calanoid copepods, and predation on age 0 fish was low. As the bloom declined, the proportion of the diet comprised of calanoid copepods declined and the occurrence of age 0 fish increased. Predation by age 1+ fish on age 0 fish was also size dependent; predation risk being substantially less for fish greater than approximately 60 mm FL. These results suggest that the survival of juvenile pink salmon (and other age 0 fish) depends largely on their growth rate prior to reaching approximately 60 mm FL and the coincident timing of the decline of the macrozooplankton bloom.

Introduction:

This project is a component of the Sound Ecosystem Assessment (SEA) program. SEA is a multi-disciplinary effort to acquire an ecosystem-level understanding of the marine and freshwater processes that interact to constrain levels of fish, and marine bird and mammal production in Prince William Sound (PWS).

The purposes of this project are to (1) determine to what extent variations in predation affect the survival of juvenile pink salmon (and other age-0 fish), and (2) identify and describe the mechanisms that cause variations in predation. Pink salmon runs to PWS failed in 1992 and 1993. These salmon run failures have drastically affected the economy of the PWS region which is largely based on the salmon 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 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.

This is a multi-year project designed to test two hypotheses regarding mechanisms that may regulate predation on juvenile salmon and other age-0 fish in PWS. Regulation of prey population size by a predator requires that prey mortality rate increase with prey population size (i.e density-dependent mortality; Holling 1959). Intense predation immediately after ocean entry may have contributed to poor survival of relatively large release groups of hatchery-reared coho salmon (Bayer 1986, Olla and Davis 1989, Pearcy 1992). Learned behavior or response to environmental cues may cause predators to aggregate in areas where prey are consistently abundant (Ware 1971, Godin 1978). Alternatively, predation on a prey population may increase when the preferred prey of potential predators is not available (Werner and Hall 1974, Ringler 1979, Winfield et al. 1983). In the northern Gulf of Alaska, predators such as juvenile walleye pollock (Armstrong and Winslow 1968) that prefer macrozooplankton (Clausen 1983, Dwyer et al. 1987, Bailey 1989) may switch to age-0 fish when macrozooplankton abundance is low. Macrozooplankton abundance was very low in PWS in 1992 indicating that predators may have switched to juvenile salmon. The following hypotheses will be tested by the project:

Hypotheses:

1. The predation rate (mortality rate) on juvenile salmon is greater when juvenile salmon abundance is high.

2. The predation rate on juvenile salmon is greater when macrozooplankton abundance is low.

This project was designed to achieve the following three objectives during the first year of study.

1. Identify the principal predators on juvenile salmon.

2. Determine the distribution, abundance, species and size composition of fish predators along the juvenile salmon migratory pathway.

3. Recommend methods for improving field sampling techniques, sampling designs, and hypothesis testing capabilities.

Methods:

Objective 1:

Identification of the principal fish predators on juvenile salmon requires estimation of the juvenile salmon consumption rate for each potential predator species along the juvenile salmon migratory pathway. Fish biomass, food consumption rate (daily ration), and diet composition must be estimated for each potential predator species to estimate juvenile salmon consumption rate. The Nearshore Fish component of the SEA program estimated fish biomass using hydroacoustic techniques. The Salmon Predation component of SEA estimated predator species/size composition, food consumption rate, and diet composition.

A stratified random sampling design was employed to estimate the juvenile salmon consumption rate during six ten-day sampling periods (Table 1). Techniques developed by Mehl and Westgard (1983) were used, i.e.

$$C_{ijk} = DR_i \; x \; B_{ijk} \; x \; P_{ijk} \qquad (1)$$

where C_{ijk} is the consumption (grams) of juvenile salmon by a predator belonging to size group j during time period i in strata k, DR_i is the daily ration (%body weight per day) during the ten-day sampling period, B_{ijk} is the biomass (grams) of the predator species within the stratum, and P_{ijk} is the proportion by weight of juvenile salmon in predator stomachs within the stratum. Total juvenile salmon consumption rate was estimated by summing among all important predator species. Variances were estimated and confidence intervals placed about the juvenile salmon consumption rate estimate for each predator species, as well as the total consumption estimate.

The daily ration of salmon predators was estimated from diel feeding periodicity studies conducted once during each ten-day sampling period. A sample of 30 individuals was collected in a single area at midnight (0000 hrs), 0400 hrs, 0800 hrs, 1200 hrs, 1600 hrs, 2000 hrs. Samples were processed as described below. The daily ration (DR_i, % body weight per day) was estimated for each ten-day sampling period (i) by

$$DR_i = \frac{Rt}{1-e^{-Rt}} \sum_{j=1}^{m} S_j(1-e^{-Rt}) \qquad (2)$$

where t is the duration of each time interval (j) over which stomach samples are collected, S_j is the mean stomach contents weight as a percent of fish body weight within time period j, m is the total number of j time intervals in a 24-h day, and R is instantaneous temperature-specific gastric evacuation rate (Elliot & Persson 1978). Water temperature was measured at the depth where fish were captured. Temperature-specific gastric evacuation rates have been estimated for walleye pollock (Dwyer et al. 1986, Smith et al. 1989) and Atlantic cod (Ursin et al. 1985).

Field studies were initiated on April 20 and continued until July 22. Approximately 180 million juvenile salmon were released from the Wally H. Noerenberg (WHN) Hatchery beginning in late April through late May. Estimates of juvenile salmon consumption rate were made for six ten-day sampling periods (Table 1) in two study areas in northwest and southwest PWS (Figure 1). The first four surveys were conducted in northwest PWS prior to June 15 when juvenile salmon released from the WHN Hatchery were likely be abundant in the area (Willette 1994). The last two surveys were conducted in southwest PWS prior to July 22 when juvenile salmon from all hatcheries in PWS were likely abundant in the area.

Six ten-day surveys were conducted to estimate the juvenile salmon consumption rate in western PWS. The stratified random sampling program was designed to minimize the variance estimate of predator biomass (Bazigos 1976) and the proportion of predator stomach contents weight comprised of juvenile salmon. As a result, strata were established based upon the abundance of predators and juvenile salmon in the study area (Smith and Gavaris 1993). Juvenile salmon abundance was estimated from hydroacoustic data, visual observations, and data on juvenile salmon migration patterns from earlier studies (Willette 1994). Application of these criteria resulted in strata established by time of day (day; night), depth, habitat type (nearshore; offshore), and geographic location (i.e., areas). Hydroacoustics were used to estimate predator biomass within each strata and locate schools of fish for net sampling (see Nearshore Fish component). The offshore boundary of the nearshore areas were defined as 300 meters from shore or 10 fathoms in depth, whichever was further from shore. Offshore areas were those more than 300 meters from shore or greater than 10 fathoms in depth.

Three vessels were employed to sample salmon predators during each ten-day predation rate survey. An approximately 25 m trawl vessel sampled fish in offshore areas using a 40 m x 28 m mid-water wing trawl equipped with a net sounder. The cod end of the trawl was lined with approximately 2.0 cm stretch-mesh web to retain small specimens. Data from the net sounder was used to determine the depth fished and to insure that the number of fish caught in each set did not greatly exceed required sample sizes. Two purse seine vessels sampled salmon predators in nearshore areas. Each vessel fished a small-mesh purse seine approximately 250 m x 30 m with 2.0 cm stretch mesh web. The small-mesh seines were also used to capture small fish that may compete with juvenile salmon for food, as well as, larger juvenile salmon later in the season.

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 for stomach analysis 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. A selected subsample from this collection was analyzed under project 94320A (Salmon Growth and Mortality) and project 94163 (Forage Fish Influence on Recovery of Injured Species). The purpose of these studies was to examine diet overlap.

For large fish (greater than 150 mm FL), stomach contents analysis was conducted on board each vessel on a randomly selected sample (n=10) from each species. 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. Total stomach contents wet weight was measured to the nearest 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. If greater than ten fish were collected for a particular species, stomachs were excised from an additional 20 randomly selected individuals, placed in cloth bags, and preserved in 10% buffered formaldehyde for later stomach contents analysis in the laboratory. Length, weight and sexual maturity was measured as described above. Laboratory analysis of these samples was similar to that conducted in the field. However, total stomach contents weight was measured to the nearest .01g. The proportion of prey in each taxonomic group was visually estimated, but prey in each taxonomic group were also weighed to the nearest .01 g. Diet composition was expressed as a proportion of total stomach contents weight. 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).

The age composition of the walleye pollock in the catch was estimated from otolith analysis and length-frequency data. Length modes are clearly separated for ages 1-3 among juvenile walleye pollock from the northwest Gulf of Alaska (Smith et al. 1984). A random sample of otoliths was obtained from 618 walleye pollock. Both otoliths were excised from each fish and placed in labeled vials containing sea water. At the end of the field season, sea water was replaced with fresh water. In the laboratory, otolith pairs were selected at random and one otolith from each fish was broken through the nucleus and burned in an alcohol flame. Otolith sections were examined using a dissecting microscope and reflected light. Ages were obtained from 472 of the original 618 samples collected. Some otoliths were not readable due to the lack of clear annuli near the otolith margin and crystalization of some otoliths. All otoliths were aged three times by a single reader and the most commonly arrived at age was tentatively accepted as valid. A subsample of 50 otoliths was sent to the National Marine Fisheries (NMFS), Alaska Fisheries Science Center for age validation.

Age-length data from 472 pollock were used to build an age length key (MacDonald and Pitcher 1979). One hundred randomly selected observations were removed from the data set for later model validation. The remaining 372 observations were used in a multinomial regression analysis with age as the response and length as the explanatory variable. Eighteen parameters were estimated, two each for age classes 2 through 10 from the model

$$E\,[\log(\frac{\pi_i}{\pi_1})] = \beta_{0i} + \beta_{1i} \cdot Length, \quad i = 2, 3, \ldots 10, \tag{2}$$

where $\pi_1 = 1 - \pi_2 - \pi_3 - \ldots \pi_{10}$

With nine equations and unknowns, the estimates can be obtained for any given length by

$$\pi_i = \frac{\exp(\hat{\beta}_{0i} + \hat{\beta}_{1i} \cdot Length)}{1 + \sum_{j=2}^{10} \exp(\hat{\beta}_{0j} + \hat{\beta}_{1j} \cdot Length)}, \quad i = 2, 3, \ldots 10, \tag{3}$$

where $\hat{\pi}_1 = 1 - \hat{\pi}_2 - \hat{\pi}_3 - \ldots \hat{\pi}_{10}$

The probability that any fish of a given length may belong to each of the ten age classes was calculated for the 100 observations that were not used to build the model. The expected number of fish in an age class was given by the sum of the probabilities for that age class. The model was then evaluated by comparing the expected number for each age class to the known proportion of the sample (n=100) in each age class.

Objective 2:

Two broad-scale surveys were conducted to determine the spatial distribution, abundance, and species/size composition of fish predators along the juvenile salmon migratory pathway. These surveys were conducted by an approximately 25m mid-water trawl vessel. The Nearshore Fish component of SEA collected hydroacoustic data along transects spaced approximately 2 nm apart. The Salmon Predation component of SEA sampled selected fish targets with a 40 m x 28 m mid-water trawl net (described above). Fish samples were processed to estimate species and size composition of hydroacoustic targets using the methods described in objective (1).

Objective 3:

Analysis of variance, multiple comparison tests and an analysis of gain in precision will be conducted to identify strata that can be combined in future years (Smith and Gavaris 1993, Cochran 1977). Post-stratification techniques based on predator and juvenile salmon abundance estimates will be applied to the 1994 data to help develop an improved stratification scheme that approaches optimal allocation (Jolly and Hampton 1990). The relative contribution of each component of juvenile salmon consumption rate (Equation 1) to the overall variance of the salmon consumption rate will be computed to identify where gains in precision can be made by increasing sample sizes.

Two methods of estimating the proportion of total stomach contents weight comprised of juvenile salmon (P) have been evaluated. The methods used in this analysis are described in Appendix II. Preliminary analyses have also been conducted to estimate minimum sample sizes needed to detect differences in total stomach contents weight and the proportion of juvenile salmon in predator stomachs among strata. This approach will allow for an evaluation of differences in predation rate among various places and times.

The feasibility of estimating the juvenile salmon consumption rate in areas of relatively low juvenile salmon abundance was evaluated. First, the proportion of total stomach contents weight comprised of juvenile salmon was estimated for each strata. The frequency distributions of the proportion of total stomach contents weight comprised of juvenile salmon (P) were compared for two areas near and distant from the WHN Hatchery. It was assumed that juvenile salmon were generally more abundant near than distant from the WHN Hatchery. For the purposes of this analysis, all strata north of offshore strata 62 were considered near the WHN Hatchery (Figure 1). All strata north of offshore strata 64 and south of offshore strata 61 were considered distant from the WHN hatchery. Second, the minimum sample size for each net set required to capture at least one predator that had consumed juvenile salmon was estimated for each sampling period. Sample size estimates were compared among sampling periods.

Results:

Objective 1:

Walleye pollock (*Theragra chalcogramma*) and squid were the most abundant fish species captured in offshore strata in western PWS (Appendix I). Abundance of both species in offshore areas declined after June 1. After the beginning of June, adult chum and pink salmon were common in offshore trawl catches (Appendix I). During late April and early May, total catch per net set was relatively consistent in offshore strata. During this time period, greater than 70% of net sets resulted in catches between 10 and 100 fish (Figure 2). Catch rates in offshore strata were more variable after the middle of May. In nearshore strata, total fish catch was low prior to the beginning of June (Figure 2). After June 1, Pacific herring (*Clupea harengus pallasi*), adult salmon, and juvenile walleye pollock were common in nearshore catches (Appendix I). Many of the fish species captured in nearshore areas were less than 150 mm FL (Appendix I).

A total of 6,796 stomach samples were collected from fish over 150 mm in length (Table 2). With the exception of 711 squid, all of these samples have been processed at this time. An additional 15,678 samples of fish less than 150 mm in length (forage fish) were collected (Table 3). A subset of these samples were analyzed for stomach contents under projects 94320A (Salmon Growth and Mortality) and 94163 (Forage Fish Influence on Recovery of Injured Species).

The walleye pollock population sampled in western PWS was dominated by age 6 fish from the 1988 year class (Table 4). The range of lengths overlapped for all age groups except age 1 and 2 (Table 4). A multinominal regression model developed from a subsample of 372 otoliths accurately predicted the age composition for the 100 specimens not used to build the model (Figure 3). Additional work is ongoing to develop variances and confidence intervals for these model estimates. Length-weight regression parameters for the total walleye pollock sample were $W = .0000196 * FL^{2.82}$ ($r^2 = .97$), where weight is in grams and fork length is in millimeters.

The juvenile salmon consumption rate of important fish predators in PWS has not been estimated at this time. Hydroacoustic estimates of biomass for important fish predator species are not yet available from the Nearshore Fish component of SEA (94320N). However, the proportion by weight of juvenile salmon in predator stomachs has been estimated for each strata in the northwest PWS study area. Walleye pollock, herring, adult pink salmon, and dolly varden trout were found to prey on juvenile salmon (Table 5). These fish were captured with purse seines in nearshore habitats and a mid-water trawl in offshore habitats. Greenling, tomcod, Pacific cod, dolly varden trout, and sculpins were also captured with hand seines set on schools of salmon fry in very nearshore areas. These fish species also consumed juvenile salmon, although they may have fed in the net. The catches and apparent feeding rate of these species mixed with schools of fry was greatest in the June 1-15 sampling period, declining sharply thereafter.

The proportion of the diet of walleye pollock comprised of juvenile salmon declined exponentially over time (Figure 4). The proportion of the diet of walleye pollock comprised of age 0 fish was inversely related to the proportion of the diet comprised of large calanoid copepods (Figure 5). The majority of the juvenile salmon found in predator stomachs were less than 60 mm FL (Figure 6). The majority of the walleye pollock with juvenile salmon in their stomachs were greater than 400 mm FL (Figure 7). Juvenile salmon were found in the stomachs of walleye pollock, herring, and all predators (combined) in approximately 30, 8, and 29% of the strata sampled, respectively (Appendix II).

Objective 2:

During each of two broad-scale surveys, fish abundance appeared to be greater in northern than southern PWS. Each of the broad-scale surveys followed a more detailed survey of the Northwest PWS Study Area. The mid-water trawl vessel simply continued southward after completing work in the northwest area. The broad-scale surveys focused primarily on collection of hydroacoustic data. Few net sets were made in the southwest portion of the survey area, because hydroacoustic data indicated a lack of fish targets. During the May survey, three mid-water trawl sets in the southwest area captured 41 walleye pollock. In the June survey, two mid-water trawl sets in the southwest area captured 37 walleye pollock.

Objective 3:

An analysis of gain in precision has not yet been conducted to identify strata that can be combined in future years. Also, the relative contribution of each component of the juvenile salmon consumption rate to the overall variance of the estimate has not be conducted. Biomass estimates for important fish predator species are needed from the Nearshore Fish component of SEA (95320N) to conduct these analyses.

An evaluation of two methods for estimating the proportion of total stomach contents weight comprised of juvenile salmon (P) identified the superior estimator. A formula approach to estimating the variance of P was identified as superior to a bootstrap approach. However, the results from these analyses are summarized in Appendix II.

The proportion of total stomach contents weight comprised of juvenile salmon (P) was estimated for 66 strata in western PWS (Appendix II). The frequency distributions of P exhibited roughly equal occurrence of zero values in the two areas near and distant from the WHN Hatchery (Figure 8). Values of P greater than 1% were more common near than distant from the WHN Hatchery.

Discussion:

Walleye pollock appeared to be the most significant fish predator on juvenile salmon in western PWS in 1994. Apparent abundance and the overall proportion of the diet comprised of juvenile salmon was greatest for this species. However, the juvenile salmon consumption rate of this species and others (Table 5) must be estimated (equation 1) to more firmly establish the relative importance of each fish predator species. The juvenile salmon consumption rate of potential fish predators in very nearshore nursery areas (greenling, tomcod, etc.) cannot be estimated from the data collected in this study, because (1) random sampling was not employed, (2) these predators may have fed on juvenile salmon in the net while being captured, and (3) abundance or biomass estimates from hydroacoustics will likely not be possible as these species are often in kelp beds. Various fixed gear types (fyke nets, hoop traps, and gill nets) will be employed in 1995 to more effectively sample these species.

In 1994, it appeared that the greatest predation on juvenile salmon occurred during the first week after the fry release (Figure 4). Walleye pollock (age 3+) captured in offshore areas appeared to be the principal predator during this early time period. Age composition of walleye pollock indicated that the 1988 year class was relatively strong (Figure 3). This year class would have recruited to the offshore population (comprised of age 3+ fish) in 1991. Juvenile pink salmon that reared in PWS during 1991 and 1992 exhibited poor survival resulting in salmon run failures in 1992 and 1993. The age composition and length-at-age of walleye pollock in the northern Gulf of Alaska (Personal Communication, Michael Martin, National Marine Fisheries Service) is similar to that observed in PWS indicating either (1) similar factors affecting growth and survival in the two areas, or (2) mixing of fish between the northern Gulf and PWS.

The results from the present study support the hypothesis that predation on age 0 fish is greater when macrozooplankton abundance is low. During the bloom, predator diets were comprised largely of calanoid copepods, and predation on age 0 fish was low (Figure 5). As the abundance of macrozooplankton declined, the proportion of the diet comprised of calanoid copepods declined and the occurrence of age 0 fish increased. Predation by age 1+ fish on age 0 fish was also size dependent; predation risk being substantially less for fish greater than approximately 60 mm FL (Figure 6). These results suggest that the survival of juvenile pink salmon (and other age 0 fish) depends largely on their growth rate prior to reaching a size of approximately 60 mm FL and the coincident timing of the decline of the macrozooplankton bloom. If the juvenile salmon (and other age 0 fish) can reach a size greater than 60 mm FL, before the decline in macrozooplankton abundance, their survival will likely be relatively high. In 1994, the mean length of the early fed juvenile pink salmon released from WHN Hatchery exceeded 60 mm FL after June 15 (See report for project 94320A). However, the proportion of large calanoid copepods in the diet of walleye pollock declined substantially during the June 1-15 sampling period. It is interesting that the apparent predation rate on juvenile salmon in very nearshore habitats (by greenling, tomcod, etc.) was greatest during this June 1-15 period.

The life history strategy employed by juvenile salmon may be related to the apparent shift in distribution of all fish species that occurred in early June. At this time, walleye pollock catches in offshore habitats initially became more variable, then declined sharply (Appendix I). At the same time, catches of herring and other fish species increased considerably in nearshore habitats. It appears that the nearshore habitats occupied by juvenile salmon during the initial 30 days of marine residence provide a refuge from predation. However, these nearshore habitats may not provide a refuge after the seasonal increase in nearshore fish abundance (Figure 2). Thus, an alternative hypothesis states that juvenile salmon growth prior to the seasonal increase in nearshore fish abundance is critical to survival.

The high apparent predation on juvenile salmon in offshore habitats by age 3+ walleye pollock in early May indicates that juvenile salmon are predated when leave the nearshore refuge. Juvenile salmon may leave nearshore refuges to migrate across passages or forage in offshore habitats. High abundances of juvenile salmon may cause more individuals to leave the refuge to seek food elsewhere (Simenstad et al. 1981). The proposed study design for 1995 will focus on the tradeoff between foraging and predation risk (Walters and Juanes 1993).

References:

Armstrong, R.H. and P.C. Winslow. 1968. An incidence of walleye pollock feeding on young salmon. Trans. Amer. Fish. Soc. 97(2): 202-203.

Bayer, R.L. 1986. Seabirds near an Oregon salmon hatchery in 1982 and during the 1983 El Nino. Fish. Bull. 84: 279-286.

Bazigos, G.P. 1976. The design of fisheries statistical surveys - inland waters: populations in non-random order, sampling methods for echo surveys, double sampling) fish. Tech. Paper 133, supp. 1, 45p.

Bailey, K.M. 1989. Interaction between the vertical distribution of juvenile walleye pollock *Theragra chalcogramma* in the eastern Bering Sea, and cannibalism. Mar. Ecol. Prog. Ser. 53: 205-213.

Cochran, W.G. 1977. Sampling Techniques. John Wiley & Sons, Inc. New York.

Clark, I. 1979. Practical Geostatistics. Applied Science, London.

Clausen, D.M. 1983. Food of walleye pollock, *Theragra chalcogramma*, in an embayment of Southwestern Alaska. U.S. Fish. Bull. 81: 637-642.

Daan, N. 1973. A quantitative analysis of the food intake of North Sea cod, *Gadus morhua*. Neth. J. Sea Res. 6: 479-517.

Dwyer, D.A., K. Bailey, P. Livingston, and M. Yang. 1986. Some preliminary observations on the feeding habits of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea based on field and laboratory studies. Int. North Pac. Fish. Comm. Bull. 45: 228-246.

Dwyer, D.A., K.M. Bailey, P.A. Livingston. 1987. Feeding habits and daily ration of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea, with special reference to cannibalism. Can. J. Fish. Aquat. Sci. 44: 1972-1984.

Elliott, J.M. and L. Persson. 1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47: 977-991.

Godin, J.J. 1978. Behavior of juvenile pink salmon (*Oncorhynchus gorbuscha*) toward novel prey: influence of ontogeny and experience. Env. Biol. Fish. 3: 261.

Healey, M.C. 1982. Timing and relative intensity of size-selective mortality of juvenile chum salmon during early sea life. Can. J. Fish. Aquat. Sci. 39: 952-957.

Holling, C.S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can. Entomol. 91: 293-320.

Johnson, R.A. and D.W. Wichern. 1988. Applied Multivariate Statistical Analysis. Prentice Hall Inc., Englewood Cliffs, N.J.

Jolly, G.M. and I. Hampton. 1990. A stratified random transect design for acoustic surveys of fish stocks. J. Fish. Aquat. Sci. 47: 1282-1291.

Langton, R.W. 1982. Diet overlap between Atlantic cod, *Gadus morhua*, silver hake, *Merluccius bilinearis*, and fifteen other northwest Atlantic finfish. Fish. Bull. 80: 745-759.

Livingston, P.A. 1983. Food habits of Pacific whiting, *Merluccius productus*, off the west coast of North America, 1967 and 1980. Fish. Bull. 81: 629-636.

Livingston, P.A. 1989. Interannual trends in Pacific Cod, *Gadus macrocephalus*, predation on three commercially important crab species in the eastern Bering Sea. Fish. bull. 87: 807-827.

MacDonald, R.D.M. and T.J. Pitcher. 1979. Age-groups from size-frequency data: a versatile and efficient method of analyzing distribution mixtures. J. Fish. Res. Board Can. 36: 987-1001.

Mehl, S. and T. Westgard. 1983. The diet and consumption of mackerel in the North Sea. Int. Counc. Explor. Sea C.M. 1983/H:34.

Olla, B.L. and M.W. Davis. 1989. The role of learning and stress in predator avoidance of hatchery-reared coho salmon (*Oncorhynchus kisutch*) juveniles. Aquaculture 76: 209-214.

Parker, R.R. 1968. Marine mortality schedules of pink salmon of the Bella Coola River, central British Columbia. J. Fish. Res. Board Can. 25: 757-794.

Parker, R.R. 1971. Size-selective predation among juvenile salmonid fishes in a British Columbia inlet. J. Rish. Res. Board Can. 28: 1503-1510.

Pearcy, W.G. 1992. Ocean Ecology of North Pacific Salmonids. University of Washington Press, Seattle, WA.

Ringler, N.H. 1979. Selective predation by drift-feeding brown trout (*Salmo trutta*) J. Fish. Res. Board Can. 36: 392.

Simenstad, C.A., W.J. Kinney, S.S. Parker, E.O. Salo, J.R. Cordell and H. Buechner. 1980. Prey comunity structure and trophic ecology of outmigrating juvenile chum and pink salmon in Hood Canal, Washington. Fisheries Research Institute Report FRI-UW-8026, University of Washington, Seattle, 113p.

Smith, G.B., G.E. Walters, P.A. Raymore, and W.A. Hirschberger. 1984. Studies of the distribution and abundance of juvenile groundfish in the northwestern Gulf of Alaska, 1980-82: Part I, Three-year comparisons. NOAA Technical Memorandum NMFS F/NWC-59, 100p.

Smith, R.L., J.M. Paul, and A.J. Paul 1989. Gastric evacuation in Walleye pollock, *Theragra chalcogramma*. Can. J. Fish. Aquat. Sci. 46: 489-493.

Smith, S.J. and S. Gavaris. 1993. Improving precision of abundance estimates of eastern Scotian Shelf Atlantic Cod from bottom trawl surveys. N. Amer. J. Fish. Management 13: 35-47.

Ursin, E., M. Pennington, E.B. Cohen, and M.D. Grosslein. 1985. Stomach evacuation rates of Atlantic cod (*Gadus morhua*) estimated from stomach contents and growth rates. Dana 5: 63-80.

Walters, C.J. and F. Juanes. 1993. Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fish. Can. J. Fish. Aquat. Sci. 50: 2058-2070.

Ware, D.M. 1971. Predation by rainbow trout (*Salmo gairdneri*): the effect of experience. J. Fish. Res. Board Can. 28: 1847.

Werner, E.E. and D.J. Hall. 1974. Optimal foraging and size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology 55: 1042.

West, C.J. and P.A. Larkin. 1987. Evidence of size-selective mortality of juvenile sockeye salmon (*Oncorhynchus nerka*) in Babine Lake, British Columbia. Can. J. Fish. Aquat. Sci. 44: 712-721.

Willette, T.M. 1994. Impacts of the Exxon Valdez oil spill on the migration, growth, and survival of juvenile pink salmon in Prince William Sound. In: Proceedings of the Exxon Valdez Oil Spill Symposium, Anchorage, Alaska, American Fisheries Society Symposium Series, (in press).

Winfield, I.J. G. Peirson, M. Cryer, and C.R. Townsend. 1983. The behavioural basis of prey selection by underyearling bream (*Abramis brama*) and roach (*Rutilus rutilus*). Freshwater Biol. 13: 139.

Table 1: Sampling periods, areas, and vessels employed in the Salmon Predation project in 1994. Mid-water trawler - AK Beauty, Purse Seiners - Goodnews, Intrepid.

Time Period	Study Area	Vessels
April 22 - April 28	Northwest PWS	AK Beauty, Goodnews
May 5 - May 12	Northwest PWS	AK Beauty, Goodnews, Intrepid
May 13 - May 16	Western PWS	AK Beauty
May 17 - May 30	Northwest PWS	AK Beauty, Goodnews, Intrepid
June 1 - June 13	Northwest PWS	AK Beauty, Goodnews, Intrepid
June 13 - June 15	Western PWS	AK Beauty
June 23 - June 30	Southwest PWS	AK Beauty, Goodnews, Intrepid
July 7 - July 21	Southwest PWS	AK Beauty, Goodnews, Intrepid

Table 2: Summary of fish (>150 mm FL) stomach samples collected in western Prince William Sound, 1994.

			Stomach Samples Excised and Preserved (Selected Species only)																	Plankton	
Stratification and Coding			110	121	130	139	190	199	233	250	270	410	420	440	450	530	710	897			
Stratum	Code	Description	Cod	Flound	Ling	Unk	Gmlng	SfCod	Herr	Tom	Pollk	King	Sock	Pink	Chum	Dolly	Sable	Squid	TotalStom	Plankton	Tucker
Date	1	April 16-30	0	0	0	0	0	0	129	0	404	0	0	0	3	1	0	2	539	7	16
	2	May 1-15	1	1	0	0	2	0	50	0	958	1	0	0	0	0	0	123	1,136	37	33
	3	May 16-31	0	0	0	0	0	0	115	0	483	3	5	0	26	3	0	141	776	39	20
	4	June 1-15	6	2	3	10	37	0	851	79	727	9	2	0	76	15	0	304	2,121	51	0
	5	June 16-30	1	0	0	3	28	9	735	17	137	2	0	147	10	52	1	141	1,283	45	2
	6	July 5-25	2	2	5	4	31	0	439	14	365	0	1	63	5	5	0	0	936	22	0
	7	August 27 - Sept 7	0	0	0	0	0	0	0	0	3	0	0	0	0	0	2	0	5	0	0
Time	1	4 am - 12 noon	6	0	4	13	55	8	483	44	1,087	5	1	88	27	21	0	53	1,895	45	31
	2	12 noon - 8 pm	3	1	4	4	41	0	260	66	334	2	4	0	54	29	0	3	805	34	13
	3	8 pm - 4 am	1	4	0	0	2	1	1,576	0	1,653	8	3	122	39	26	1	655	4,091	122	27
Habitat	1	Nearshore	10	1	8	17	98	9	2,243	110	253	10	8	119	114	76	3	2	3,081	199	0
	2	Offshore	0	4	0	0	0	0	75	0	2,806	5	0	91	6	0	0	709	3,696	2	71
Site Habitat	1	Shallow Bay	0	1	2	1	21	0	99	0	50	0	4	5	1	10	0	0	194	9	0
	2	Mod Slope Pass	4	0	0	11	52	0	458	68	32	3	2	16	45	22	0	1	714	57	0
	3	Steep Slope Pass	6	0	6	3	18	0	565	22	35	6	0	2	45	5	0	1	714	52	0
	4	Offshore	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Area	1	Esther	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2	Culross Island	0	0	0	1	2	0	224	0	30	5	0	0	45	1	0	0	308	20	0
	3	Main Bay	0	1	0	0	0	0	104	0	16	2	0	0	15	2	0	0	140	20	0
	4	Chenega Island	2	0	0	6	5	0	208	4	9	1	0	2	25	1	0	2	265	31	0
	5	So. Knight Island	0	0	0	0	6	0	272	0	7	1	6	0	6	9	0	0	307	22	0
Gear	1	Purse seine	8	1	5	17	91	1	2,248	102	252	10	8	119	114	76	3	2	3,057	201	0
	4	Set gillnet	2	0	3	0	6	0	0	6	0	0	0	0	0	0	0	0	17	0	0
	47	Mid-water trawl	0	4	0	0	0	0	71	0	2,824	5	0	91	6	0	0	709	3,710	0	71
	50	Fyke net	0	0	0	0	1	8	0	2	1	0	0	0	0	0	0	0	12	0	0
	55	Tucker trawl	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Boat	1	Alaska Beauty	0	4	0	0	0	0	71	0	2,824	5	0	91	6	0	0	709	3,710	0	71
	2	Intrepid	1	1	0	0	2	0	885	0	161	6	1	94	50	20	0	2	1,223	108	0
	3	GoodNews	1	0	0	0	1	9	1,148	2	92	4	7	25	64	38	3	0	1,394	93	0
	4	Auklet	8	0	8	17	95	0	215	108	0	0	0	0	0	18	0	0	469	0	0
Total			10	5	8	17	98	9	2,319	110	3,077	15	8	210	120	76	3	711	6,796	201	71

Table 3: Summary of fish (< 150 mm FL) stomach samples collected in western Prince William Sound, 1994.

Stratification and Coding			Forage Fish Samples (Preserved Whole)															
			Cod	Herr	Tom	Pollk	Kng	Sock	Coho	Pink	Chum	STng	Smlt	Rnbw	Cap	Sndl	Stklbk	
Stratum	Code	Description	110	233	250	270	410	420	430	440	450	509	510	513	516	517	660	Total
Date	1	April 16-30	0	0	0	0	0	0	0	0	0	66	0	0	0	0	0	66
	2	May 1-15	1	10	0	0	0	0	0	164	52	294	0	3	58	0	145	727
	3	May 16-31	19	111	15	3	3	0	2	232	146	15	3	8	78	55	28	718
	4	June 1-15	210	787	60	423	5	201	32	622	423	0	13	0	4	132	12	2,924
	5	June 16-30	300	394	1,090	3,457	0	714	0	797	87	1	0	0	104	197	0	7,141
	6	July 5-25	236	77	1,073	2,302	5	27	0	192	13	0	0	0	44	132	1	4,102
	7	August 27 - Sept 7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Time	1	4 am - 12 noon	299	321	473	1,628	0	158	16	700	176	72	0	1	17	222	93	4,176
	2	12 noon - 8 pm	344	199	270	250	3	152	8	1,056	296	0	0	5	41	245	84	2,953
	3	8 pm - 4 am	123	859	1,495	4,307	10	632	10	251	249	304	16	5	230	49	9	8,549
Habitat	1	Nearshore	765	1,345	2,227	5,213	13	888	34	2,001	721	0	16	11	275	516	186	14,211
	2	Offshore	1	34	11	972	0	54	0	6	0	376	0	0	13	0	0	1,467
Site Habitat	1	Shallow Bay	86	79	259	222	7	27	21	206	72	0	0	0	0	105	1	1,085
	2	Mod Slope Pass	353	532	209	386	0	92	8	880	166	0	12	8	118	248	55	3,067
	3	Steep Slope Pass	186	338	144	371	1	161	5	551	382	0	4	2	15	109	123	2,392
	4	Offshore	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Area	1	Esther	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2	Culross Island	14	157	15	47	4	0	5	168	177	0	1	1	12	23	26	650
	3	Main Bay	1	31	0	0	0	5	10	90	80	0	0	1	1	1	109	329
	4	Chenega Island	95	271	32	292	2	136	10	249	207	0	3	1	55	40	21	1,414
	5	So. Knight Island	3	393	0	8	2	59	3	269	75	0	5	7	63	29	21	937
Gear	1	Purse seine	765	1,376	2,178	5,213	13	942	34	2,007	721	0	16	11	275	516	186	14,253
	4	Set gillnet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	47	Mid-water trawl	1	3	11	972	0	0	0	0	0	376	0	0	13	0	0	1,376
	50	Fyke net	0	0	49	0	0	0	0	0	0	0	0	0	0	0	0	49
	55	Tucker trawl	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Boat	1	Alaska Beauty	1	3	11	972	0	0	0	0	0	376	0	0	13	0	0	1,376
	2	Intrepid	72	194	820	3,020	5	303	10	95	102	0	0	3	107	7	20	4,758
	3	GoodNews	107	952	999	2,092	8	639	11	246	183	0	16	8	164	46	166	5,637
	4	Auklet	586	230	408	101	0	0	13	1,666	436	0	0	0	4	463	0	3,907
Total			766	1,379	2,238	6,185	13	942	34	2,007	721	376	16	11	288	516	186	15,678

Table 4: Mean length at age of walleye pollock collected in western Prince William Sound, 1994.

Age	Frequency	Minimum Length (mm)	Mean Length (mm)	Maximum Length (mm)	Standard Deviation
1	57	155	178.7	210	16.1
2	21	245	283.1	316	18.8
3	21	304	336.1	376	19.5
4	39	327	414.7	490	38.1
5	62	385	448.8	510	27.0
6	195	423	479.9	551	25.5
7	33	462	511.8	580	33.1
8	32	483	544.1	585	29.3
9	8	505	590.5	630	47.8
10	4	610	620.8	635	11.5

Table 5: Summary of diet composition (% by weight) for four species of fish found to prey on juvenile salmon in western Prince William Sound, 1994. Data from all strata combined.

Species	Lg. Cop	Amph.	Euph.	Juvenile Salmon	Total Catch
Pacific Herring	20.26	0.31	19.89	0.01	110,165
Walleye Pollock	34.80	2.07	20.77	1.80	10,454
Pink Salmon	0.01	3.14	15.11	0.42	1,310
Dolly Varden	2.30	1.37	9.38	1.31	77

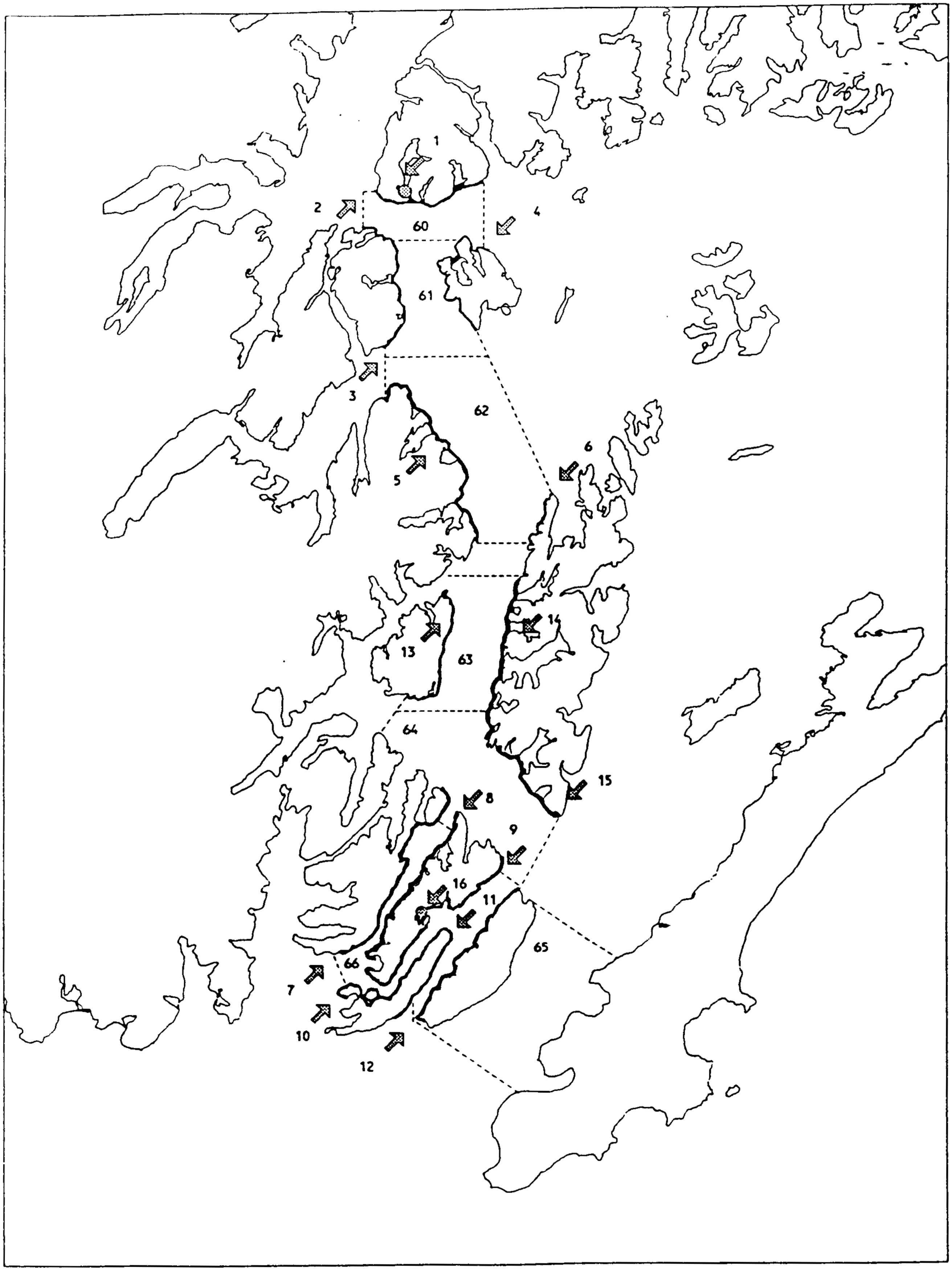

Figure 1: Nearshore and offshore strata established to estimate the juvenile salmon consumption rate of fish predators in western Prince William Sound, 1994.

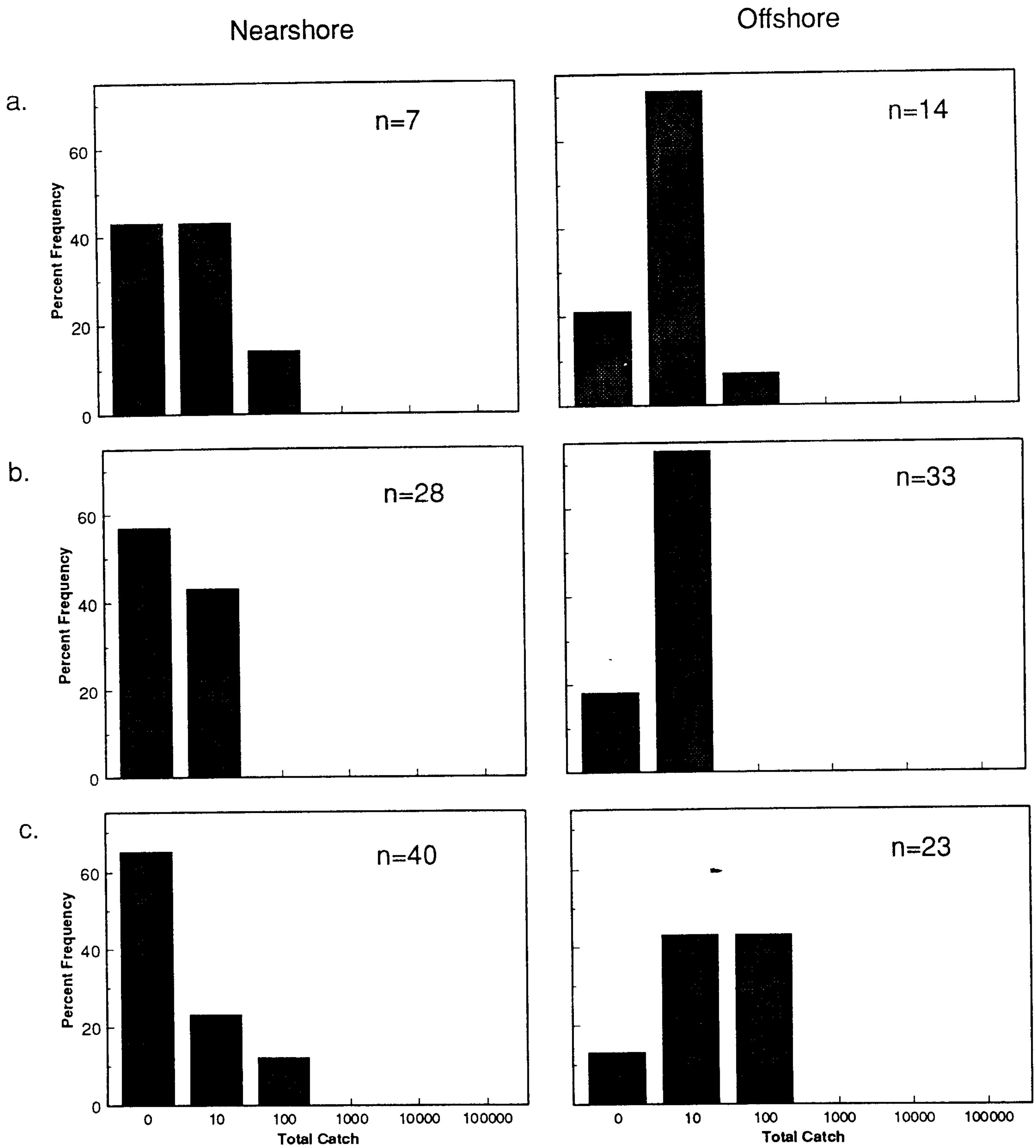

Figure 2: Frequency of occurence of total fish catch (>150 mm FL) in western Prince William Sound by sampling period (a) April 24-30, (b) May 1-15, (c) May 15-30, (d) June 1-15, (e) June 15-30, and (f) July 5-20. Sample sizes indicate number of net sets.

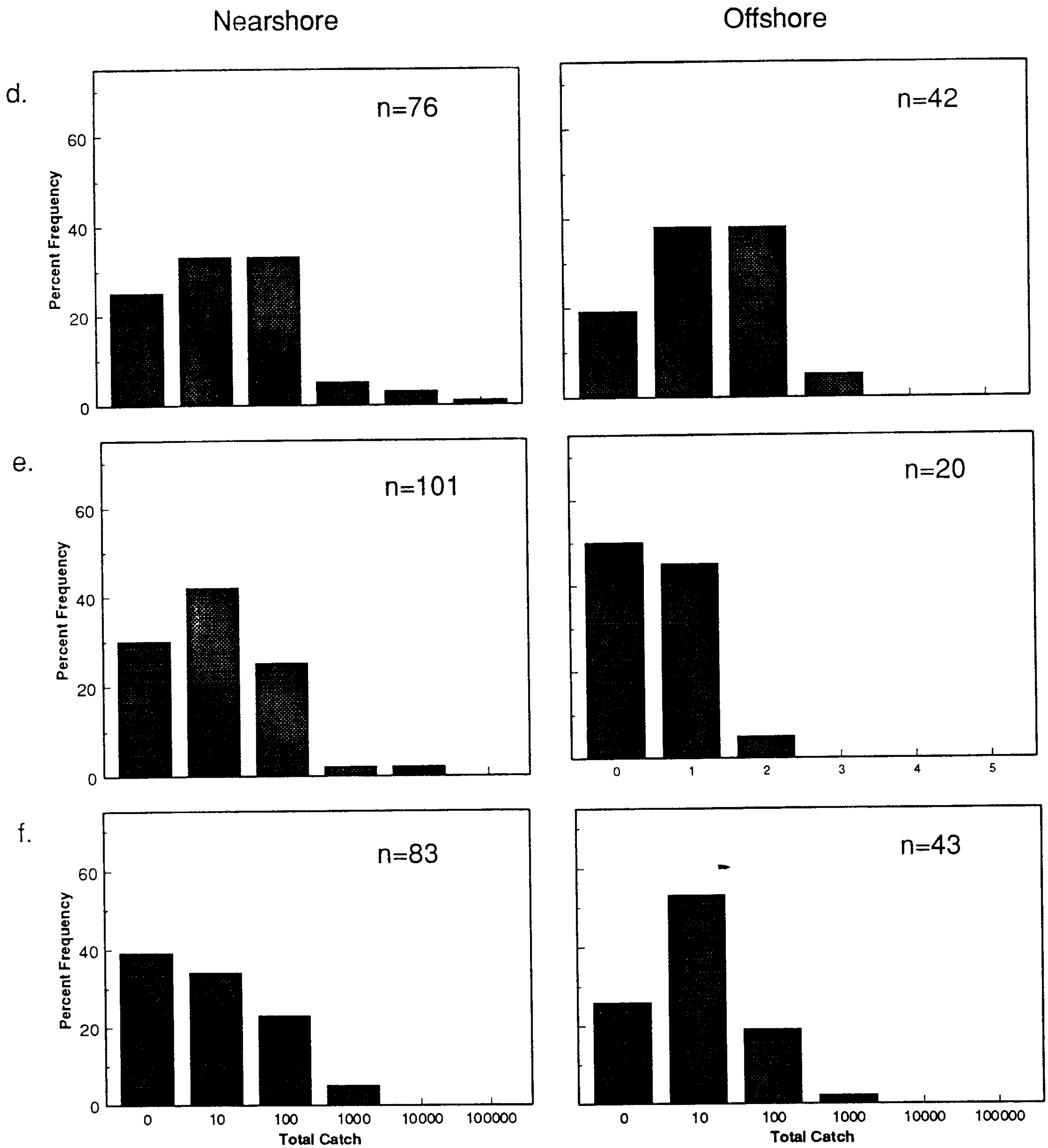

Figure 2: continued.

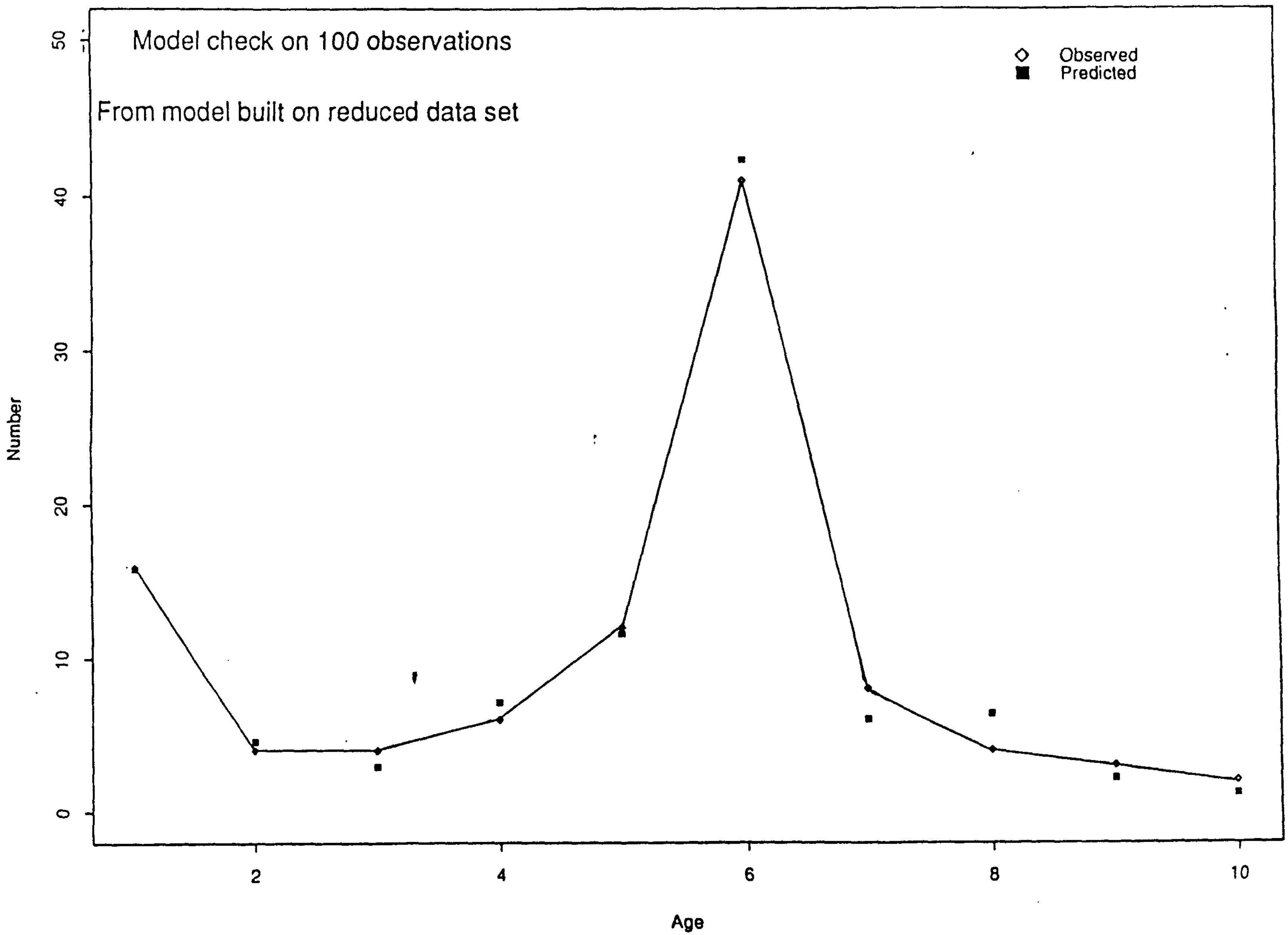

Figure 3: Observed age composition of walleye pollock in western Prince William Sound and predicted age composition from lengths of 100 walleye pollock not used to build an age-length multinomial regression model.

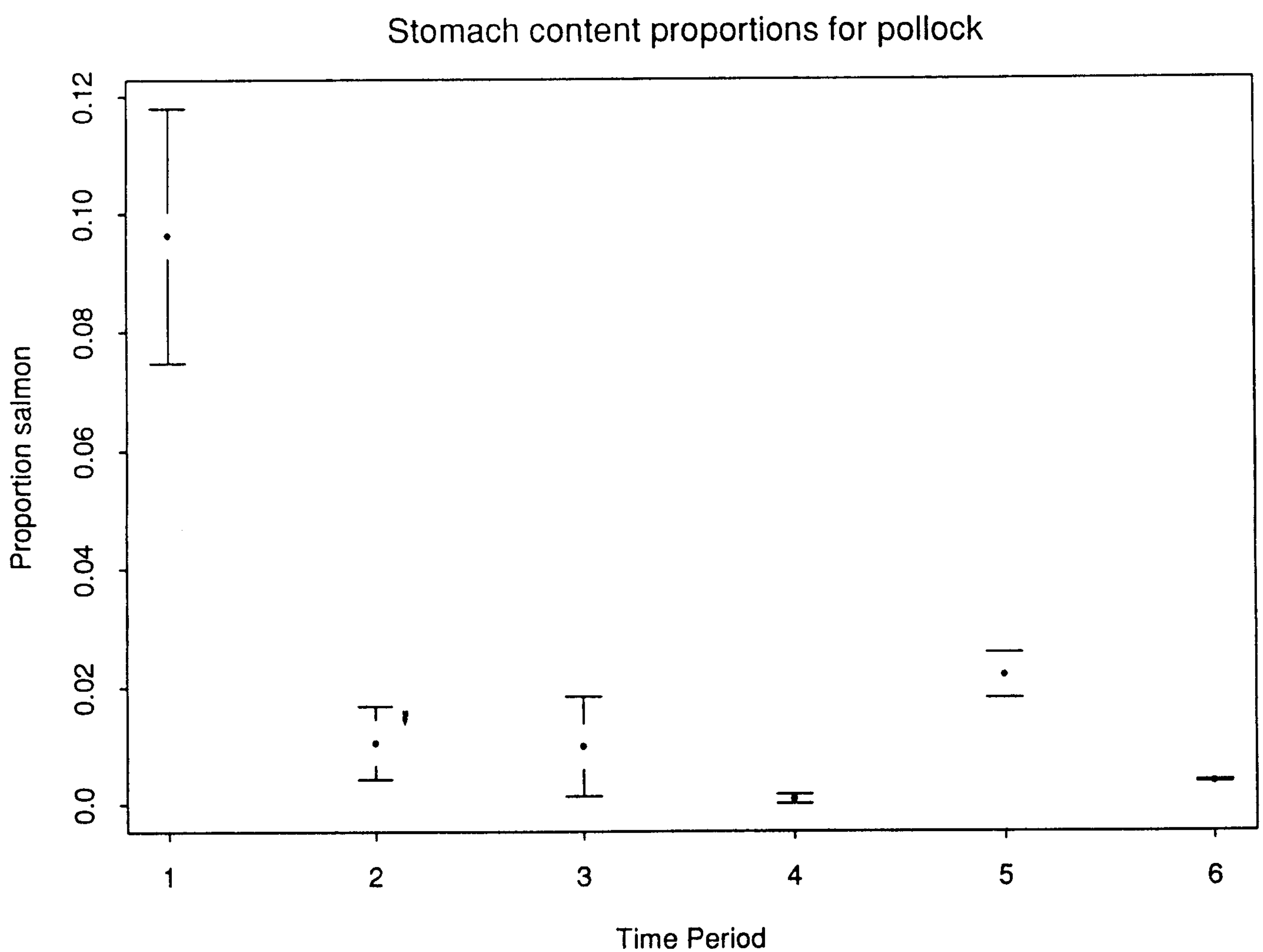

Figure 4: Estimated proportion of total stomach contents weight comprised of juvenile salmon for walleye pollock in western Prince William Sound during six sampling periods.

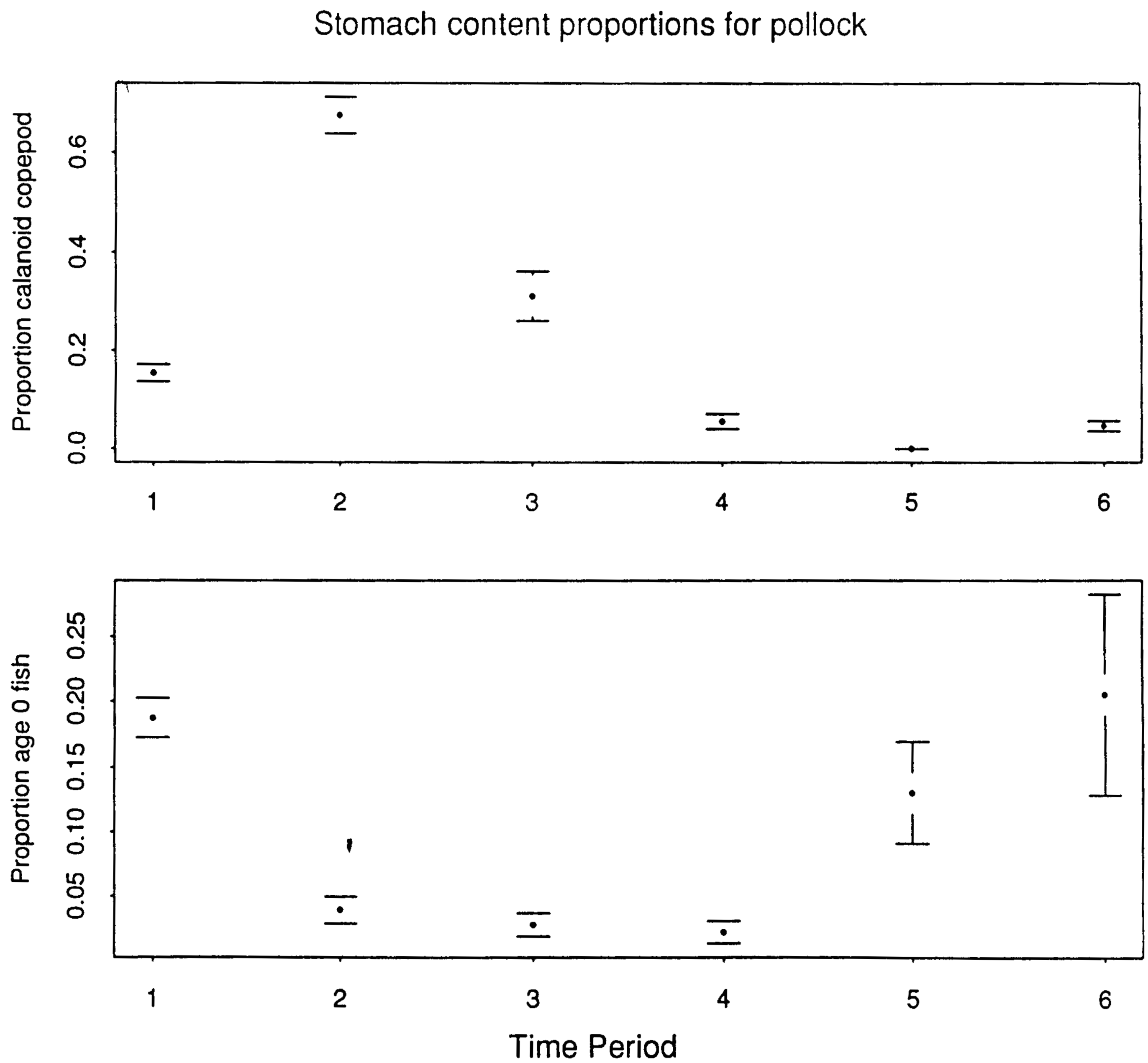

Figure 5: Estimated proportion of total stomach contents weight comprised of (a) calanoid copepods and (b) age 0 fish for walleye pollock in western Prince William Sound during six sampling periods.

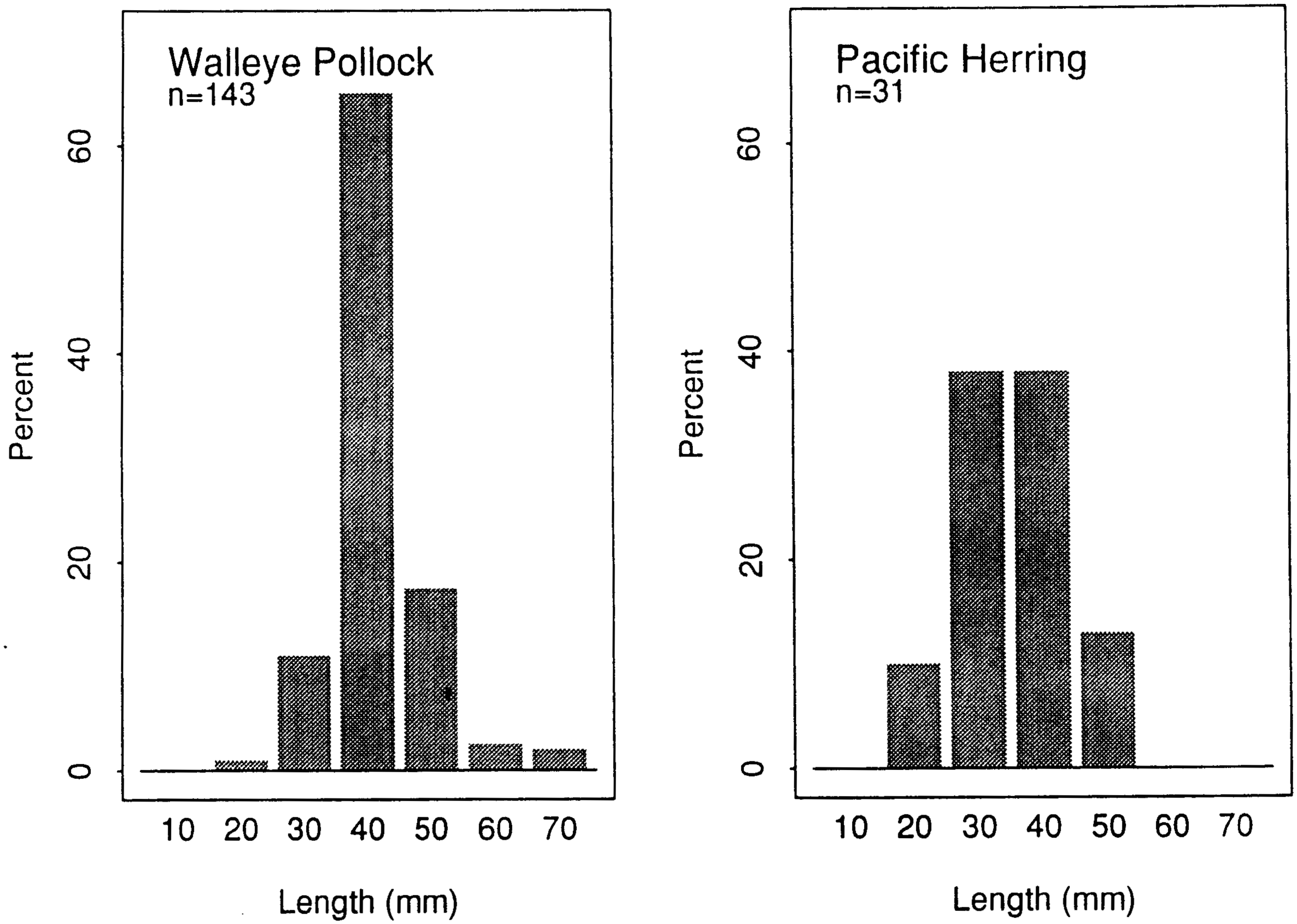

Figure 6: Length frequency distributions of juvenile salmon found in stomachs of walleye pollock and Pacific herring in western Prince William Sound, 1994.

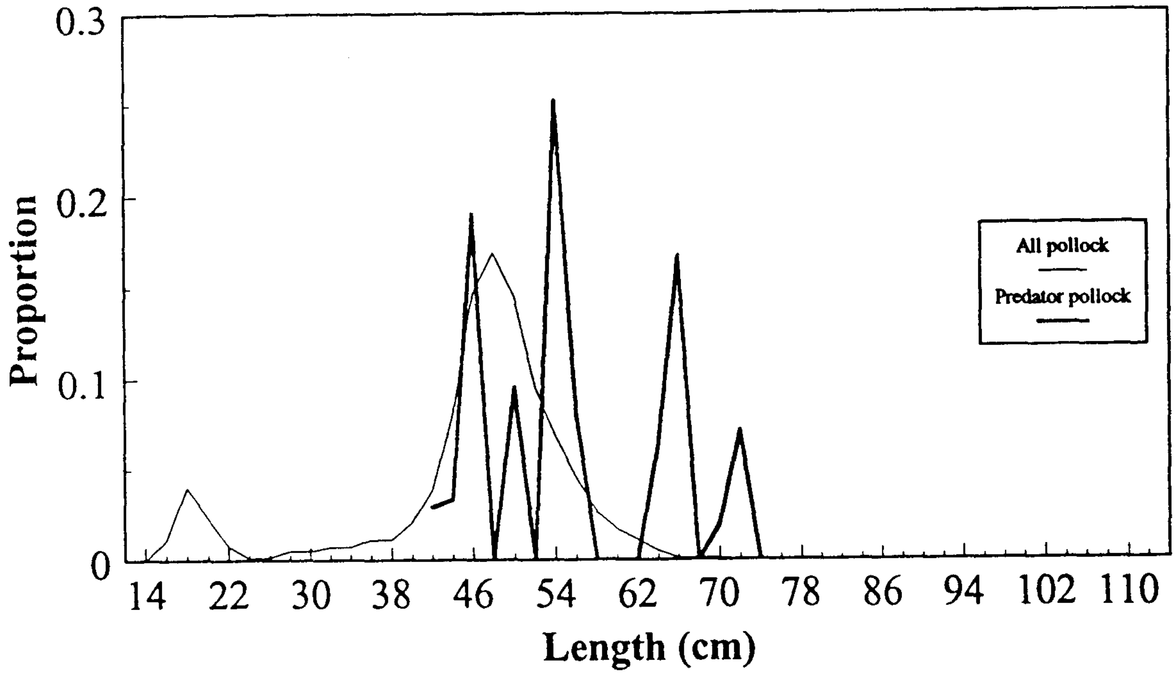

Figure 7: Comparison of length frequency distributions between all walleye pollock and pollock found to consume juvenile salmon in western Prince William Sound, 1994.

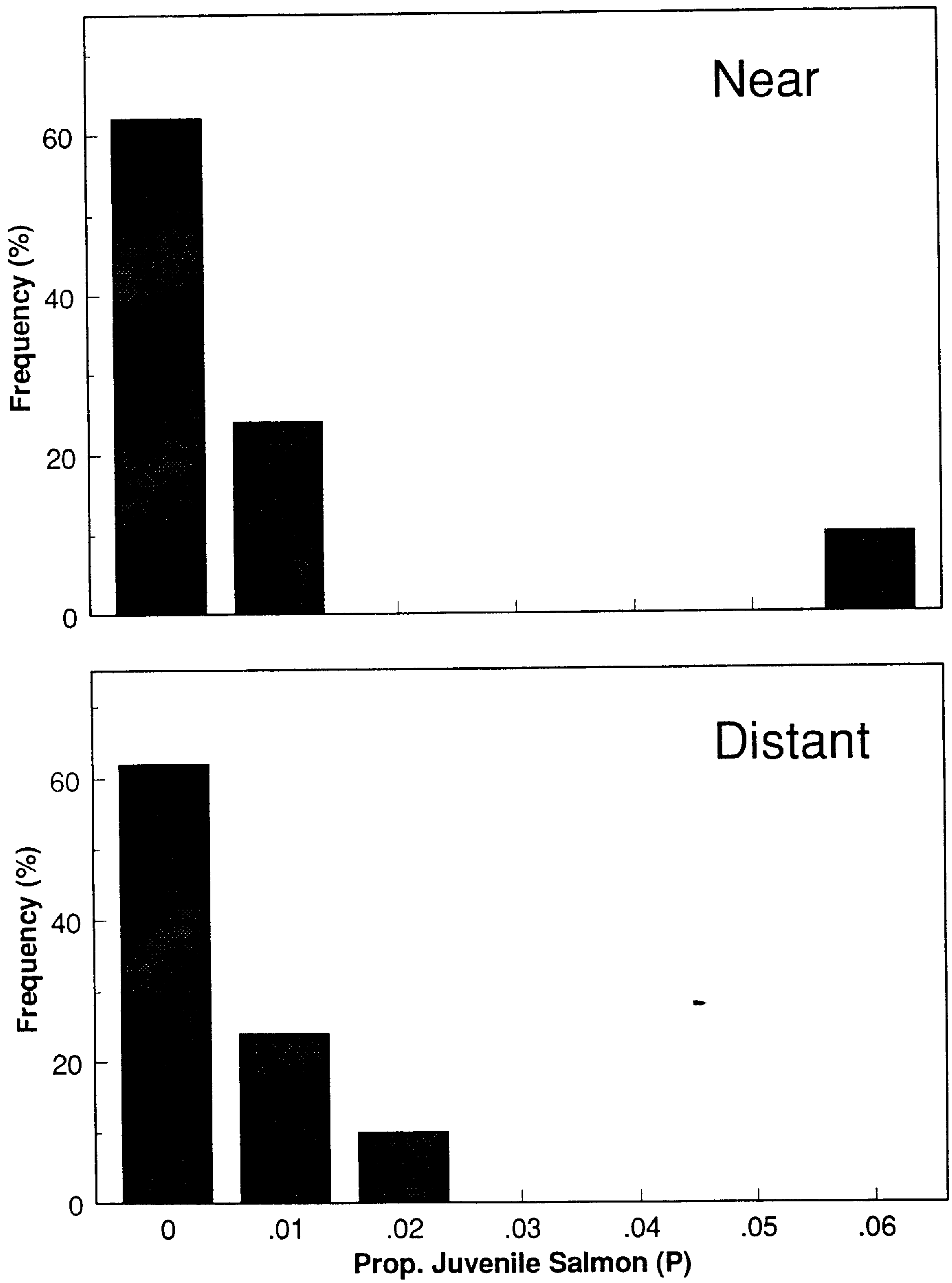

Figure 8: Comparison of frequency distributions of the proportion of total stomach contents weight comprised of juvenile salmon (P) between two areas near and distant from the Wally H. Noerenberg Hatchery.

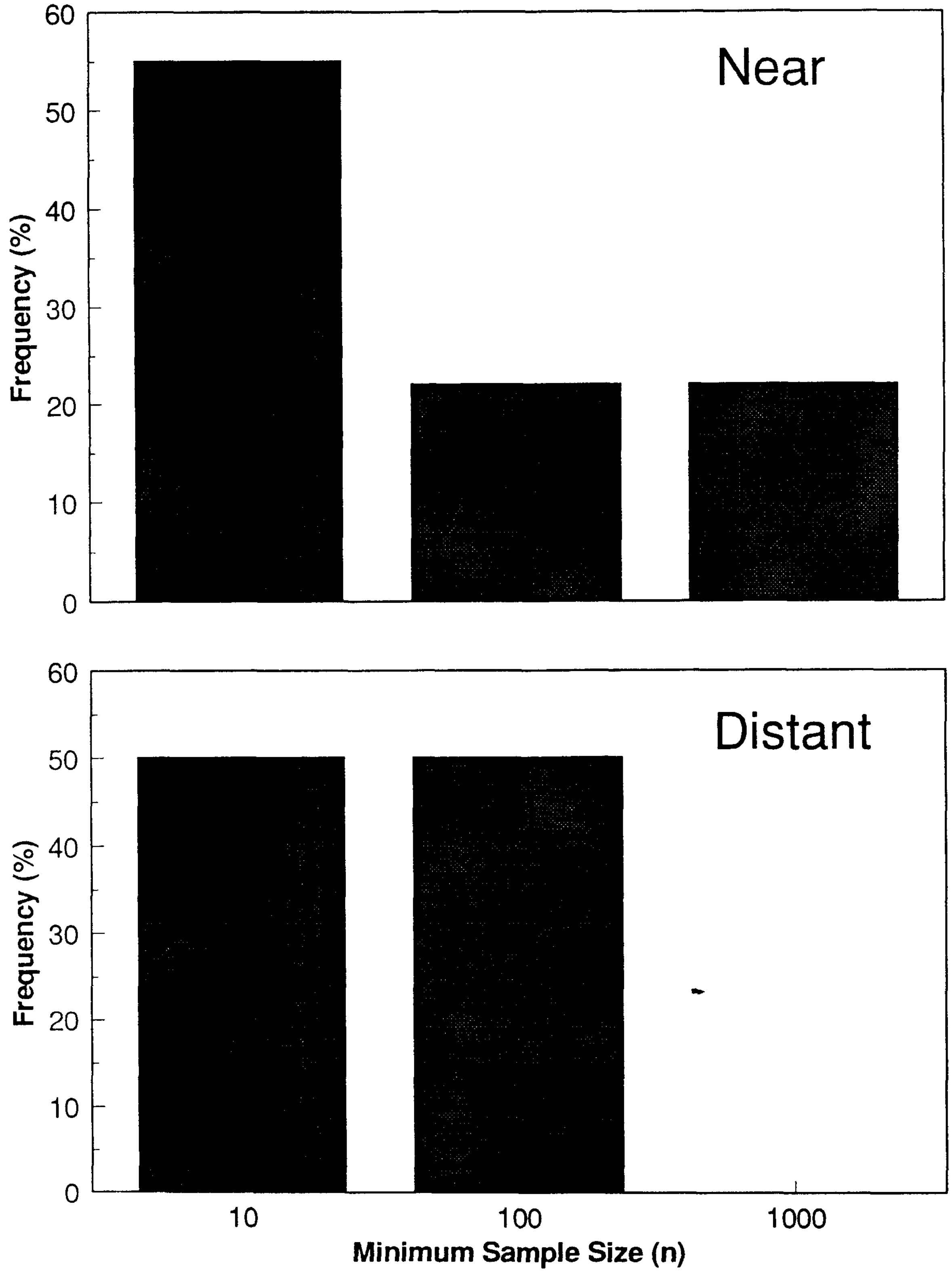

Figure 9: Comparison of frequency distributions of minimum sample sizes needed per net set to capture at least one predator that had consumed juvenile salmon between two areas near and distant from the Wally H. Noerenberg Hatchery.

Appendix I: Summary of total fish catch in Salmon Predation project in western Prince William Sound, 1994.

Table 1: Summary of total fish catch (<150 mm FL) in Salmon Predation project in western Prince William Sound, 1994.

Time Period	Stratum	Species	Total Catch
1	1	Pacific Herring	91
	60	Pacific Herring	4,763
		Pacific Sandlance	18
		Pink Shrimp	1,755
		Unidentified Shrimp	170
		Unidentified Smelt	10
		Unidentified Squid	43
	62	Unidentified Squid	1
2	2	Pacific Herring	3
		Pink Salmon	45,177
		Soft Sculpin	3
		Threespine Stickleback	43
		Unidentified Fish	23
		Unidentified Shrimp	1
	3	Chum Salmon	1,950
		Dolly Varden	1
		Irish Lord	4
		Pacific Spiny	1
		Pink Salmon	93,726
		Threespine Stickleback	65
		Unidentified Eel	1
		Unidentified Fish	7
		Unidentified Shrimp	2
	4	Capelin Smelt	65
		Dusky Rockfish	3
		Pacific Staghorn	1
		Prowfish	1
		Quillback Rockfish	1
		Sharpnose Sculpin	1
		Threespine Stickleback	7
		Unidentified Prickleback	2
		Unidentified Snailfish	1

Table 1: Continued

Time Period	Stratum	Species	Total Catch
		Unidentified Squid	655
	61	Unidentified Squid	59
3	2	Capelin Smelt	19
		Northern Smoothtongue	8
		Pacific Herring	5
		Threespine Stickleback	7
		Unidentified Snailfish	2
	3	Capelin Smelt	1
		Threespine Stickleback	4
	4	Capelin Smelt	9
		Chum Salmon	933
		Dolly Varden	3
		Pacific Herring	56
		Pacific Sandlance	2
		Pacific Spiny	1
		Pink Salmon	7,844
		Silverspotted Sculpin	1
		Threespine Stickleback	12
		Unidentified Fish	6
		Unidentified Greenling	1
		Unidentified Salmon	3
		Unidentified Snailfish	1
		Unidentified Squid	7
	5	Capelin Smelt	66
		Chum Salmon	81
		Dolly Varden	1
		Irish Lord	5
		Pacific Sandlance	7
		Pacific Spiny	2
		Pink Salmon	29,867
		Possible Salmon	4
		Sockeye Salmon	8
		Threespine Stickleback	13
		Unidentified Eel	3
		Unidentified Flatfish	1
		Unidentified Gadidae	1
		Unidentified Greenling	2
		Unidentified Rockfish	5
		Unidentified Snailfish	2
		Walleye Pollock	4

Table 1: Continued

Time Period	Stratum	Species	Total Catch
		Pink Salmon	4,814
		Sockeye Salmon	1
		Unidentified Squid	1
		Walleye Pollock	3
	4	Capelin Smelt	1
		Chinook Salmon	1
		Chum Salmon	1,853
		Crested Sculpin	1
		Pacific Herring	40,303
		Pacific Sandlance	273
		Pink Salmon	42,699
		Prowfish	2
		Quillback Rockfish	1
		Sockeye Salmon	2,108
		Threespine Stickleback	7
		Unidentified Fish	3
		Unidentified Gadidae	42,767
		Unidentified Greenling	3
		Unidentified Prickleback	3,000
		Unidentified Squid	8
		Walleye Pollock	53,101
	5	Bering Wolfish	1
		Chinook Salmon	1
		Chum Salmon	108
		Coho Salmon	1
		Dolly Varden	9
		Pacific Herring	1,052
		Pacific Sandlance	4
		Pink Salmon	39,036
		Quillback Rockfish	1
		Sockeye Salmon	902
		Spot Shrimp	1
		Unidentified Fish	201
		Unidentified Gadidae	1
		Unidentified Greenling	1
		Unidentified Rockfish	1
		Unidentified Salmon	2,337
		Walleye Pollock	7
	6	Chum Salmon	5
		Coho Salmon	3
		Pacific Herring	48

Table 1: Continued

Time Period	Stratum	Species	Total Catch
	6	Lingcod Greenling	2
		Threespine Stickleback	1
		Unidentified Greenling	1
	14	Capelin Smelt	1
		Chum Salmon	85
		Pacific Herring	4
		Pacific Sandlance	41
		Pink Salmon	30,023
		Unidentified Fish	1
		Unidentified Gadidae	15
		Unidentified Greenling	1
	60	Unidentified Lanternfish	5
		Unidentified Squid	18
	61	Capelin Smelt	22
		Northern Smoothtongue	5
		Unidentified Squid	553
4	1	Capelin Smelt	1
		Chinook Salmon	150
		Chum Salmon	7,677
		Coho Salmon	1
		Pink Salmon	72
	2	Bering Wolfish	4
		Chinook Salmon	4
		Dolly Varden	1
		Pacific Herring	85
		Pacific Sandlance	1
		Pink Salmon	10
		Sockeye Salmon	1
		Threespine Stickleback	6
		Unidentified Eel	1
		Unidentified Fish	3
		Unidentified Gadidae	3,151
		Unidentified Greenling	1
		Unidentified Snailfish	2
		Unidentified Squid	1
	3	Chinook Salmon	1
		Chum Salmon	1,977
		Coho Salmon	29
		Pacific Herring	39
		Pacific Sandlance	2

Table 1: Continued

Time Period	Stratum	Species	Total Catch
		Pacific Sandlance	1
		Pink Salmon	67,195
		Prowfish	1
		Unidentified Gadidae	3
		Unidentified Greenling	2
		Unidentified Smelt	7
		Unidentified Squid	2
		Walleye Pollock	5
	7	Chum Salmon	1,105
		Pacific Sandlance	1
		Pink Salmon	15,275
		Unidentified Gadidae	1
	13	Capelin Smelt	3
		Chum Salmon	6
		Coho Salmon	1
		Pacific Herring	5
		Pacific Sandlance	1
		Pink Salmon	76,867
		Sockeye Salmon	1
	14	Chum Salmon	102
		Pacific Sandlance	1
		Pink Salmon	43,651
		Unidentified Gadidae	1
	60	Unidentified Squid	12
	62	Pacific Herring	1
		Unidentified Gadidae	1
		Unidentified Squid	17
5	4	Chum Salmon	196
		Pacific Sandlance	1
		Pink Salmon	24,474
		Unidentified Gadidae	271
	5	Chum Salmon	1
		PacifiC Sandlance	954
		Pink Salmon	23,349
		Unidentified Gadidae	1
	6	Chum Salmon	3
		PacifIC Sandlance	2,199
		Pink Salmon	120,994
		Sockeye Salmon	1
		Unidentified Gadidae	4

Table 1: Continued

Time Period	Stratum	Species	Total Catch
	7	Chum Salmon	3
		Crested Sculpin	1
		Dolly Varden	16
		Pacific Sandlance	4
		Pink Salmon	36,406
		Prowfish	6
		Rock Greenling	6
		Sockeye Salmon	600
		Soft Sculpin	1
		Unidentified Fish	3
		Unidentified Gadidae	17,830
		Unidentified Rockfish	1
		Unidentified Smelt	2
		Unidentified Snailfish	4
	8	Chum Salmon	359
		Coho Salmon	2
		Crested Sculpin	1
		Pacific Sandfish	2
		Pacific Sandlance	1,678
		Pink Salmon	89,990
		Prowfish	1
		Rock Greenling	2
		Sockeye Salmon	6
		Unidentified Fish	2
		Unidentified Gadidae	7,993
	9	Bigmouth Sculpin	1
		Crested Sculpin	5
		Pacific Sandlance	150
		Pacific Spiny	2
		Pacific Tomcod	3,413
		Pink Salmon	302
		Prowfish	3
		Unidentified Gadidae	21,950
		Unidentified Rockfish	2
		Unidentified Salmon	9
		Unidentified Snailfish	2
	10	Capelin Smelt	3,024
		Crested Sculpin	1
		Dolly Varden	1
		Lingcod Greenling	2
		Pacific Sandlance	2

Table 1: Continued

Time Period	Stratum	Species	Total Catch
		Pacific Tomcod	900
		Prowfish	5
		Sockeye Salmon	1
		Unidentified Fish	2
		Unidentified Gadidae	51,989
		Unidentified Rockfish	1
		Unidentified Smelt	2
	11	Crested Sculpin	1
		Lingcod Greenling	2
		Pacific Spiny	1
		Prowfish	2
		Rock Greenling	15
		Sablefish	1
		Unidentified Gadidae	32,135
		Unidentified Rockfish	1
		Unidentified Salmon	5
		Unidentified Smelt	2
		Unidentified Snailfish	4
	12	Lingcod Greenling	10
		Pacific Herring	1
		Pacific Sandfish	1
		Pink Salmon	7
		Prowfish	5
		Unidentified Fish	1
		Unidentified Gadidae	18,380
		Walleye Pollock	1
	13	Chinook Salmon	10
		Chum Salmon	35
		Crested Sculpin	10
		Dolly Varden	2
		Great Sculpin	1
		Pacific Herring	5,406
		Pacific Tomcod	7
		Pink Salmon	6,396
		Prowfish	17
		Sockeye Salmon	20,514
		Threespine Stickleback	3
		Unidentified Eel	1
		Unidentified Fish	3
		Unidentified Flatfish	1
		Unidentified Gadidae	140,584

Table 1: Continued

Time Period	Stratum	Species	Total Catch
		Unidentified Greenling	2
		Unidentified Rockfish	13
		Unidentified Salmon	661
		Unidentified Sculpin	4
	14	Capelin Smelt	6
		Chum Salmon	2
		Pacific Herring	5
		Pacific Sandlance	4
		Pink Salmon	75,694
		Prowfish	2
		Unidentified Eel	4
		Unidentified Gadidae	26,892
	15	Capelin Smelt	1
		Crested Sculpin	3
		Possible Herring	4
		Prowfish	10
		Unidentified Eel	1
		Unidentified Gadidae	19,200
		Unidentified Rockfish	1
		Unidentified Salmon	45
		Unidentified Smelt	3
	16	Capelin Smelt	9
		Coho Salmon	11
		Pacific Sandlance	1
		Prowfish	2
		Unidentified Gadidae	272
	63	Unidentified Gadidae	2,111
	64	Quillfish	9
		Unidentified Gadidae	4
		Unidentified Squid	65
	65	Bigmouth Sculpin	1
		Capelin Smelt	2
		Eulachon Smelt	1
		Pacific Tomcod	7
		Prowfish	6
		Unidentified Gadidae	3
		Unidentified Squid	8
		Walleye Pollock	170
	66	Pacific Herring	1
		Unidentified Gadidae	4
		Unidentified Sculpin	1

Table 1: Continued

Time Period	Stratum	Species	Total Catch
		Unidentified Squid	7
6	6	Chum Salmon	1
		Crested Sculpin	7
		Pacific Tomcod	400
		Pink Salmon	4,492
		Prowfish	60
		Sockeye Salmon	181
		Unidentified Gadidae	21,476
		Walleye Pollock	2,800
	7	Chum Salmon	3
		Pink Salmon	22,510
		Unidentified Euphausiid	2
		Unidentified Gadidae	1,378
		Unidentified Prickleback	1
		Unidentified Salmon	776
	8	Chum Salmon	3
		Northern Ronquil	7
		Pacific Sandlance	346
		Pink Salmon	100,184
		Sockeye Salmon	918
		Unidentified Euphausiid	1
		Unidentified Gadidae	9,383
		Unidentified Salmon	104
	9	Chinook Salmon	11
		Northern Ronquil	4
		Pacific Sandlance	1
		Pacific Tomcod	10
		Pink Salmon	21,446
		Sockeye Salmon	6,060
		Unidentified Gadidae	7,626
		Unidentified Salmon	10
		Unidentified Smelt	1
	10	Capelin Smelt	1
		Northern Ronquil	6
		Pacific Herring	1
		Pacific Sandlance	432
		Pink Salmon	98,099
		Prowfish	1
		Sockeye Salmon	162
		Unidentified Gadidae	9,283

Table 1: Continued

Time Period	Stratum	Species	Total Catch
		Unidentified Salmon	130
	11	Lingcod Greenling	1
		Northern Ronquil	11
		Pacific Sandfish	1
		Prowfish	6
		Sockeye Salmon	7,031
		Unidentified Fish	1
		Unidentified Gadidae	2,037
		Unidentified Salmon	444
		Unidentified Smelt	1
	12	Capelin Smelt	1
		Northern Ronquil	8
		Pacific Herring	7
		Pacific Sandfish	13
		Pacific Tomcod	8
		Pink Salmon	4,606
		Prowfish	1
		Sockeye Salmon	101
		Unidentified Gadidae	5,456
		Unidentified Salmon	205
		Walleye Pollock	120
	13	Chum Salmon	1
		Pacific Herring	10
		Pink Salmon	2,584
		Unidentified Gadidae	4,521
		Unidentified Salmon	1,160
		Walleye Pollock	758
	14	Chum Salmon	82
		Pacific Sandlance	1
		Pink Salmon	24,451
		Sockeye Salmon	1
		Unidentified Gadidae	6,570
	15	Chum Salmon	104
		Pacific Sandlance	881
		Pink Salmon	42,241
		Unidentified Gadidae	5,567
	16	Lingcod Greenling	1
		Pacific Herring	1
		Unidentified Gadidae	541
		Unidentified Salmon	513
	61	Unidentified Flatfish	1

Table 1: Continued

Time Period	Stratum	Species	Total Catch
		Walleye Pollock	20
	62	Unidentified Gadidae	5,000
	63	Prowfish	1
		Unidentified Gadidae	9,000
		Walleye Pollock	1
	64	Unidentified Gadidae	4,350
		Unidentified Smelt	400
	65	Capelin Smelt	1
		Unidentified Gadidae	800
	66	Capelin Smelt	10
		Pink Shrimp	122
		Prowfish	3
		Unidentified Fish	2
		Unidentified Gadidae	206
		Walleye Pollock	14

Table 2: Summary of total fish catch (>150 mm FL) in Salmon Predation project in western Prince William Sound, 1994.

Time Period	Stratum	Species	Total Catch
1	1	Chum Salmon	3
		Dolly Varden	1
		Pacific Herring	131
	60	Unidentified Squid	6
		Walleye Pollock	1,365
	62	Walleye Pollock	10
2	2	Pacific Herring	10
		Unidentified Squid	7
	3	Dolly Varden	2
		Pacific Herring	2
		Pacific Tomcod	1
		Walleye Pollock	8
	4	Pacific Cod	1
		Pacific Herring	7
		Starry Flounder	1
		Unidentified Squid	3
		Walleye Pollock	6
	5	Pacific Herring	38
		Unidentified Fish	1
		Walleye Pollock	1
	6	Dolly Varden	1
		Walleye Pollock	7
	9	Pacific Herring	27
		Unidentified Greenling	2
		Walleye Pollock	3
	60	Arrowtooth Flounder	1
		Chinook Salmon	1
		Walleye Pollock	1,164
	61	Unidentified Squid	6
		Walleye Pollock	1,011
	62	Walleye Pollock	773
	64	Walleye Pollock	33
	66	Walleye Pollock	7
3	1	Pacific Herring	1
	2	Chinook Salmon	1
		Chum Salmon	20
		Pacific Herring	93
		Unidentified Squid	2
	3	Dolly Varden	1

Table 2: Continued

Time Period	Stratum	Species	Total Catch
		Pacific Herring	4
		Walleye Pollock	2
	4	Lingcod Greenling	1
		Pacific Herring	135
		Quillback Rockfish	1
		Threespine Stickleback	3
		Unidentified Squid	19
		Walleye Pollock	3
	5	Chum Salmon	3
		Dolly Varden	1
		Pacific Herring	152
		Unidentified Eel	1
		Walleye Pollock	4
	6	Dolly Varden	3
		Walleye Pollock	2
	14	Unidentified Prickleback	1
	60	Chinook Salmon	1
		Walleye Pollock	413
	61	Chinook Salmon	1
		Walleye Pollock	3
4	1	Chinook Salmon	4
		Chum Salmon	75
		Pacific Herring	3
	2	Chum Salmon	250
		Pacific Herring	5,586
		Unidentified Squid	40
		Walleye Pollock	32
	3	Arrowtooth Flounder	1
		Chinook Salmon	1
		Chum Salmon	73
		Dolly Varden	2
		Pacific Herring	25,129
		Unidentified Squid	7
		Walleye Pollock	1
	4	Crested Sculpin	1
		Lingcod Greenling	3
		Pacific Cod	3
		Pacific Herring	70,099
		Pacific Staghorn	1
		Pacific Tomcod	1

Table 2: Continued

Time Period	Stratum	Species	Total Catch
		Pink Salmon	7
		Unidentified Greenling	4
		Unidentified Squid	3
		Walleye Pollock	2
	5	Chum Salmon	2
		Coho Salmon	1
		Crested Sculpin	1
		Dolly Varden	1
		Pacific Herring	1,247
		Pacific Sandlance	5
		Pacific Tomcod	5
		Sockeye Salmon	1,001
		Threespine Stickleback	2
		Unidentified Greenling	2
		Walleye Pollock	3
	6	Pacific Cod	3
		Pacific Staghorn	3
		Pacific Tomcod	37
		Salmon Shark	1
		Unidentified Greenling	5
	13	Pacific Herring	35
		Walleye Pollock	15
	60	Arrowtooth Flounder	1
		Pacific Herring	10
		Walleye Pollock	1,647
	61	Walleye Pollock	586
	62	Chinook Salmon	1
		Salmon Shark	1
		Walleye Pollock	121
	63	Walleye Pollock	35
	66	Walleye Pollock	1
5	5	Unidentified Greenling	1
	6	Unidentified Greenling	1
	7	Chinook Salmon	1
		Chum Salmon	5
		Dolly Varden	2
		Pacific Herring	26
		Pink Salmon	40
		Sockeye Salmon	11
	8	Chum Salmon	110

Table 2: Continued

Time Period	Stratum	Species	Total Catch
		Grunt Sculpin	1
		Pacific Herring	2
		Pacific Tomcod	1
		Pink Salmon	992
		Sockeye Salmon	20
		Unidentified Greenling	3
		Unidentified Rockfish	1
	9	Dolly Varden	3
		Pacific Herring	74
		Pink Salmon	24
		Sockeye Salmon	4
		Unidentified Rockfish	2
		Unidentified Salmon	30
		Walleye Pollock	5
	10	Capelin Smelt	3,000
		Chinook Salmon	6
		Chum Salmon	7
		Pacific Herring	12
		Pink Salmon	287
		Unidentified Salmon	4
		Walleye Pollock	1
	11	Chum Salmon	2
		Dolly Varden	2
		Pacific Herring	14
		Pink Salmon	32
		Sockeye Salmon	2
		Unidentified Salmon	3
		Unidentified Snailfish	1
	12	Chum Salmon	1
		Pacific Herring	11
		Pink Salmon	11
		Sockeye Salmon	1
	13	Chum Salmon	55
		Dolly Varden	5
		Pacific Herring	5,451
		Pink Salmon	39
		Sockeye Salmon	3
		Unidentified Greenling	1
		Unidentified Salmon	195
		Walleye Pollock	39
	14	Pacific Herring	9,448

Table 2: Continued

Time Period	Stratum	Species	Total Catch
		Pink Salmon	18
		Prowfish	3
		Unidentified Salmon	76
		Unidentified Squid	2
		Walleye Pollock	2
	15	Dolly Varden	2
		Pacific Herring	162
		Pink Salmon	468
		Unidentified Rockfish	1
		Unidentified Salmon	34
		Unidentified Smelt	3
		Walleye Pollock	4
	16	Dolly Varden	9
		Pink Salmon	5
		Walleye Pollock	50
	63	Chinook Salmon	1
		Pink Salmon	19
		Salmon Shark	1
		Walleye Pollock	5
	64	Pink Salmon	15
		Unidentified Squid	3
		Walleye Pollock	3
	65	Chum Salmon	2
		Pacific Herring	8
		Pink Salmon	23
		Unidentified Squid	1
		Wolf Eel	1
	66	Walleye Pollock	42
6	6	Pacific Cod	8
		Pacific Herring	70
		Pink Salmon	57
		Prowfish	1
		Sockeye Salmon	1
		Walleye Pollock	1
		Wolf Eel	1
	7	Chum Salmon	1
		Pacific Herring	623
		Pink Salmon	22
		Walleye Pollock	48
	8	Chum Salmon	1

Table 2: Continued

Time Period	Stratum	Species	Total Catch
		Dolly Varden	3
		Lingcod Greenling	1
		Pink Salmon	9
		Sockeye Salmon	3
		Unidentified Greenling	2
		Unidentified Sculpin	1
		Walleye Pollock	19
	9	Pacific Herring	34
		Pink Salmon	21
		Unidentified Salmon	440
		Walleye Pollock	6
	10	Chum Salmon	55
		Lingcod Greenling	1
		Pacific Herring	3
		Pink Salmon	127
		Sockeye Salmon	105
		Unidentified Greenling	2
		Unidentified Salmon	1,830
	11	Pacific Herring	1
		Pink Salmon	1
	12	Chum Salmon	10
		Pink Salmon	70
		Unidentified Salmon	190
		Walleye Pollock	24
	13	Pacific Herring	2
		Pink Salmon	10
		Salmon Shark	3
		Unidentified Salmon	1
		Unidentified Sculpin	1
		Walleye Pollock	2,000
	14	Lingcod Greenling	2
		Unidentified Greenling	1
	15	Lingcod Greenling	1
		Pacific Herring	210
		Unidentified Greenling	1
	16	Pacific Herring	98
		Pink Salmon	203
		Walleye Pollock	3
	60	Unidentified Squid	2
		Walleye Pollock	31
	61	Walleye Pollock	11

Table 2: Continued

Time Period	Stratum	Species	Total Catch
	62	Chum Salmon	1
		Unidentified Squid	35
		Walleye Pollock	20
	63	Pink Salmon	15
		Unidentified Squid	110
		Walleye Pollock	10
	64	Pink Salmon	10
		Unidentified Squid	142
		Walleye Pollock	42
	65	Black Rockfish	1
		Eulachon Smelt	51
		Pink Salmon	5
		Unidentified Squid	32
		Walleye Pollock	114
	66	Arrowtooth Flounder	2
		Chum Salmon	3
		Pacific Herring	336
		Pink Salmon	3
		Walleye Pollock	511

Appendix II

Several options for analyzing stomach content data have been discussed and this effort is intended to shed some light on the relative merits of each. Specifically, we are interested in obtaining an estimate of p, the proportion of a predator's diet that is a particular prey species. For the purposes of this discussion, I would like to consider estimates for a single stratum, i.e., a single time period and location combination. Once we determine the best approach at this level we can consider how to compare time periods and/or locations.

Sampling scheme

We have a two-stage sampling scheme within each stratum. Primary units were sets with several sets taken in each stratum. Individual fish were the secondary units with anywhere from zero to thousands of fish in a set. Some subset of the fish from a set were sampled for stomach content analysis with the entire set taken in some cases.

The estimators for this sampling scheme generally utilized the number of possible primary units and the total number of secondary units. In our particular case, this meant we needed the total number of possible sets and the total number of fish in each stratum. For this analysis, we could estimate the number of possible sets by dividing the volume of water in a stratum by the average volume of water filtered by a set. The total number of fish in the stratum could then be estimated as the average number of fish in each set that was taken times the total number of possible sets.

There are a couple of ways to estimate p, the proportion of a particular prey species in the stomach of a particular predator species. The first is to estimate the total stomach content weight of the predator and the weight of the prey species in the stomach of the predator and then divide the latter estimate by the former. The second is to calculate a p for each individual predator sampled and then consider this the response to be estimated. To see the difference, consider a fish with only a small amount of prey in its stomach, but of only one prey species. It adds a small observation to both estimates of the first approach, but a large observation (100%) to the second. The first approach would seem to be more resilient to such a case and might be preferred for this reason.

Methods

Formula approach

Notation at the stratum level:

- N = total number of sets in the stratum
- n = number of sets taken in the stratum
- M_i = total number of fish caught in the i^{th} set
- m_i = number of fish sampled in the i^{th} set
- y_{ij} = response measured for the j^{th} fish in the i^{th} set

Note: y_{ij} can be any response measured on an individual fish, such as the total stomach content weight of a fish, total weight of a given prey species in its stomach, or the proportion of its stomach content that is a given prey species.

In general form, the estimator of the population mean to be used is

$$\bar{y}_r = \frac{\sum_{i=1}^{n} M_i \bar{y}_i}{\sum_{i=1}^{n} M_i}, \tag{1}$$

where

$$\bar{y}_i = \frac{1}{m_i} \sum_{j=1}^{m_i} y_{ij} .$$

The estimator for the variance of $\bar{y}_r$ is

$$\hat{V}(\bar{y}_r) = \left(\frac{N-n}{N}\right) \frac{1}{n\bar{M}^2} s_r^2 + \frac{1}{nN\bar{M}^2} \sum_{i=1}^{n} M_i^2 \left(\frac{M_i - m_i}{M_i}\right) \frac{s_i^2}{m_i}, \tag{2}$$

where

$$\bar{M} = \frac{1}{n} \sum_{i=1}^{n} M_i ,$$

$$s_r^2 = \frac{1}{n-1} \sum_{i=1}^{n} M_i^2 (\bar{y}_i - \bar{y}_r)^2 ,$$

$$s_i^2 = \frac{1}{m_i - 1} \sum_{j=1}^{m_i} (y_{ij} - \bar{y}_i)^2 .$$

If w_1 is the weight of a prey species in a stomach, w_2 is the total stomach content weight, and p is the proportion w_1/w_2, then the estimators become

$$\bar{w}_1 = \frac{\sum_{i=1}^{n} M_i \bar{w}_{1i}}{\sum_{i=1}^{n} M_i} \qquad \text{where } \bar{w}_{1i} = \frac{1}{m_i} \sum_{j=1}^{m_i} w_{1ij} , \tag{3}$$

$$\overline{w}_2 = \frac{\sum_{i=1}^{n} M_i \overline{w}_{2i}}{\sum_{i=1}^{n} M_i} \qquad \text{where } \overline{w}_{2i} = \frac{1}{m_i}\sum_{j=1}^{m_i} w_{2ij}\,, \tag{4}$$

$$\overline{p} = \frac{\sum_{i=1}^{n} M_i \overline{p}_i}{\sum_{i=1}^{n} M_i} \qquad \text{where } \overline{p}_i = \frac{1}{m_i}\sum_{j=1}^{m_i} p_{ij}\,, \tag{5}$$

so that

$$\hat{p}_1 = \frac{\overline{w}_1}{\overline{w}_2} \text{ and } \hat{p}_2 = \overline{p}. \tag{6}$$

The variance for $\hat{p}_2$ is obtained directly from (2). In the case where p is estimated as the ratio of two estimates, we can use a Taylor approximation or the Delta method to approximate its variance. The general form of this approximation is

$$Var\left(\frac{\mu_1}{\mu_2}\right) \cong \left(\frac{\mu_1}{\mu_2}\right)^2 \left[\frac{Var(\mu_1)}{\mu_1^2} + \frac{Var(\mu_2)}{\mu_2^2} - 2\frac{Cov(\mu_1,\mu_2)}{\mu_1\mu_2}\right]. \tag{7}$$

Plugging in estimates, we have

$$\hat{V}(\hat{p}_1) = \hat{V}\left(\frac{\overline{w}_1}{\overline{w}_2}\right) = \left(\frac{\overline{w}_1}{\overline{w}_2}\right)^2 \left[\frac{\hat{V}(\overline{w}_1)}{\overline{w}_1^2} + \frac{\hat{V}(\overline{w}_2)}{\overline{w}_2^2} - 2\frac{\hat{C}(\overline{w}_1,\overline{w}_2)}{\overline{w}_1\overline{w}_2}\right], \tag{8}$$

where $\overline{w}_1$ and $\overline{w}_2$ come from (3) and (4), $\hat{V}(\overline{w}_1)$ and $\hat{V}(\overline{w}_2)$ come directly from (2), and $\hat{C}(\overline{w}_1,\overline{w}_2)$ is a modification of (2):

$$\hat{C}(\overline{w}_1,\overline{w}_2) = \left(\frac{N-n}{N}\right)\frac{1}{n\overline{M}^2} s_{\overline{w}_1,\overline{w}_2} + \frac{1}{nN\overline{M}^2}\sum_{i=1}^{n} M_i^2 \left(\frac{M_i - m_i}{M_i}\right)\frac{s_{w_1,w_2}}{m_i}, \tag{9}$$

where

$$\overline{M} = \frac{1}{n}\sum_{i=1}^{n} M_i\,,$$

$$s_{\overline{w}_1,\overline{w}_2} = \frac{1}{n-1}\sum_{i=1}^{n} M_i^2 (\overline{w}_{1i} - \overline{w}_1)(\overline{w}_{2i} - \overline{w}_2),$$

$$s_{w_1,w_2} = \frac{1}{m_i - 1}\sum_{j=1}^{m_i}(w_{1ij} - \overline{w}_{1i})(w_{2ij} - \overline{w}_{2i}).$$

We now have two estimates of *p* with variances as calculated by formula. Functions were written in S-plus to generate these estimators.

Bootstrap approach

The second approach is to use a bootstrap to address the same question. Each set was sampled with replacement for as many fish as were originally taken. For each realization of the bootstrap, $\hat{p}_1$ and $\hat{p}_2$ were calculated as in (6). This was repeated 1000 times. The averages of $\hat{p}_1$ and $\hat{p}_2$ were then determined and variances calculated from the distributions of the 1000 replications. Additionally, the realizations were sorted lowest to highest and 95% confidence interval lower and upper limits were taken as the 25th and the 975th points, respectively. Functions were again written in S-plus to perform these bootstraps.

Results

Formula approach

For the purposes of these calculations, a unique estimate of N was not obtained for each stratum. Rather an approximation was made for one stratum which was applied to all strata. The volume of water in this stratum to a depth of 20 m was estimated as 6,245,148,800 m^3. Considering a trawl size of 18 m by 26 m and a trawl length of 10km, one set filtered an estimated 4,680,000 m^3 of water. There were then an estimated 1335 possible sets in this stratum. Calculations were run for N=1000 and N=2000.

Estimates were generated for predator species 270 (pollock) and 233 (herring) and prey species 460 (salmon), 670 (all fish), and 301 (large copepods). Additionally, a set of estimates was obtained for all predators with salmon as the prey species. If $\overline{w}_2$ was zero, then $\hat{p}_1$ was undefined. When this occurred, $\hat{p}_1$ was set to zero. An "NA" occurred in the output when the estimate was undefined, which could happen in several ways. $\hat{V}(\hat{p}_1)$ was undefined if either $\overline{w}_1$ or $\overline{w}_2$ were zero. It was also undefined if either *n* or m_i was one so that s_r^2 and/or s_i^2 were undefined. One important point to keep in mind is that *n*=1 does not necessarily mean only one set was taken in that stratum. It means that only one set in that stratum had any of the particular predator species that is being considered. For any calculation, the data set is reduced to only those sets that caught the desired predator species. Also, if M_i was unknown for a particular set, it was eliminated from the current calculation.

There were several instances where $\hat{p}_1$ was two to three times $\hat{p}_2$ (e.g., strata 160, 161, 462). There are also cases where the two estimates are very similar (e.g., strata 261, 262), and where $\hat{p}_2$ is considerably larger than $\hat{p}_1$ (e.g., strata 460, 660).

Bootstrap approach

Bootstrap estimates were generated for predator species 270 on prey species 460, 670, and 301 and for predator species 233 on prey species 460 and 670. Additionally, a set of estimates was obtained for all predators with salmon as the prey species. The strata with "NA" for output did not have any sets with the desired predator species that were listed in the catch totals table, i.e., M_i was not known.

Considering the output for predator=270 and prey=460, the same relationships can be seen as pointed out above. The relative magnitudes of $\hat{p}_1$ and $\hat{p}_2$ are the same as in the formula approach. In fact, the point estimates are very close between the two methods.

Discussion

The difference between $\hat{p}_1$ and $\hat{p}_2$ seemed to be substantial considering that neither was always greater than or less than the other. The relationship between them depends on the specific counts and weights in the stratum. I looked at the raw data for two sets to see what some of the factors might be in varying this relationship. Set number 941056 was in stratum 660 where $\hat{p}_1$ was less than $\hat{p}_2$. Out of 19 fish caught, one had stomach contents of 50% salmon (50/100), while the other 18 fish had no salmon. Estimating p for this one set using both methods yielded $\hat{p}_1$=0.0088 and $\hat{p}_2$=0.0263. Another set, number 9410103, was in stratum 462 where $\hat{p}_1$ was greater than $\hat{p}_2$. Out of 9 fish, one had stomach contents of 50% salmon (850/1700), while the other 8 fish had no salmon. Estimating p yielded $\hat{p}_1$=0.1856 and $\hat{p}_2$=0.0556. In both cases, one fish in the set had 50% salmon while the rest had none so that $\hat{p}_2$ did not change much. However, $\hat{p}_1$ increased by more than 20 times as the actual amount of salmon in that one stomach increased considerably.

Consider some artificial data where there were 10 fish sampled in a set, 9 of them with 100 mg in their stomachs, but none of it salmon. By varying the numbers for the 10th fish, we can calculate both estimators to see a little more clearly how they respond. Three situations were considered:

w_1 (1-9)	w_2 (1-9)	w_1 (10)	w_2 (10)	$\hat{p}_1$	$\hat{p}_2$
100	0	100	50	0.05	0.05
100	0	200	100	0.091	0.05
100	0	50	25	0.026	0.05

In all cases the 10th fish had 50% salmon in its stomach, but the actual weights differed. The estimator based on a p for each individual fish, $\hat{p}_2$, did not vary since it does not consider the actual weights involved. In contrast, $\hat{p}_1$ changed considerably, reflecting the relative magnitude of the amount of salmon in the 10th fish and the total stomach contents of all fish.

It is perhaps helpful to consider how this estimate is to be used in the overall study plan. An estimate of the consumption of juvenile salmon by a particular predator species in a particular stratum is defined as $C = DR \times B \times p$, where C is consumption (grams), DR is the daily ration (% body weight per day), and B is the biomass (grams) of the predator species within the stratum. It seems reasonable to expect the estimate of C to vary for the three different situations considered above since the goal is to estimate the amount of salmon consumed which relates to the sum of the w_2's. It seems that p is the only term that can provide different estimates for C, and that only happens when $\hat{p}_1$ is used. We want to estimate the proportion of total prey that is salmon, and this seems to further point to $\hat{p}_1$ as the estimator to use.

There is a relationship between these two estimators that is worth pointing out. Consider the slightly simpler task of estimating p for a single set. The two estimators would be

$$\hat{p}_1 = \frac{\overline{w}_1}{\overline{w}_2} = \frac{\sum w_{1i}}{\sum w_{2i}} \qquad \text{and} \qquad \hat{p}_2 = \frac{1}{n}\sum p_i = \frac{1}{n}\sum \frac{w_{1i}}{w_{2i}}.$$

Every observation has equal weight in $\hat{p}_2$, no matter what the prey weight or total stomach weight. If we weight each observation by total stomach weight so that those fish with more prey in their stomachs get more weight, then we have

$$\hat{p}_2 = \frac{\sum w_{2i} p_i}{\sum w_{21}} = \frac{\sum w_{2i} \frac{w_{1i}}{w_{2i}}}{\sum w_{2i}} = \frac{\sum w_{1i}}{\sum w_{2i}} = \hat{p}_1 .$$

Again, since we eventually want to estimate the biomass of one prey species consumed from an estimate of total prey biomass, we should consider the actual weights involved and use $\hat{p}_1$.

In addition, Steve Thompson states that "the population ratio is commonly estimated by dividing the total of the y-values by the total of the x-values in the sample." In our case, this would be the total of the w_1's divided by the total of the w_2's which is equivalent to $\hat{p}_1$. Proportions and ratios are pretty tricky to deal with considering they are decidedly non-normal with a range of 0 to 1. It would seem then that $\hat{p}_1$ is the appropriate estimator to use.

The formula approach and the bootstrap method seemed to give very similar results. Considering the large number of zeros for w_1, which created a high proportion of repeated values, there was some question of the appropriateness of the bootstrap. Since the two methods were so consistent, I would be inclined to use the formula approach since its estimates are presumably exact and computer calculation time is actually less.

The difference in variance estimates between N=1000 and N=2000 seem to be extremely minute. For predator=270 and prey=460, variances from only two strata changed appreciably (161 and 612) and in both cases the variance was extremely low (10^{-6}). It would seem that a reasonable approximation of N will suffice. We have latitude and longitude for the beginning and ending of each set, so we can easily calculate the average length of trawl in each set to estimate the number of possible trawls.

Output from formula estimation

N=1000

predator=270
prey =460

period	location	ratio	var.ratio	p.hat	v.p.hat	n.caught	n.sampled
1	60	0.09934494	0.00054415	0.05986843	0.00005623	1278	357
1	61	0.06329787	0.00000149	0.03500000	0.00000043	87	30
1	62	0.00000000	NA	0.00000000	0.00000000	10	10
2	3	0.00000000	NA	0.00000000	NA	8	6
2	4	0.00000000	NA	0.00000000	NA	6	6
2	5	0.00000000	NA	0.00000000	NA	1	1
2	6	0.04712644	0.00000000	0.04285714	0.00000000	7	7
2	9	0.00892351	NA	0.10000000	NA	3	3
2	60	0.01631844	0.00017660	0.00766537	0.00002944	1387	487
2	61	0.00840576	0.00001667	0.00690963	0.00001228	1019	250
2	62	0.00011530	0.00000001	0.00014575	0.00000002	542	150
2	65	0.00000000	NA	0.00000000	0.00000000	33	29
2	66	0.00000000	NA	0.00000000	0.00000000	7	7
3	3	0.00000000	NA	0.00000000	NA	2	2
3	4	0.00000000	NA	0.00000000	0.00000000	3	2
3	5	0.00000000	NA	0.00000000	NA	2	2
3	60	0.01494706	0.00016688	0.00209674	0.00000391	474	311
3	61	0.00000000	NA	0.00000000	0.00000000	239	151
4	2	0.00000000	NA	0.00000000	0.00000000	30	30
4	4	0.00000000	NA	0.00000000	NA	1	1
4	13	0.00000000	NA	0.00000000	0.00000000	15	5
4	60	0.00008057	NA	0.00019071	NA	1855	372
4	61	0.00000000	NA	0.00000000	0.00000000	378	217
4	62	0.01582711	0.00025322	0.00509259	0.00002580	120	86
4	66	0.00000000	NA	0.00000000	NA	1	1
5	9	0.09282700	NA	0.04222649	NA	5	5
5	10	0.00000000	NA	0.00000000	NA	1	1
5	12	0.00000000	NA	0.00000000	NA	1	1
5	13	0.16071430	NA	0.07268722	NA	6	6
5	14	0.00000000	NA	0.00000000	NA	1	1
5	15	0.00000000	NA	0.00000000	NA	3	1
5	16	0.02277022	NA	0.00601469	NA	50	46
5	63	0.00000000	NA	0.00000000	NA	4	4
5	64	0.00000000	NA	0.00000000	NA	46	33
6	7	0.00000000	NA	0.00000000	0.00000000	45	23
6	8	0.00000000	NA	0.00000000	0.00000000	19	19
6	9	0.00000000	NA	0.00000000	NA	6	6
6	12	0.09688290	0.00000742	0.04347826	0.00000159	144	23
6	13	0.00000000	NA	0.00000000	0.00000000	2754	42
6	16	0.00000000	NA	0.00000000	NA	3	3
6	60	0.00795100	0.00000123	0.02292020	0.00001777	31	23
6	61	0.00000000	NA	0.00000000	0.00000000	31	11
6	62	0.00000000	NA	0.00000000	NA	20	20
6	63	0.00000000	NA	0.00000000	NA	10	10
6	64	0.00000000	NA	0.00000000	0.00000000	42	27
6	65	0.00000000	NA	0.00000000	NA	113	55
6	66	0.00000000	NA	0.00000000	0.00000000	523	125

predator=233
prey=460

period	location	ratio	var.ratio	p.hat	v.p.hat	n.caught	n.sampled
1	1	0.00000000	NA	0.00000000	0.00000000	34	27
2	2	0.00000000	NA	0.00000000	NA	12	10
2	3	0.00000000	NA	0.00000000	0.00000000	2	2
2	4	0.00000000	NA	0.00000000	0.00000000	5	4
2	5	0.00000000	NA	0.00000000	0.00000000	34	29
2	9	0.00000000	NA	0.00000000	0.00000000	24	21
3	2	0.00000000	NA	0.00000000	0.00000000	98	16
3	3	0.00000000	NA	0.00000000	NA	2	1
3	4	0.00000000	NA	0.00000000	NA	173	51
3	5	0.00378377	NA	0.00701684	NA	145	66
4	2	0.00000000	NA	0.00000000	0.00000000	5669	148
4	3	0.00000000	NA	0.00000000	0.00000000	25146	51
4	4	0.00000000	NA	0.00000000	NA	110442	110
4	5	0.00000000	NA	0.00000000	NA	2265	162
4	6	0.00000000	NA	0.00000000	0.00000000	127	45
4	13	0.00000000	NA	0.00000000	0.00000000	35	20
4	60	0.00000000	NA	0.00000000	0.00000000	10	10
4	61	0.00000000	NA	0.00000000	0.00000000	7	4
5	7	0.00000000	NA	0.00000000	NA	25	22
5	9	0.00000000	NA	0.00000000	0.00000000	74	31
5	10	0.00000000	NA	0.00000000	NA	11	11
5	11	0.00000000	NA	0.00000000	NA	14	12
5	12	0.00000000	NA	0.00000000	NA	11	10
5	13	0.00000000	NA	0.00000000	NA	8468	162
5	14	0.00559410	0.00003344	0.00272571	0.00000885	453	123
5	15	0.00000000	NA	0.00000000	NA	157	75
5	16	0.01114404	NA	0.00607814	NA	76	57
5	65	0.00000000	NA	0.00000000	0.00000000	69	28
6	6	0.00000000	NA	0.00000000	0.00000000	77	69
6	7	0.00000000	A	0.00000000	0.00000000	2763	106
6	9	0.00000000	NA	0.00000000	NA	33	32
6	10	0.00000000	NA	0.00000000	NA	2	1
6	11	0.00000000	NA	0.00000000	NA	1	1
6	12	0.00000000	NA	0.00000000	NA	8	6
6	13	0.00000000	NA	0.00000000	0.00000000	2	2
6	15	0.00000000	NA	0.00000000	0.00000000	610	42
6	16	0.00000000	NA	0.00000000	NA	99	42
6	66	0.00000000	NA	0.00000000	NA	328	19

predator=all
prey=460

period	location	ratio	var.ratio	p.hat	v.p.hat	n.caught	n.sampled
1	1	0.00000000	NA	0.00000000	0.00000000	34	29
1	60	0.06064349	0.00023080	0.05245818	0.00001659	8249	369
1	61	0.06134021	0.00000134	0.03181818	0.00000035	89	33
1	62	0.00000000	NA	0.00000000	0.00000000	11	11
2	2	0.00000000	NA	0.00000000	NA	90	18
2	3	0.00963575	NA	0.00294727	NA	93	21
2	4	0.00000000	NA	0.00000000	NA	99	29
2	5	0.02956055	NA	0.01361149	NA	68	47
2	6	0.04651540	0.00000059	0.03281250	0.00003351	8	10
2	9	0.00180444	0.00000113	0.00763116	0.00002416	37	32
2	60	0.00305882	0.00000823	0.00105024	0.00000084	10140	550
2	61	0.00819424	0.00001855	0.00563231	0.00001118	1409	272
2	62	0.00005473	0.00000000	0.00005445	0.00000000	1404	168
2	65	0.00000000	NA	0.00000000	0.00000000	33	30
2	66	0.00000000	NA	0.00000000	0.00000000	8	8
3	1	0.00000000	NA	0.00000000	NA	1	1
3	2	0.00000000	NA	0.00000000	NA	159	43
3	3	0.00000000	NA	0.00000000	NA	12	11
3	4	0.00000000	NA	0.00000000	NA	323	80
3	5	0.00106587	NA	0.00369844	NA	262	94
3	6	0.00000000	NA	0.00000000	NA	12	9
3	60	0.01080767	0.00009581	0.00128568	0.00000149	616	370
3	61	0.00000000	NA	0.00000000	NA	878	163
4	1	0.00000000	NA	0.00000000	0.00000000	352	22
4	2	0.00000000	NA	0.00000000	NA	9371	202
4	3	0.00000000	NA	0.00000000	NA	25400	71
4	4	0.00000000	NA	0.00000000	NA	211676	140
4	5	0.00000000	NA	0.00000000	NA	5876	193
4	6	0.00000000	NA	0.00000000	NA	155	51
4	13	0.00000000	NA	0.00000000	NA	53	27
4	60	0.00008382	0.00000001	0.00019193	0.00000004	2054	399
4	61	0.00000000	NA	0.00000000	0.00000000	943	200
4	62	0.00486934	NA	0.00087873	NA	569	104
4	64	0.00000000	NA	0.00000000	NA	35	1
4	66	0.00000000	NA	0.00000000	0.00000000	1	2
5	7	0.00000000	NA	0.00000000	NA	18571	73
5	8	0.00000000	NA	0.00000000	NA	9159	19
5	9	0.00109149	NA	0.00021230	NA	25981	58
5	10	0.00000000	NA	0.00000000	NA	59246	30
5	11	0.00011095	NA	0.00006251	NA	32225	35
5	12	0.00000000	NA	0.00000000	NA	18459	31
5	13	0.00438960	NA	0.00030182	NA	178913	250
5	14	0.01313009	NA	0.00311789	NA	36456	148
5	15	0.00000000	NA	0.00000000	NA	19942	90
5	16	0.01986955	NA	0.00968793	NA	435	120
5	63	0.00000000	NA	0.00000000	NA	2539	32
5	64	0.00000000	NA	0.00000000	NA	190	28
5	65	0.00000000	NA	0.00000000	NA	300	56
5	66	0.00000000	NA	0.00000000	NA	2	2
6	6	0.00000000	NA	0.00000000	NA	28500	90
6	7	0.00000000	NA	0.00000000	NA	4986	142
6	8	0.00000000	NA	0.00000000	NA	4973	31
6	9	0.00000000	NA	0.00000000	NA	26832	55
6	10	0.00000000	NA	0.00000000	NA	37919	21
6	11	0.00000000	NA	0.00000000	NA	9535	13
6	12	0.03820214	NA	0.00269642	NA	5053	41
6	13	0.00000000	NA	0.00000000	NA	8680	57
6	15	0.00000000	NA	0.00000000	NA	5360	46
6	16	0.00000000	NA	0.00000000	NA	1361	52
6	60	0.00775261	0.00000175	0.02045455	0.00002782	33	25
6	61	0.00000000	NA	0.00000000	0.00000000	32	13
6	62	0.00000000	NA	0.00000000	NA	5056	25
6	63	0.00000000	NA	0.00000000	NA	9137	35
6	64	0.00000000	NA	0.00000000	NA	5794	50
6	65	0.00000000	NA	0.00000000	NA	204	71
6	66	0.00000000	NA	0.00000000	NA	1156	164