Exxon Valdez Oil Spill
Restoration Project Final Report

Forage Fish Diet Overlap, 1994-1996

Restoration Project 97163C
Final Report

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Study History: "Forage fishes are abundant, schooling fishes preyed upon by many species of seabirds, marine mammals, and other fish species. They provide important ecosystem functions by transferring energy from primary or secondary producers to higher trophic levels," (Springer and Speckman, 1997). A number of these planktivorous species inhabit Prince William Sound (PWS), some supporting important commercial fisheries and all contributing to food webs leading to apex predators. The population dynamics of these forage resources can thus influence the health of their predator populations. Forage fish studies in PWS grew out of observations that seabird populations have failed to recover several years after the acute, massive damage caused by the oil spill, and that their trophic resources have shifted between the late 1970's and the 1990's (Piatt and Anderson, 1996; Oakley and Kuletz, 1996; Bechtol, 1997; Anderson et al, 1999). Researchers felt that an ecosystem study was needed to understand the linkages between these observations.

The initial investigation began in 1994 as Forage Fish Influence on Recovery of Injured Species: Forage Fish Diet Overlap (Sound Ecosystem Assessment (SEA) Restoration Project 94163; Willette et al, 1995). This project was designed to assess the abundance, species composition, distribution and diet overlap of forage fish species within PWS to increase understanding of recent declines in their predators (Springer, 1992; Anderson et. al, 1997; Bechtol, 1997). It was conducted by Alaska Department of Fish and Game (Cordova) concomitantly with two other SEA projects, Salmon Predation (94320E) and Salmon Growth and Mortality (94320A). The National Marine Fisheries Service, Auke Bay Laboratory (NMFS-ABL) and the University of Alaska, Fairbanks, Institute of Marine Science (UAF-IMS) were contracted to process forage fish stomach and prey samples collected by SEA in 1994. In August and November of 1994, the forage fish project was replaced by a multi-agency pilot project that jointly examined seabirds and forage fish. This second project evolved into the Alaska Predator Ecosystem Project (APEX). APEX focuses on the trophic interactions of seabirds and the forage species they depend on. The interconnected components of the five-year study are designed to examine fish ecology, seabird foraging at sea, and seabird reproductive success and colony dynamics on land (Duffy, 1998). In the two years that fish diet overlap studies were part of APEX, the fish population segment of the project (163A) was headed by the University of Alaska, Juneau Center for Fisheries and Ocean Science (JCFOS), and ABL assumed responsibility for the diet overlap sub-project.

Abstract: The Forage Fish Diet Overlap component of the Alaska Predator Ecosystem Experiment (APEX) investigated the trophic interactions of forage fish prey of seabird populations which were impacted during the *Exxon Valdez* oil spill. We analyzed more than 5000 specimens of 14 forage species, and zooplankton and epibenthic prey samples from Prince William Sound (PWS), 1994-96. Forage fish were collected monthly in western PWS with purse seines in 1994 and in three regions of PWS (southwestern, central and northeastern) with a mid-water trawl in 1995 (summer and autumn) and with a beach seine in 1996 (summer). The species examined were mainly young-of-the-year (YOY) and age-1 walleye pollock (*Theragra chalcogramma*), Pacific herring (*Clupea pallasi*), Pacific sandlance (*Ammodytes hexapterus*), pink salmon (*Oncorhynchus gorbuscha*), chum salmon (*O. keta*), sockeye salmon (*O. nerka*), Pacific cod (*Gadus macrocephalus*), Pacific tomcod (*Microgadus proximus*), prowfish (*Zaprora

silenus), northern smoothtongue (*Leuroglossus schmidti*), eulachon (*Thaleichthys pacificus*), capelin (*Mallotus villosus*), threespine stickleback (*Gasterosteus aculeatus*), and Pacific sandfish (*Trichodon trichodon*). We compared seasonal size, diet composition and diet overlap between species from May-November, 1994; described the diets, prey fields and prey selection of juvenile pollock and herring in summer and autumn, 1995 and of juvenile herring, sandlance and pink salmon in summer, 1996; examined for prey shifts and feeding declines when the 1995-96 fish occurred in multi-species aggregations (sympatrically) compared to when they occurred in single species aggregations (allopatrically) to test for competition; and compared diet composition interannually for several species in July of the three years.

Most forage fish species were planktivorous during the six months sampled in 1994, with large and small calanoid copepods a consistent component of prey biomass. Small calanoids were predominantly *Pseudocalanus*, but a succession of large calanoids were consumed throughout the season. *Neocalanus* spp. were prominent in May and *Metridia* spp. were conspicuous in summer and autumn. Species' diets shifted to a variety of macrozooplankters in summer and autumn, but in different months. Pacific tomcod and salmonids were the least planktivorous forage species, but piscivory was occasionally observed among other species. Food webs were the most complex in June, when both significant diet overlap and prey partitioning were commonly observed. Diet overlap between species pairs shifted monthly, and herring and pollock diets overlapped the most consistently. Herring, tomcod, capelin, and pink and chum salmon diets differed each year in July, but sandlance and pollock diets were consistent between years.

Evidence for trophic competition was found from comparisons between the diets of YOY forage species in allopatric and sympatric aggregations in 1995 and 1996. Small calanoid copepods were the predominant zooplankter available in both summer and autumn, but YOY herring and pollock preferred larger prey in autumn. Summer diets of allopatric pollock and herring overlapped by 76% biomass, mainly on the basis of small calanoids. Autumn diets of sympatric pollock and herring also overlapped (mean 55-88% biomass of prey species), the common prey being large calanoids, larvaceans and euphausiids. In autumn, YOY herring and pollock consumed greater numbers of prey in allopatric aggregations than in sympatric aggregations, indicating that competitive interactions inhibited the feeding of both species during this period of declining prey abundance.

In summer, 1996, trophic interactions of three forage species were compared between allopatric and sympatric aggregations. Prey partitioning was indicated by low interspecific diet overlap between sympatric species pairs. Intraspecific comparisons showed that sandlance shifted diets in the presence of other planktivores, but pink salmon and herring diets remained similar whether they occurred allopatrically or sympatrically. Juvenile sandlance and herring consumed small calanoids and larvaceans in proportion to their availability in the zooplankton; juvenile pink salmon strongly selected larvaceans, avoided small calanoids and sometimes consumed fish. Changes in prey composition, changes in diet similarity, and feeding declines indicated that competitive trophic interactions occur among herring, pink salmon and sandlance in summer. Significant declines in food quantity and stomach fullness for all three species in sympatric aggregations were the most dramatic indication of competition, and may have been related to a trend for decreased zooplankton densities in areas of sympatric aggregations.

Our results show that food webs in PWS are complex. Although shifts in diet may compensate to some degree, competitive interactions among forage species can result in reduced feeding. If sympatry occurs regularly under conditions of limited food availability, interspecific competition could affect the carrying capacity of PWS for these species. Density dependent effects have not been thoroughly examined. However, the migration of the majority of juvenile pink salmon to the Gulf of Alaska earlier in the summer reduces their interactions with other planktivorous forage fish in PWS.

Key Words: allopatric and sympatric, competition, diet composition, diet overlap, forage fish trophic interactions, prey fields, prey selection, Prince William Sound, seasonal changes in diet.

Project Data: *Description of data* - The forage fish size and stomach contents data, zooplankton prey field data and epibenthic prey field data were generated from laboratory measurements and microscopic analysis of samples collected by the SEA and APEX projects in 1994-1996. Food habits raw data consist of counts of prey organisms with prey weights estimated from literature values and data on file. *Format* - Data generated by Auke Bay Laboratory for the sample years 1994-1996 and by the University of Alaska, Institute of Marine Science Fairbanks Laboratory for 1994 were finalized in Microsoft ACCESS databases. *Custodian* - Contact Molly Sturdevant, Fisheries Research Biologist, Auke Bay Laboratory, NWAFSC/NMFS/NOAA, 11305 Glacier Highway, Juneau, Alaska, 99801-8626 (work phone: (909) 789-6041, FAX: (907) 789-6094, EMAIL: molly.sturdevant@noaa.gov). *Availability* - Data summaries are available upon written request.

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INTRODUCTION

Seabirds are sensitive to food quality, abundance and distribution. The carrying capacity of the forage environment for pigeon guillemots (*Cepphus columba*), for example, is believed to be higher when greater populations of pelagic (high lipid) forage fish are present. Decadal-scale shifts in the Gulf of Alaska (GOA) oceanographic regime are believed to play a role in the trophic shifts documented for seabirds (Piatt and Anderson, 1996). Declines in lipid-rich capelin and other forage species and increases in lipid-poor gadids and flatfish are well-documented, but it remains uncertain whether these community shifts were caused by the major oceanographic changes in the region (Duffy, 1998; Anderson et al, 1999). Similarly, the effects of the forage fish community shift on forage fish trophic dynamics are unknown. Bottom-up and top-down controls are currently being debated (e.g., McRoy et al, 1999). The prey resources of forage fish must also respond to oceanographic changes, the densities of their own prey, and to densities and distributions of their predators and competitors (e.g.., Brodeur and Ware, 1992; Tanasichuk 1998a, b; Mohammadian et al, 1997; Frost and Bollens, 1992). If oceanographic regime shifts did cause these GOA fish community changes, we may also ask how they influenced the zooplankton food available to forage fish species, whether competitive interactions between forage species shifted as community composition changed, and whether interactions between members of the changing community of planktivorous forage species that comprise seabird prey resources could influence their foraging and reproductive success. These complicated questions cannot be answered without information about the food habits and feeding biology of the fish, as well as studies on the biology of their prey resources. The goal of the forage fish diet study was to provide basic information on forage fish trophic ecology to this end.

This final report consists of three chapters which synthesize the principal findings of three years of forage fish diet data. All of the APEX diet data has previously been reported in annual reports (APEX Projects 95163C-98163C), but SEA Project 94163 has not been completely reported on. Chapter 1 is the first presentation of this data set. Interim reports of the 1994 forage fish diet data were presented before sample processing was completed (Sturdevant, 1995) . The annual report of 94163 included only the late summer data (Willette et al, 1995; Willette et al, 1997), and other data subsets were included in the Salmon Growth and Mortality Project 94320A annual report (Willette et al, 1995). Chapter 1 describes the overall sizes, diet composition, and diet overlap of the 14 forage fish species examined over three years by the Forage Fish Diet Overlap project from monthly, pooled SEA-APEX data. The biomass summary presented here was also incorporated into the trophic mass-balance model of Alaska's PWS Ecosystem (Okey and Pauley, 1998). Chapters 2 and 3 are more in-depth drafts of manuscripts from APEX data with specific analyses that compare principal forage species in allopatric and sympatric aggregations and describe zooplankton prey fields; these manuscripts are in review prior to journal publication. Chapter 2 examines YOY herring and pollock in summer and autumn, while chapter 3 examines juvenile herring, sandlance and pink salmon in summer. In addition, the annual report of APEX Project 98163S (Purcell et al., 1999) utilizes the 1995-96 data to examine the trophic structure of PWS and the potential competition of forage fish and jellyfish by comparing diets of herring, pollock, sandlance and pink salmon to those of *Aurelia*, *Cyanea*, *Aequorea*, and *Pleurobrachia*.

OBJECTIVES

The forage fish diet component of APEX was directed under the hypothesis that "planktivory is the factor determining abundance of the preferred forage species of seabirds." The objectives of the diet study were to collect samples of forage fish for analysis of stomach contents; collect samples from prey fields (zooplankton, epibenthos) for analysis of available prey taxa; to perform laboratory analyses of stomach and prey field samples; and to describe the food habits, prey partitioning, preferred prey items, diet overlap and potential competition between forage species. Providing such information is a first step toward unraveling a trophic cascade that may contribute to lack of seabird recovery.

METHODS

The complete methods employed by SEA 94163 and APEX 163A-C and involved in producing this report appear in the annual reports and the written protocols (see Sturdevant, 1997) for each sub-project. These are briefly summarized below.

Sample collection -- In the first year of PWS forage fish studies, SEA samples were collected opportunistically in conjunction with other projects. Forage fish specimens were collected approximately monthly, between April and September, 1994 in western PWS, using multiple gear types. The samples analyzed were caught principally with two sizes of purse seines (see Chapter 1, this report; Willette et al., 1995). A stratified sampling design was employed in that year, with month and habitat type (shallow bay, moderate slope passage, steep-slope passage) as strata. In August-September, 1994, SEA sampling focused on forage fish sampling, including collection of zooplankton and epibenthic prey fields and a 24-hour diel study at a shallow bay site (Iktua Bay). The project was redirected in July and November, 1994. At these times, a mid-water trawl was used on a pilot basis to survey three geographic regions of PWS (southwestern, central and northeastern) along a parallel transect grid (Haldorson, 1995). Diet samples were collected only in the latter cruise. In summer and autumn, 1995, APEX Project 95163C used the mid-water trawl to fish on hydroacoustic targets along the same transect grid (see Haldorson, Shirley and Coyle, 1996). In summer, 1996, APEX Project 96163C surveyed the offshore area and a shoreline grid of zig-zag transect lines with two sets of hydroacoustic gear. Forage fish samples were collected principally with beach and purse seines (Haldorson, Shirley, Coyle and Thorne, 1997). A diel study of fish feeding was conducted opportunistically at two beach seine sites, with samples collected every four hours over a 24-hour period. Zooplankton prey samples were also collected at sites where fish were caught in 1995-96. No other directed sampling was conducted (see annual reports for specific methodology).

All prey and fish samples (10-15 individuals per size class and species) were preserved in the field in 10% formalin solution and returned to the laboratory for processing. If multiple size classes in the catch were obvious, we preserved each. However, it was not possible to analyze all of the extensive collections in 1994; fish were prioritized based on the quality of information expected to be gained from processing them. The few samples from April, 1994 were not examined. After 1996, although APEX forage fish population assessments continued, forage fish diet overlap studies were discontinued due to budget constraints and limitations for field sampling and laboratory processing.

Laboratory processing --Preserved fish were measured and weighed and the stomachs were excised and transferred to alcohol. Stomachs were weighed before and after removal of contents to obtain an estimate of wet weight by subtraction. Stomach fullness and condition of the contents (relative state of digestion) were ranked according to indices. Contents were teased apart under the microscope, subsampled when necessary, and organisms identified to genus or species where possible. Prey taxa were also assigned to size groups or life history stage when appropriate (see Sturdevant, 1997 for codes and descriptions of taxa). Total weights per taxon were estimated by multiplying numbers observed by individual mean weights from the literature and data on file. Diet composition of forage species was described as the percentage contribution of taxa pooled into major taxonomic groups; grand values were estimated for pooled specimens of a species or mean values were estimated for specific aggregations, depending on the analysis (see chapters). Diet overlap and prey selection were compared between species by month or between groups of allopatric and sympatric species (see chapters for measures used). The quantities and composition of food consumed by fish from allopatric and sympatric aggregations were also compared to assess for competitive interactions. A variety of ANOVA methods and chi-square tests were used for statistical analyses in chapters 2 and 3.

RESULTS

Chapter 1. Diet Composition, Diet Overlap, and Size of 14 Species of Forage Fish Collected Monthly in Prince William Sound, Alaska, 1994-1996.

Authors: M. V. Sturdevant and T. M. Willette

Abstract - Chapter 1

This report summarizes the results of three years of forage fish diet studies sponsored by the *Exxon Valdez* oil spill Trustee Council. Forage Fish Influence on Recovery of Injured Species: Forage Fish Diet Overlap (Restoration Project 94163) investigated the trophic interactions of forage fish prey of seabird populations which were impacted during the *Exxon Valdez* oil spill. Forage fish were collected monthly in western PWS principally with purse seines in 1994. Its successor, Alaska Predator Ecosystem Project (APEX), collected forage specimens in three regions of PWS (southwestern, central and northeastern) principally with a mid-water trawl in 1995 (summer and autumn) and with a beach seine in 1996 (summer). Fish were young-of-the-year (YOY) to age-2 of 14 species, including walleye pollock (*Theragra chalcogramma*), Pacific herring (*Clupea pallasi*), Pacific sandlance (*Ammodytes hexapterus*), pink salmon (*Oncorhynchus gorbuscha*), chum salmon (*O. keta*), sockeye salmon (*O. nerka*), Pacific cod (*Gadus macrocephalus*), Pacific tomcod (*Microgadus proximus*), prowfish (*Zaprora silenus*), northern smoothtongue (*Leuroglossus schmidti*), eulachon (*Thaleichthys pacificus*), capelin (*Mallotus villosus*), threespine stickleback (*Gasterosteus aculeatus*), and Pacific sandfish (*Trichodon trichodon*). We compared seasonal size, diet composition and diet overlap between pooled species from May-November, 1994 and compared diet composition interannually for several species in July of the three years.

Most forage fish species were planktivorous during the six months sampled in 1994, with large and small calanoid copepods a consistent component of prey biomass. Small calanoids were predominantly *Pseudocalanus*, but a succession of large calanoids were consumed throughout the season. *Neocalanus* spp. were prominent in May and *Metridia* spp. were conspicuous in summer and autumn. Large calanoid biomass declined in the diets after spring, and macrozooplankters such as hyperiids, euphausiids and decapods were prominent in summer and autumn. Pacific tomcod, salmonids and sandfish were the least planktivorous forage species, but piscivory was also occasionally observed among other species. Food webs were the most complex in June, when both significant diet overlap and prey partitioning were commonly observed. The July diets of herring, tomcod, capelin, and pink and chum salmon diets differed each year, but sandlance and pollock diets were consistently dominated by small calanoids. Pollock and herring exhibited the most consistent diet overlap by prey biomass. Since different zooplankters have different nutritional profiles, the nutritional quality of planktivorous forage species could be influenced by several diet attributes, including seasonal shifts in diet overlap between species based on ontogenetic prey requirements and fish movement, shifts in diet based on prey availability and competitive interactions with co-occurring species, and the onset of piscivory.

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Introduction - Chapter 1

This report, "Diet Composition, Diet Overlap, and Size of 14 Species of Forage Fish Collected Monthly in Prince William Sound, Alaska, 1994-1996, " summarizes results from three years of Forage Fish Diet Overlap projects. Its purpose is to provide an overview of food habits and potential competition between forage species using combined project data. The species examined include juveniles from several Teleost families: the Salmonidae-- pink salmon (*Oncorhynchus gorbuscha*) chum salmon (*O. keta*), and sockeye salmon (*O. nerka*); the Osmeridae-- eulachon (*Thaleichthys pacificus*) and capelin (*Mallotus villosus*); Bathylagidae-- northern smoothtongue (*Leuroglossus schmidti*); the Gadidae-- pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*) and Pacific tomcod (*Microgadus proximus*); the Clupeidae-- Pacific herring (*Clupea pallasi*); the Ammodytidae-- Pacific sandlance (*Ammodytes hexapterus*); the Zaproridae-- prowfish (*Zaprora silenus*); the Gasterosteidae-- threespine stickleback (*Gasterosteus aculeatus*); and the Trichodontidae-- Pacific sandfish (*Trichodon trichodon*). Each of these species is commonly encountered in the area and/or abundant at some time within the study period. The < 150 mm size range of forage fish means that some species (e.g.., herring, pollock, salmon) are seabird prey as juveniles, then outgrow the classification, while others are considered to be forage species throughout their life history (e.g.., capelin and sandlance). Some species may be more familiar than others, and some may not be thought of as traditional "forage fish" (Springer and Speckman, 1997). The salmonids, for example, are well-known, commercially important as adults, planktivorous, "small schooling species" during their early marine period of residency (Groot and Margolis, 1991), and can contribute large proportions to the diets of piscivorous seabirds (Scheel and Hough, 1997). They are also important because of their high densities during the period of spring outmigration when the habitats they transition are also utilized by "traditional" forage species for feeding. Prowfish and sandfish are two of the little known forage species which are sometimes pelagic and sometimes cryptic because of their association with either jellyfish or sediments, respectively. Prowfish can be frequent or infrequent dietary components of diving seabirds, but provided 25% of dietary biomass delivered to tufted puffin (*Lunda cirrhata*) chicks (Hatch and Sanger, 1992; Roseneau et al, 1998). Sandfish occurred in diets of nearshore diving birds, such as pigeon guillemots foraging on demersal or schooling species (Golet et al, 1998). Because differences in the quality of forage fish are sufficient to influence prey selection by seabirds (Roby et al, 1998), their trophic relationships with one another are important to consider in an ecosystem study. Summarizing by month allows diet comparisons by season between individual species or family groups and by year for a few species examined interannually in July.

The annual report of the 1994 Forage Fish Diet Overlap project (Willette et al., 1995) limited results principally to the August-September directed sampling collections, which included zooplankton and epibenthic prey samples and thus allowed an investigation of prey selection (Willette et al., 1995). Prey field samples that directly correspond to the catches from May-July, 1994, are not available. Nonetheless, a seasonal and interannual assessment of food habits, diet overlap and prey partitioning among forage fish is important. Trophic interactions between species cannot be understood without an understanding of which species are common and abundant and how often their distributions overlap in space and time. For example, the carrying capacity of PWS to support numerous planktivore species may reach its limits when densities of fish are greatest, such as when strong year classes of herring or capelin appear or during the peak outmigration of juvenile salmon in spring, or in years when zooplankton production is lower than average. Even though biologists studying apex predators are most interested in the abundance and distribution of the forage available during the birds' summer breeding season, the interactions that take place among forage species at other times of the year will influence their summer populations. We have therefore summarized the seasonal diets and diet overlap of these forage species without information on prey selection/preferences or the potential effects of co-occurrence with another species.

Methods - Chapter 1

Data analyzed in this chapter is based on laboratory stomach analysis of forage fish specimens from six, monthly collections in 1994, summer and autumn collections in 1995, and a summer collection in 1996. Field methods are described above in the overall methods for the final report. Fish were identified in the field and preserved in 10% formalin solution; identifications were checked according to a variety of standard keys when fish were measured and weighed in the lab. After stomach analysis in the laboratory, diet composition was computed as percent biomass, percent numbers and percent frequency of occurrence of major prey categories for each forage species in each month. Diet overlap between species pairs was computed for each month in 1994 as the Percent Similarity Index (PSI) of Schoener (1970; Krebs, 1989):

$$PSI_{jk} = \sum \min(p_{ij}, p_{ik} = 1 - 0.5*(\sum |p_{ij} - p_{ik})$$

where p is the pooled biomass proportion of the i^{th} prey taxon in n taxonomic categories consumed by fish species j and k.

Results - Chapter 1

Fish Size

Stomach analysis was performed on a total of 5110 forage fish specimens representing 14 species in nine sampling periods spanning the three years from 1994-1996 (Table 1). June represented the most intense effort, with up to 496 per species (herring) and a total of 1673 specimens examined. Mean size per species ranged from a low of 31 mm FL for Pacific cod in May, 1994 to a high of 163 mm FL for Pacific tomcod in July, 1995, thus spanning individuals from age-0 to at least age-2. None were noted as gravid or otherwise sexually mature. Seasonal size trends varied among the forage species. Between spring and autumn, 1994, mean sizes of five of the eight forage species consistently caught increased by more than a factor of two (Table 1). They included the gadids and salmonids. Other species either showed inconsistencies in growth across months or were not examined in multiple months.

All three gadids were similar in size and had similar trends of size increase across months of 1994: Pacific cod mean size increased from 31 to 92 mm FL (May-September); Pacific tomcod increased from 47 to 100 mm FL (June-September); and walleye pollock mean size increased from 42 to 107 mm FL (June-November). These fish were principally age-0 (Smith, 1981; Walters, 1984; Lee, 1985). In July and October, 1995, we also examined small sets of age-1 or age-2, trawl-caught gadids, including tomcod 163 mm mean FL and pollock up to approximately 200 mm FL. Adult Pacific tomcod are the smallest of these gadids, reaching approximately 30 cm length compared to approximately 90-100 cm length for Pacific cod and walleye pollock (Hart, 1983).

Juveniles of two salmonid species also had similar sizes and trends of increase. Mean size of both pink and chum salmon increased from less than 50 mm FL in May to more than 130 mm FL by September, 1994. The salmonids thus tended to be larger in size in a given month than the gadids. The large mean size of chum salmon compared to pink salmon juveniles in July is based on only six specimens (Table 1). The juvenile sockeye salmon examined from June were approximately twice the length of the pink and chum salmon juveniles (104 mm FL) in that month. The pink and chum salmon were YOY fish, while the sockeye salmon could have been age-0 or age-1, since sockeye juveniles can spend a winter in fresh water or go to salt water in their first year of life (Groot and Margolis, 1991). As adults, pink salmon reach a size of approximately 50-60 cm, while chum salmon are larger, up to approximately 80 cm, and sockeye salmon are generally in between these size ranges (Groot and Margolis, 1991).

The mean sizes of three forage species, Pacific herring, capelin and Pacific sandlance, did not increase steadily over the spring-autumn time period in 1994. Pacific herring mean size remained between 123-133 mm FL in the six months between May-November; capelin decreased from 116 mm FL in May to 89 mm mean FL in July; and Pacific sandlance mean size increased from 94 mm FL in May to 127 mm mean FL in June and July, then decreased to 88 mm FL in September. The herring and sandlance were probably age-0 to age-2 (Stokesbury et al, 1998; Dick and Warner, 1982). As adults, herring can reach 38 cm in length and sandlance can reach 26 cm in length. Most capelin were YOY to age-2 pre-spawning adults (Pahlke, 1985; Hatch and Sanger, 1992). Capelin size to 22 cm has been reported from the northern Pacific Ocean (Hart, 1983).

No seasonal size trends were available for five forage species studied: three schooling species (northern smoothtongue, eulachon smelt, threespine stickleback), a nearshore demersal species (Pacific sandfish), and a pelagic species associated with large jellyfish (prowfish). They were all "forage sized," between 80-130 mm mean FL, but tend to be less common in seabird diets. Northern smoothtongue from May, 1994 had mean FL of 80 mm. Smoothtongue mature at 140-170 mm (Hart, 1983), indicating that our samples were juveniles. Eulachon smelt were caught in autumn of 1994 and 1995 at a mean FL of approximately 80 mm. At this size, eulachon in British Columbia were likely age-1 or age-2 (Barraclough, 1964); adults attain lengths of approximately 200 mm (Hart, 1983). Sticklebacks as adults are among the smallest of the species examined, ranging from 25-87 mm (Hart, 1983). Our specimens from May could thus have been adults. Sandfish from July, 1996 were probably age-1 at their 84 mm size (Paul et. al, 1997). Adult sandfish reach approximately 300 mm (Hart, 1983). Prowfish from both July and October, 1996 were 74-92 mm in length. Prowfish to a length of 880 mm have been recorded, but little is known of their life history (Hart, 1983).

Diet Composition

Seasonal prey composition is presented as percent biomass (Table 2; Figure 1), percent number (Table 3), and percent frequency of occurrence (Table 4) of major prey categories. Monthly diet overlap between forage species by prey biomass appears in Table 5. All diet composition values represent monthly pooled samples for each forage species without regard for possible intra-specific differences in diet between size classes, spatial differences in feeding habitat or prey fields available, prey species selected from within categories, forage fish school composition, or diel feeding period. The prey percent biomass measure of diet composition best represents the energy consumed by the fish, but diet composition as percent numbers or frequency of occurrence of prey often present a different picture of common prey items.

Diet composition varied among the forage species and over time. Most were principally planktivorous during the periods sampled. Calanoid copepods were the most consistent zooplankters in the diet. Both large and small calanoid taxa were consumed (total length, TL > 2.5 mm vs. TL < 2.5 mm; weight approximately 30:1). Although large taxa often dominated the calanoid prey biomass, May was the only month in which large calanoids were consumed in greater numerical proportions (Table 3) and more frequently (Table 4) than small calanoids, reflecting the seasonal peak in abundance of *Neocalanus plumchrus/flemingeri -Calanus marshallae/pacificus* (hereafter referred to as *Neocalanus/Calanus* spp.; Cooney, 1993). Members of each category of calanoids were difficult to identify when distorted by digestion, and the majority were generalized. However, several genera and species were commonly identified. Among the large calanoid category, these included *C. pacificus, C. marshallae, N. plumchrus/flemingeri, Metridia pacifica* and *M. ochotensis;* less commonly observed species were *Epilabidocera longipedata, Eucalanus bungii, and Euchaeta elongata.* Small calanoids were principally *Pseudocalanus* spp., with contributions from *Acartia clausi, A. longiremis*, and *Centropages abdominalis*, as well as the cyclopoid copepod, *Oithona similis*.

Among the gadids, large calanoids declined in prominence from May to September, 1994. Pacific cod, the only gadid examined from May, consumed almost entirely large calanoids in that month, mostly *Neocalanus* spp., but large calanoids were absent from their diet by September. In June and July, *Neocalanus cristatus* and *N. plumchrus/flemingeri, C. marshallae, Epilabidocera* and *Metridia* spp. all contributed to cod diet. Other prominent prey of Pacific cod included gammarid amphipods and gastropods (the pteropod, *Limacina helicina*, and unidentified benthic snails) in June and July, and both malacostracans and other epibenthic/epiphytic prey in September. The September epibenthic/epiphytic prey included gammarid and caprellid amphipods, isopods, bivalves, harpacticoid copepods, cumaceans, and polychaetes. For pollock, small calanoids as well as large calanoids contributed substantial prey biomass to the diet, but the biomass proportions of both declined seasonally. Pollock consumed different species of large calanoids each month: in June, *C. pacificus* and *Neocalanus* spp.; in July, *C. pacificus*, *Neocalanus* spp. and *Epilababidocera*; in August, *M. pacifica* and *Euchaeta*; in September, *C. pacificus;* and in October (1995) and November, *M. pacifica.* By late summer, macrozooplankters or fish appeared in pollock diet in larger biomass proportions: hyperiid amphipods in August, fish in September, and euphausiids in November. Pacific tomcod were the least planktivorous of the gadids, with fish prey dominating their diets in three out of four months of 1994. Most prey fish by far were unidentified larvae 10-20 mm in length, but salmonids, gadids, sandlance and capelin were also observed in stomachs of tomcod and other piscivores. Unlike the other two gadids, Pacific tomcod predation on calanoids was minimal. Like Pacific cod, Pacific tomcod diets commonly included epibenthic/epiphytic organisms, notably gammarids and gastropods, but like pollock, they also ate more pelagic hyperiids. The hyperiids consumed by pollock were *Parathemisto* and other adult species, while those consumed by tomcod were unidentified small juveniles in July and larger specimens later.

The salmonids were consistently piscivorous compared to other forage species excepting Pacific tomcod (Figure 1). Fish were eaten by salmonids in every sampling period. Across the months of 1994, pink salmon diets were approximately one-third fish biomass, one-third calanoid biomass, and one-third other zooplankter biomass (decapods, euphausiids, gastropods, hyperiids). In July, 1996, fish made up approximately 80% of pooled prey biomass of pink salmon. Similarly, chum salmon diets were dominated by fish prey from May-July, and in September, 1994, about 40% of their diverse diet was fish biomass. For sockeye salmon, fish made up over 85% of June prey biomass. Although fish biomass often dominated salmon diets, the frequency of occurrence and percent numbers of fish consumed were usually low (Tables 3 and 4). Fish occurred most frequently in chum salmon diets in May (34%), and least frequently in September (3%); fish occurred in < 12% of pink salmon in all months except September, when 61% of the stomachs contained fish; fish were consumed by approximately 43% of June sockeye specimens (Table 4). Among other prey of salmonids, chum salmon diets never included small calanoid biomass, and large calanoids were minor prey biomass components in diets during all months except August, when they made up approximately 50%. For both pink and chum salmon, large calanoids mainly included *Neocalanus/Calanus* spp. in May; *Epilabidocera* and *Neocalanus* spp. in June; *Epilabidocera*, *Calanus* spp. and *Metridia* spp. in July; *M. pacifica* in August; and in September, *Epilabidocera* for pink salmon and *Euchaeta* for chum salmon.

Pacific herring, capelin and sandlance were planktivorous, the most prominent taxa in their diets usually being calanoid copepods. Fish were rarely important components of these three species' diets and did not contribute to their diets in the same months. For herring, large calanoids remained prominent in the diets from May throughout the summer, with no obvious decline in utilization until autumn. The succession of identified large calanoids by month for herring was, in May and June, *Neocalanus* spp./*C. marshallae;* in July, *Neocalanus/Calanus* spp. and *Epilabidocera*; in August and September, the last three genera and *M. pacifica*; in October, 1995, *M. pacifica*, and in July, 1996 *Metridia* spp. and *Epilabidocera*. Sandlance diet was clearly dominated by calanoid biomass except in June. Large calanoids were most prominent in May, with *Neocalanus* spp., *N. cristatus*, *Metridia* spp., and *C. marshallae* all appearing in sandlance diet. For capelin, large calanoids formed the largest proportion of prey biomass later than for sandlance, in June. Large calanoids in capelin diet included *Neocalanus/Calanus* spp. in May and June, but *Metridia* was prominent in July. Other prey in herring, sandlance and capelin diets varied seasonally. Fish contributed to herring prey biomass only in July (~20%), to capelin prey biomass in May (~60%) and June (~25%), and to sandlance prey biomass in June (~80%). Unidentified malacostraca were prominent in spring diets of herring, while hyperiids, euphausiids and larvaceans became more prominent in late summer-autumn. Capelin tended to consume more of the larger prey taxa earlier in the year than herring. Hyperiids, fish, and euphausiids were large components of prey biomass for capelin in May, June, and July, 1994 compared to later for herring. Euphausiid were also dominant in October, 1995. For sandlance, other taxa besides calanoids occasionally contributed to prey biomass: fish in June, larvaceans and invertebrate eggs in July, and malacostracans in September. Capelin had higher rates of empty stomachs than herring and sandlance. In autumn, herring, capelin and eulachon had the greatest proportions of emtpy stomachs observed for all species and all time periods (Table 1).

Seasonal diet trends could not be evaluated for five forage fish species that were examined from only one or two months. The diets of these species are of interest because they are sometimes abundant in the same areas as more commonly-eaten forage species and may therefore compete with them. The diet of northern smoothtongue in May, 1994 was composed of 45% large calanoids (Figure 1, Table 2), predominantly *Metridia ochotensis*. Other prominent taxa included fish, euphausiids, hyperiids and malacostracans. However, 51% of smoothtongue stomachs were empty (Table 1). Sticklebacks consumed nearly half their prey biomass from large calanoids and 40% from fish in May. In autumn of 1994 and 1995, eulachon stomachs contained euphausiids and unidentified malacostracans, but 55-80% of stomachs were empty. Sandfish collected in July, 1996 were piscivorous, with fish occurring in 100% of stomachs (Table 4) and as 97% of prey biomass (Figure 1; Table 2). Small calanoids, decapods and gammarid amphipods occurred frequently and in large numerical proportions, but contributed minor proportions to prey biomass of sandfish. Prowfish prey biomass in July and October, 1995 was more than 80% hyperiid amphipods, principally *Hyperia*. Prowfish also consumed small biomass proportions of larvaceans, small calanoids and pelagic gastropods (the pteropod, *Limacina helicina*). Gut contents of prowfish also had unquantifiable, gelatinous material that appeared to be from "tentacle-nibbling" the jellyfish.

Diet Overlap

Diet overlap between species was most common in June, 1994, when nine species were examined. Diets of one-third of all species pairs (12/36) overlapped significantly (> 60% PSI), with many values in excess of 75%. The degree of similarity varied mostly with the proportion of large calanoids and fish in the diets, and sometimes the proportion of small calanoids. Sandlance and capelin diets each overlapped with three different species, but not with each other. Capelin diet overlapped with Pacific cod, walleye pollock and Pacific herring diets (60-84%). Sandlance diet overlapped with Pacific tomcod, and sockeye and chum salmon diets (76-87%). Pacific cod and Pacific tomcod also overlapped with three different species each. Pacific cod overlapped with herring, pollock and capelin 60-66%, while tomcod overlapped with sockeye, chum and sandlance 80-87%. Pollock and chum salmon diets each overlapped with three species, but not with each other. Pollock diet overlapped with Pacific cod and herring by 65-66% and with capelin diet by 84%. Chum salmon diet overlapped with Pacific tomcod, sockeye salmon, and sandlance diets by 84-85%.

Few other patterns in diet overlap were observed. In May, threespine stickleback diet overlapped with three species (pink salmon, northern smoothtongue, and capelin) by 62-73%. Significant diet overlap was scattered among other species pairs in May: pink salmon overlapped with smoothtongue (69%), sandlance with Pacific cod (84%), and chum salmon with capelin (75%). In July, sandlance diet overlapped with pollock's (81%), Pacific tomcod overlapped with Pacific cod, pink salmon and herring (61-68%), and pink salmon overlapped with Pacific cod and Pacific tomcod (60-65%). Diet overlap between species pairs was rarely consistent across months. The most consistent species pairs for which we have data are pollock and herring, whose diets overlapped significantly in June and November, 1994 and in July and October, 1995. Pacific tomcod and pink salmon diets overlapped in July and August, 1994. Sandlance and herring diets overlapped significantly in September 1994 and July, 1995, but not in July, 1996. Capelin diet overlapped with both sandlance and herring in July, 1995.

Interannual Diet Patterns

Some species showed interannual consistencies in diet while others showed interannual differences. Interannual patterns of consistent diet composition were noted for pollock and sandlance in July, 1994-1996, when small calanoids predominated in their diets and large calanoids made up smaller biomass proportions. Larvaceans (a small prey) were numerically prominent and contributed notable biomass to sandlance diet in July of all three years. Pollock diets were also very similar in November, 1994 and October, 1995. In contrast, interannual differences between July diets were observed for Pacific tomcod, Pacific herring, capelin, and pink and chum salmon. For tomcod, the prey taxa present in July diets were highly diverse, and July, 1996 was the only period in which fish were not present in the diet. For herring, calanoids were the predominant taxon in July of each year, but diets differed in the proportions of large and small calanoids consumed, and in the appearance of decapods, fish or gastropods in the diet. Similarly, in October-November of the two years, large calanoids and euphausiids were each consumed but the proportions differed. Capelin diets differed radically between the years. Large prey were consumed in July, 1994 (large calanoids and euphausiids) and small prey were consumed in July, 1995 (small calanoids). Pink salmon were much more piscivorous in July, 1996 than in 1994 or 1995; in the first two years, diets were very similar based on large calanoids, fish and gastropods. On-the-other-hand, chum salmon were least piscivorous in 1996. Their diets included more prey biomass from hyperiids and either chaetognaths or decapods in July of 1995 and 1996 compared to mostly fish in July, 1994.

Discussion - Chapter 1

Collectively, the 1994-1996 Forage Fish Diet Overlap investigations confirm that the 14 forage species examined are largely planktivorous from May-November in their first two-three years of life. Common prey items included large and small calanoids, pteropod gastropods, hyperiid amphipods, euphausiid larvae in summer and older stages in autumn, and larvaceans. Prey composition changed seasonally for the eight species examined monthly from April-September. The biomass composition of large calanoids in the diet generally declined after spring, prey became more diverse, and macrozooplankters became common in diets.

Seasonal size trends are important to note because fish body size is often correlated with diet composition. Just as trends of increasing mean size across several months reflect growth, lack of growth can indicate the influx (recruitment) of YOY fish or an inshore spawning migration of adults. In some months, catches of the three species with little apparent growth over the months (herring, capelin and sandlance) include bi-modal size distributions representing multiple age classes (data on file). This is suggested by the wide size range and by standard deviations up to approximately 20% of the mean. Monthly changes in mean size of the species examined are influenced by factors such as differences in the onset and duration of spawning time and the appearance of the larvae, ontogenetic changes in spatial distribution, and size selectivity of the gear. Some of these life history traits, such as spawning, are controlled by temperature. Northern smoothtongue spawning, for example, begins in mid-autumn and ends in spring (Sobolevsky and Sokolovskaya, 1996), while herring spawn in mid-spring (Brown et al, 1996) and capelin in late spring and summer (Pahlke, 1985). A wide size range of larvae and juveniles of species with protracted spawning periods could occur in an area at the same time. The co-occurrence of species or certain size groups of species with another may also be influenced by growth rates. Walters (1984) found that of YOY pollock, cod and tomcod in Port Townsend, Washington, the cod grew the fastest and were the first to begin leaving the nearshore nursery areas shared in summer; pollock left later, followed by tomcod late in the year (Walters, 1984). Size-diet trends among these forage species will be investigated in future.

Forage fish diet composition in PWS was similar to that reported from studies done elsewhere. Juvenile pollock in the Gulf of Alaska are commonly reported to feed on small calanoids in summer and euphausiids in autumn, with size related shifts in prey (e.g., Kamba, 1977; Krieger, 1985; Merati and Brodeur, 1996). Although studies on pollock have increased in recent years, little has been published on the morphologically similar, but not commercially important, juvenile Pacific cod and tomcod. A study on the Olympic Peninsula, Washington examined all threegadid species from May -September (Walters, 1984). Juvenile Pacific cod fed mainly on small calanoids, harpacticoids, mysids and gammarid amphipods. Calanoids became less important as mysids and gammarids became more important in larger juveniles' diets, and shrimp and polychaetes appeared in the largest individuals. Growing Pacific cod thus exhibited an increasingly benthic feeding mode as well as prey size increase. In the same study, pollock and tomcod fed on the same prey categories as cod, but pollock, and tomcod to a lesser degree, continued to prey on calanoid copepods longer than cod. Unlike in our study, euphausiids were not important in these species diets (Walters, 1984). In Kamchatkan waters, cod up to 200 mm principally consumed amphipods, mysids, and euphausiids (77-91% biomass) and some fish (Tokranov and Vinnikov, 1991). The diet was more similar to cod in our study. In the eastern Bering Sea, cod and pollock up to 75 mm TL were studied in summer (Lee, 1985). Prey composition was related to differences in prey availability as well as to morphological differences in the fish (gill rakers) that influenced prey size selection. Pollock were adapted to feeding efficiently on small organisms; they had greater numbers of gill rakers closely-spaced compared to fewer rakers widely-spaced in Pacific cod (Lee, 1985). Diet overlap was high for individuals < 40 mm TL. At approximately that size, cod diet changed abruptly to larger food items, including fish prey; at the same time, the spacing between gill rakers in cod increased with growth, again indicating an adaptation to predation on macrozooplankton and piscivory (Lee, 1985; Tokranov and Vinnikov, 1991). We found tomcod to be generalists, feeding on benthic and pelagic prey--even the large copepods they ate ranged from surface swarming *Epilabidocera* to the strong vertical migrators, *Metridia* spp. Pollock, on the other hand, had a narrower prey suite that was restricted to smaller items for a longer period. The details of such prey size preferences need further study.

Copepods are commonly reported to be the main food of other young fish. For Pacific sandlance, small calanoids and other small taxa are prevalent; epibenthic taxa can be important in both fall and winter and euphausiids can be important in winter (Field, 1988; LeBrasseur et al, 1969; Craig, 1987). Few studies have compared Pacific sandlance feeding to other forage species (Simenstad et al., 1979; McGurk et al, 1992). In a study of neritic fish assemblages in Puget Sound, juvenile Pacific herring, Pacific Sandlance, and pink salmon were grouped into one functional feeding group, pelagic planktivores (Simenstad et al., 1979). Sandlance and herring were defined as obligate, while pink salmon were considered facultative planktivores. The diets of all were dominated by calanoid copepods, although overlap was not reported (Simenstad et. al, 1979). Further north, in a southeast Alaska bay, juvenile herring and capelin diets overlapped in spring when both fed in the water column (Coyle and Paul, 1992), then diverged when the water column stratified; herring then fed at the surface, while capelin continued to feed in the water column. In April, large calanoids were the most important prey of capelin, and were less important in herring diet. In May and June, small calanoids were important in both species diets, and herring switched from barnacle nauplii to barnacle cyprids. Juvenile sockeye salmon in the same study foraged near the surface in June, mainly on oikopleurans and barnacle cyprids, and their diets overlapped substantially with juvenile herring diet at that time (Coyle and Paul, 1992). In another study of herring and capelin in early summer in the Barents Sea, prey biomass was comprised mainly of calanoids, oikopleurans and larval euphausiids, with diet overlap highest among specimens 80-135 mm in length. Diet shifted ontogenetically and similarly, with consumption of calanoids declining and consumption of euphausiids increasing with size (Huse and Toresen, 1996). These studies and ours show that, like the gadids, the trophic relationships of these co-occurring species change over time and with size. Huse and Toresen (1996) concluded that herring and capelin could compete for food when planktivores were abundant or prey resources were limited.

Pink and chum salmon are typically planktivorous during their early marine period. These two species often very similar diets (e.g., Murphy et al, 1988; Landingham et al, 1998). However, juvenile chum salmon commonly feed more on epibenthos than do pink salmon (e.g., Murphy et al, 1988), and are size selective predators (Groot and Margolis, 1991). Both species were planktivorous in PWS, but pink salmon preyed more on small calanoids and chum salmon preyed more on large calanoids (Sturdevant et al, 1996). Their diets also varied with habitat, both species consuming more epibenthic prey in low-gradient habitats than in medium- and steep-gradient habitats. Both pink and chum salmon fry feed heavily on epibenthic prey in some regions (Groot and Margolis, 1991). Sockeye salmon juveniles typically eat macrozooplankton and fish, and calanoids are not important prey (Groot and Margolis, 1991). However, Landingham et al (1998) found interannual changes in the July-August diet for all three species, from crustaceans to fish, and their diets overlapped significantly. In our study, chum salmon were more piscivorous at a smaller size than pink salmon (Figure 1).

In a separate analysis of the August-September, 1994 data, Willette et al. (1995; 1997), used principal components analysis (PCA) and cluster analysis to identify similar diet composition between juvenile pink and chum salmon, between juvenile Pacific herring and walleye pollock, and between capelin and sandlance. Higher diet overlap was identified between the first two species pairs than between other species pairs, and between sympatric species pairs than for allopatric species pairs. Small calanoid copepods in general (and *Pseudocalanus* spp. specifically) and larval fish prey were partitioned (PCA). Juvenile herring and pollock consumed more calanoid biomass than juvenile salmon, while juvenile salmon consumed more larval fish biomass. Juvenile chum salmon also preferred gelatinous prey, such as ctenophores, cnidaria, and larvaceans. Diet composition and overlap changed significantly over a diel period (Willette et al., 1995; 1997).

Smoothtongue diet in our study was similar to their diets in other parts of the north Pacific. In the Strait of Georgia in April, northern smoothtongue stomachs contained euphausiids, copepods, barnacle larvae and fish eggs (Hart, 1980). In the Bering Sea in June, large calanoids (*Metridia pacifica*) comprised more than 50% and oikopleurans comprised 12% of prey biomass in northern smoothtongue diet (Gorbatenko and Il'inskii, 1991). Diets differed between summer and autumn (Balanov et. al, 1995b). The dominant food organisms by weight included euphausiids and two large calanoid species, *(Neo)Calanus cristatus* and *Eucalanus bungii*, in summer and 90% euphausiids in autumn. In another Bering Sea study in autumn, euphausiids, jellyfish and *Oikopleura labradoriensis* were the predominant prey (Balanov et al, 1995a), while in eastern Kamchatka in early winter, cnidarians and ctenophores contributed more than 65% biomass of diet in northern smoothtongue. Smoothtongue is a mesopelagic species that performs a strong vertical migration. Smoothtongue predation on the large calanoid, *Metridia ochotensis*, in our study can be explained by the overlap in vertical distribution of these two migrators. Although significant diet overlap was observed between smoothtongue and pink salmon, the large calanoids on which it was based were mostly different species, since pink salmon mainly ate *Neocalanus*. These diet differences indicate that they fed at different depths in the water column. Sobolevskii and Senchenko (1996) found no more than 45% overlap between the diets of northern smoothtongue and either pink or chum salmon or walleye pollock. However, the autumn diet change reported by Balanov et al (1995), along with our results, suggest that smoothtongue diet could overlap with pollock, herring and capelin then. More information on this species is needed to clarify trophic relationships.

Threespine sticklebacks are a very generally distributed fish found in both fresh and saltwater. Their diet of large calanoids and fish overlaps with nearly all the other forage species based on one of the two categories. Other studies showed that stickleback diet consists mainly of copepods in spring and autumn, but a wide variety of small, marine and brackish water crustaceans and young fish are also prey (Hart, 1983). They have been shown to compete with sockeye salmon in freshwater (Groot and Margolis, 1991). Diet overlap with small individuals in early spring seems likely, but we have no data to support this.

Eulachon are potential competitors of capelin, herring, smoothtongue, and pollock for euphausiid prey in autumn. In other studies, juvenile and adult eulachon also ate euphausiids and copepods (Hart, 1983). Juvenile eulachon from the echo scattering layers in the coastal waters of British Columbia had guts full of the euphausiids abundant in these layers (Barraclough, 1964). However, the high frequency of empty stomach that we observed suggests that feeding is reduced in autumn for both capelin and eulachon (Winters, 1970). Eulachon is another species for which additional studies are required to improve our understanding of trophic interactions.

Sandfish are a little-known, burrowing, intertidal species often caught in small numbers in beach seines. Their diet was very similr to pink salmon in July, 1996 (Figure 1). Although young sandfish do school with pink salmon (Bailey et al, 1983), we could not determine whether the individuals we caught were in the water column or were buried in the sandy gravel. They were smaller than mean size of salmonids, slightly larger than mean size of herring and tomcod, and similar to mean size of sandlance. However, at a mean length of 85 mm, they were larger than the fish they directly co-occurred with on western Bligh Island, sandlance (72 mm) and herring (48 mm). In another study, young sandfish (33-42 mm SL) were sympatric with pink salmon (40-59 mm SL) from Southeast Alaska in June. These sandfish were completely planktivorous, and diet overlap with the pink salmon was nearly 70% by number (Bailey et al, 1983). Shared prey included euphausiid larvae, calanoid and harpacticoid copepods, and larvaceans; fish did not appear in either species' diet (Bailey et al, 1983). By contrast, Paul et al (1997) found that sandfish < 100 mm (62-99 mm FL) consumed shrimp, euphausiids and decapod larvae most often, with sandlance occurring in approximately 9% of the stomachs; sandfish > 100 mm (115-303 mm FL) were primarily piscivorous on sandlance and other fish. An examination of numerical or frequency composition of prey for these species in our study gave similar results. In July, 1996, sandfish diet was 75% small calanoids by number (Table 3) but gammarids occurred most frequently after fish prey (46%; Table 4); pink salmon diet was 88% larvaceans by number, with the frequency of gastropods, small calanoids and larvaceans between 41-83%, respectively. The highly similar diets of sandfish and pink salmon that we have shown were therefore not based on the most prevalent prey taxa. All three of these studies point to the high potential for competition between juvenile pink and chum salmon and sandfish, because of their similar habitat and diets during the salmonid's early marine period, particularly at times or in areas where fish prey are not available. What is not obvious is the numerical diet overlap between the sandfish, sandlance and herring that actually co-occurred. All three of these species consumed more than 75% small calanoids by number (Table 3), and although the sandlance and herring diets were also dominated by small calanoid biomass (≥ 61%), sandfish diet biomass was primarily fish present as ≤ 1% numbers.

The presence of gelatinous material and *Hyperia medusarum* in prowfish stomachs suggest that prowfish take advantage of the parasitoid relationship between jellyfish and some hyperiids (Brusca, 1981) while obtaining shelter from the jellyfish. Most other forage species that sometimes consume hyperiids are not associated with jellyfish and are therefore unlikely to compete with prowfish. Pollock associate loosely with jellyfish for shelter (e.g.., Brodeur, 1998), but salmonids are not associated with jellyfish. Prowfish diet did not overlap significantly with other July species, although pink and chum salmon and pollock also ate hyperiids. In fact, the hyperiid fauna were partitioned, since pink and chum salmon principally consumed *Themisto pacifica* and *T. libellula*. Hyperiids were < 10% of prey biomass pollock diets. Of interest, these other forage species also eat gelatinous prey at times. Chum salmon prey on the salps with which *T. pacifica* is associated (Brusca, 1981). Juvenile chum consumed up to 6% of prey biomass from such gelatinous taxa in late summer, 1994 (Table 1; see also Willette et al, 1995; ibid, 1997). We observed up to 4% prey biomass from cnidarian/ctenophore tissue in pollock guts (November, 1994).

Planktivorous forage species shifted diets seasonally from predominantly calanoid biomass to predominantly macrozooplankton biomass. The shift was more gradual for species such as herring and pollock than for some others. However, large and small calanoids were consumed throughout the spring, summer and autumn, and a variety of different macrozooplankters were consumed summer through autumn. Forage species preyed on a succession of large calanoids as they became available, yet some partitioning among the species occurred. Facultative predation on *Neocalanus* spp. was observed when this genus was abundant in May and June (e.g., Cooney, 1993). Chum salmon and capelin were the only fish species that did not consume substantial large calanoid biomass; both were largely piscivorous in May. When large calanoids were the common prey category between species with high diet overlap, the actual degree of diet overlap could be much lower than we estimated from pooled taxa. For example, in May, more than 30% of smoothtongue diet biomass was a large calanoid species not consumed by other fish (*Metridia ochotensis*), thus reducing the amount of actual overlap with pink salmon or stickleback. Also unlike the other species, sandlance consumed a diverse array of large calanoid species in addition to *Neocalanus* in that month. The calorie-dense large calanoids were less prominent in forage fish diets in summer when the peak bloom of *Neocalanus* spp. had passed but fish were larger. Other large calanoid species were more common than *Neocalanus* spp. in summer and autumn, especially *M. pacifica* and *Calanus* spp., but generally did not contribute as much prey biomass as did *Neocalanus* spp. in the spring. In June, sandlance and the salmonids consumed only small proportions of large calanoids. In July, different fish species tended to share different large calanoid resources, ie., prey species overlap was limited to a few fish species. In July, 1994, for example, herring mainly consumed *Neocalanus/Calanus*, while capelin mainly consumed *Metridia*, but pink and chum salmon preyed on *Epilabidocera, Calanus* spp. and *Metridia* spp. These differences could represent stratification of feeding by depth in the water column (Coyle et al, 1992) as well as oceanographic influences on copepod distribution and availability to predators. As mentioned above, however, fish size and ontogenetic diet shifts are also important to consider. The interannual consistency of sandlance and pollock diets in July compared to the interannual variation of herring and capelin diet suggests that for some species, prey composition was influenced by size differences as well as species interactions. Herring mean size was smaller in successive months of July, 1994-96 (130 mm-75 mm FL), yet much of their prey biomass was consistently calanoids. Capelin were age-1 in July, 1994 compared to age-0 in July, 1995, and the interannual differences in diet composition reflect ontogenetic shifts in prey size selection (Figure 1). However, sandlance mean size indicates fish were age-2 in 1994 compared to age-1 in 1995 and 1996, yet diet was quite constant in the three July months. Thus, species must be considered individually in the context of their life histories.

Most forage species were planktivorous at the times and in the size ranges we sampled. The least planktivorous species were the tomcod, salmonids and sandfish. However, both opportunistic piscivory and size-related shifts to piscivory were observed among the planktivores. Opportunistic piscivory was exhibited by some species that did not consume fish in the summer but did prey on fish larvae in spring, such as sandlance in June and capelin in May. Even though it was earlier in the year, the mean size of these fish was larger at the time they ate substantial biomass proportions of fish compared to when they did not, again suggesting a bi-modal size in the specimens examined. Size -related shifts to piscivory were clearly observed for species such as pollock and herring when they were beyond the general size maximum of seabird prey, approximately 150 mm FL (Sturdevant, 1995; Sturdevant and Willette, 1995; Chapter 1, this report). A trend for partitioning by prey size and type is also suggested in Figure 1 for herring, capelin and sandlance. Overall, sandlance consumed smaller prey more often than the other two species, and capelin tended to consume larger prey earlier in the year than herring. Unlike the gadids, mean size of these species did not obviously increase over time and diet trends for these species also suggest that multi-modal size classes were examined. Spring herring, capelin and sandlance diets included relatively large biomass and frequency of fish that are not observed in later months (Figure 1, Tables 2-4).

Prey fish in the size range that subadult forage fish can consume include the larvae and fry of numerous taxa. Fish larvae are most abundant in the ichthyoplankton in spring (May/June) in the upper 50 m (Haldorsen et al, 1993; Norcross and Frandsen, 1996), but in PWS, oceanographic features also influence the distribution, density and species composition of ichthyoplankton from April to October (Norcross and Frandsen, 1996). Spatial differences in the density/availability of fish larvae may explain the patchiness of piscivory among large fish specimens at some stations compared to others (e.g.., pink salmon in July, 1996). Fish grow faster when piscivorous than when zooplanktivorous (Juanes and Conover, 1994; Mittelbach and Persson, 1998), but despite the ontogenetic increase in mean prey size of piscivores, many species continue to select small prey (Juanes, 1994). We observed this in the salmonids and tomcod, for example. The onset of piscivory in fish is generally believed to occur earlier and at smaller sizes in species that are born larger and have bigger gapes, and different piscivores of similar size consume similar sized prey (Mittlebach and Persson, 1998).

Few investigations of carrying capacity have included the consumptions of as many fish species as we have studied. Since population estimates of most forage and other fish species for PWS are not available, it is difficult to estimate the impact of their feeding on one another in the sound. The food requirements of numerous species have not been well-documented, not only in terms of prey composition but in terms of daily ration. The carrying capacity of PWS for juvenile Pacific salmon has been estimated, however. Cooney (1993) estimated that juvenile salmon (mostly pinks) with growth rates averaging 3-4% of body weight daily use up to 3.2% of the total 'herbivore' production and up to 10.0% of the annual macrozooplankton production in the region, when mortality is accounted for. Since the planktivorous and piscivorous feeding of juvenile salmon overlaps with a number of other forage species, some of this mortality will be impacted by trophic interactions among the fish, both through food competition and predation. Although most of the other forage populations are likely not as large as the salmonids', more than half of which comes from hatchery production (Cooney, 1993), if each of the 10 or so other species included in this study consumes just half the maximum estimate for juvenile salmon, then approximately 1/4 of the total herbivore production and 3/4 of the macrozooplankton production would be consumed. As noted above, some of these species, including the salmonids, also utilize some ichthyoplankton prey resources during their period of residency. In addition, some forage species live longer than pink salmon, but mature at smaller size, and, unlike the salmon, remain in PWS to complete their life history. In other areas of the northwestern Pacific, researchers have provided evidence that juvenile salmon crop the epibenthic and neritic prey resources they utilize; declining foraging success and the availability of preferred prey organisms related directly to migration rates of juvenile salmon out of estuarine and nearshore areas (Simenstad and Salo, 1982) and distribution and residency were food-limited at certain times (Healey, 1982). An impact of salmonid feeding was also documented in the Gulf of Alaska, where they continued to depress macrozooplankton stocks (Shiomoto et al, 1997), but limits to the ocean's carrying capacity continue to be debated (Heard, 1998). In all of these areas where salmon impact their feeding environments, forage species and other residents will also experience the decline in prey resources, but how the inevitable trophic interactions affect forage fish availability to seabirds has not been studied. We need long term studies of fish feeding and both mesozooplankton and macrozooplankton trends.

Jellyfish competition with forage fish is a new aspect of the PWS ecosystem being investigated (Purcell et al, 1999). The summer diets of four large species of pelagic cnidarians (*Aurelia, Cyanea and Aequorea*) and a ctenophore (*Pleurobrachia*) were compared to those of juvenile walleye pollock, sandlance, herring and pink salmon. Collectively, both predator groups principally ate small calanoid copepods and larvaceans. Other jellies that occur in the nearshore feeding zones occupied by small forage species, such as the small medusa, *Irene* spp., probably also consume small zooplankters. The similarity between diets of these jellyfish and forage fish suggest the two groups may compete for food resources in areas or times of low plankton abundance. Other recent studies suggest that forage fish populations may also compete with marine organisms besides jellyfish for zooplankton, including chaetognaths (Baier and Purcell, 1997), euphausiids (Atkinson and Cripps, 1999), aquatic insects (Herwig and Schindler, 1996), and hydroids (Madin et al., 1999). Further multi-species studies which examine competitive interactions of planktivores at several trophic levels are needed to examine the carrying capacity of PWS for forage fishes.

Diet overlap changed between species pairs each month and sometimes reflected growth patterns. Lee (1985) concluded that competition between co-occurring cod and pollock would vary according to their size combinations, and would be greatest when individuals of both species were < 40 mm. In our study, the gadids were in this size range in May and June (Table 1), but no pollock were examined from May. Indeed, the only time we observed significant diet overlap (66%) between cod and pollock was in June, when they were smallest. Then in July, cod and tomcod diet overlapped significantly (61%), reflecting cod's change to larger prey and the onset of piscivory at larger size (Figure 1). Pollock switched to large prey later than cod and tomcod. Pollock began to eat macrozooplankton at 73 mm in length and fish at 92 in mm length, compared to the 55 mm length of the other gadids. Consequently, pollock and tomcod diets overlapped in September (75%). Pollock are significant piscivores and cannibals as adults (Dwyer et al, 1987).

June appeared to be a time when food webs were most complex. June was also the month when the quality of capelin for piscivorous seabirds was highest (Roby et al, 1998). Numerous factors can influence fish diets. For example, the prey suite available to fish in an area may change with time or may vary in different habitats; growth to larger body size may be accompanied by increased swimming speed and mouth gape, which facilitate predation on different taxa; increasing energy requirements may be more efficiently met by consuming larger items if the costs of consuming them are not too great; and forage fish interactions with other species may prompt shifts in prey consumption to avoid potential competition. Investigation of these possibilities was beyond the scope of this chapter. Calanoids, fish and macrozooplankton were used to varying degrees by all forage fish species, but as prey composition changed monthly and with size, diets of different species pairs overlapped. Herring and pollock were the most consistent pair with overlapping diets. Chapters 2 and 3 discuss the importance of considering the frequency and duration of species co-occurrence to evaluate the importance of diet similarity.

The influences of different diets of forage species on their nutritional quality and growth are an area of study needing more intensive study. Energy assimilated from the diet can be allocated for lipid storage, such as for gamete production, or for somatic growth of fish. The diets of forage fish could influence both their nutritional quality and, through size of fish, their effective availability as forage for seabirds. Payne et al's (1997) studies of the proximate composition of 14 forage species in the northeastern Pacific showed large differences between species. The smelts/osmerids had the highest oil content, sandfish/pricklebacks/sandlance were intermediate in oil content, and pollock/herring/prowfish were among those species with the lowest oil content. The generally high lipid content of pelagic species maturing at small size (herring, sandlance and capelin) nonetheless varied intraspecifically with age, sex and collection site (Anthony and Roby, 1997; Roby et al, 1998). Roby et al. (1999) found both interspecific and intraspecific differences in lipid content of seabird prey dry mass (2-61%), resulting in a fivefold difference in energy density. Seabird prey choice could thus reflect huge differences in forage fish quality and influence reproductive parameters.

Heintz et. al (1999) were able to detect fine-scale spatial differences in the triglyceride (TAG) content of sandlance collected from adjacent bays in southwestern PWS, yet sympatric herring and sandlance both had greater amounts of TAG than allopatric herring and sandlance. This result suggests that prey availability affects nutritional content more than trophic interactions between planktivores do. Yet our observations of subtle shifts in prey composition, and especially, the declines in food quantity consumed by sympatric forage species compared to allopatric forage species (Chapter 3) suggest that competition is a mechanism by which diet can influence nutritional content. Studies on the chemical composition of zooplankton showed that copepods contain the largest fraction of lipid, while protein content varied relatively little between copepods, pteropods, polychaetes, amphipods, cnidarians and ctenophores (Ikeda, 1972; Lee, 1974). Protein was highest and lipid was among the lowest values for euphausiids and chaetognaths (Ikeda, 1972). Copepods stored lipid, while other zooplankters (ostracods, pteropods, euphausiids amphipods and decapods) stored triglycerides (Lee, 1974) and oikopleurans did not store lipid (Deibel et al, 1992). Lipid content in zooplankters, as in fish, is related to ontogenetic stage (Deibel et al, 1992). In addition to their nutritional content, the relative abundances of preferred zooplankters vary. In particular, long-term studies of zooplankton production in PWS have revealed that the standing stock of large calanoids (*Calanus/Neocalanus*) and small calanoids (*Pseudocalanus*) not only varies interannually but varies with regard to which category predominates (Cooney et al, 1994). Other taxa are no doubt similarly variable. Since small calanoids are the predominant taxon available in summer and autumn zooplankton (see Chapters 2 and 3), non-selective feeding at high rates on small calanoids could favor small forage fish with high-lipid requirements without high energy expenditure. Even if other taxa provide more calories in larger packages, feeding on small calanoids for lipid combined with other abundant zooplankters, such as gastropods, oikopleurans or euphausiids, for other nutrients may supply the most advantageous diet. Similarly, diet may explain monthly variation in lipid content and energy density (Roby et al, 1998), since the proportional biomass of calanoids in the diet of forage species declined seasonally and other prey varied monthly. Something other than diet must explain the very different proximate compositions of planktivores such as herring and pollock that have similar diets at similar size/age.

We do not have lipid content or energy density values for the forage specimens whose diets we examined. However, lipid content was generally ranked highest for adult eulachon/lanternfish, second for herring, third for sandfish, sandlance and capelin, fourth for prowfish, and fifth for salmonids and gadids (Roby et al, 1998). Young fish generally had lower lipid content than larger/older fish (Roby et al, 1998). Given our diet information and the nutritional profiles noted above, diets of forage species may be adapted to their life history strategies. A diet high in protein, as is supplied by fish prey, allows faster growth (Harris et al, 1986). Faster growth allows young fish a predation refuge from size-selective piscivores that prey on smaller individuals (Hargreaves and LeBrasseur, 1986). Gadids and salmonids mature at larger size than herring, capelin or sandlance. The salmonids in our study were most piscivorous, with growth advantages that are important for their long migration to the Gulf of Alaska. The other species do not perform such an extensive migration and can afford to remain planktivorous longer, yet the higher lipid content of such a diet may allow earlier maturity. The timing of reproduction may be timed according to forage species seasonal diet shifts and predation on a succession of prey resources. Gamete production requires high energy intake, so fish maturing at small size should do better as planktivores that feed on high lipid plankters such as copepods or maturing macrozooplankton instead of on fish larvae. The late copepodite stages of *Neocalanus* consumed in spring are a prime example. Ontogenetic partitioning of prey resources among forage species may thus be advantageous for both strategies. Selective predation by piscivores on the faster growing, larger forage specimens that prey on fish and larger taxa when younger and smaller, would tend to select for slower growth rates and planktivorous life style forage species.

Other effects on diet and nutrition may be density dependent. For example, in years with high abundances of forage species having inferior nutritional quality, such as 1995 appeared to be for YOY pollock (Haldorsen et al, 1996), competition for similar prey between pollock and nutritionally superior species, such as herring, could influence both the energy content and size of the birds' preferred forage species. Herring energy density differed between 1995 and 1996 (Roby et al, 1998), but our interannual diet data are limited to the months of July and come from different areas of the sound. We observed interannual differences in prey consumed during July by tomcod, pink and chum salmon, and herring, indicating that the lipid and therefore energy content of forage fish could vary between years. However, these species sizes also varied between years. Tomcod were much larger in 1995 than in the other two years, pink salmon were smallest in 1994, chum salmon were largest in 1996, and herring size declined from 1994-1996. Pollock size differed little between July, 1994 and July, 1995. Roby et al. (1998) showed that younger fish generally had lower lipid content. Since fish grow faster on fish prey, the onset of piscivory or switch from predation on mesozooplankton (copepods) to macrozooplankters could also influence forage fish effective availability to seabirds which provision their nestlings with fishes in certain size ranges during the brief summer. The area fished and the gear used also differed between years, so our samples are not equally representative of species' size classes. Our results indicate that planktivory is a factor that can determine the abundance of the preferred forage species of seabirds, but that careful consideration must be given to many factors, including sampling methodology, spatial and temporal distribution, allopatry vs. sympatry, school density, size distribution, and the prey available when evaluating results of diet analyses, and that directed sampling and perhaps manipulative studies are necessary to further elucidate the impacts of these variables.

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Acknowledgments - Chapter 1

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Table 1. Sizes of forage fish analyzed for diet composition, Prince William Sound, 1994-1996. n = number of fish, FL = mm fork length, range = smallest to largest specimens, SD = standard deviation of the mean, %empty = percentage of stomachs with < trace contents.

Forage Species Species code	Pacific cod (110)	Prow-fish (197)	Pacific Herring (233)	Pacific Tomcod (250)	Walleye Pollock (270)	Sockeye Salmon (420)	Pink Salmon (440)	Chum Salmon (450)	Smooth-tongue (509)	Eulachon (511)	Capelin (516)	Sand-lance (517)	Stickle-back (660)	Sand-fish (699)	Total n per month
1994 SEA data															
							May								
n	10	--	41	--	--	--	61	50	55	--	41	34	80	--	372
mean FL	31	--	130	--	--	--	42	49	80	--	116	94	65	--	
range FL	26-38	--	100-156	--	--	--	29-60	32-68	54-107	--	63-133	49-128	47-79	--	
SD FL	4.1	--	18.9	--	--	--	8.3	6.9	13.5	--	21.0	27.0	5.4	--	
%empty	0.0	--	14.6	--	--	--	13.1	10.0	50.9	--	39.0	0.0	5.0	--	
							June								
n	84	--	496	153	252	181	244	111	--	--	32	120	--	--	1673
mean FL	56	--	124	57	42	104	64	55	--	--	95	127	--	--	
range FL	30-83	--	89-159	31-152	22-158	76-125	35-110	36-73	--	--	39-137	106-180	--	--	
SD FL	11.9	--	11.0	25.2	25.6	9.2	13.9	7.7	--	--	27.8	16.0	--	--	
%empty	0.0	--	20.6	2.0	10.9	12.8	18.9	17.1	--	--	43.8	1.7	--	--	
							July								
n	90	--	36	200	206	--	154	6	--	--	15	90	--	--	797
mean FL	72	--	124	71	61	--	77	109	--	--	89	127	--	--	
range FL	53-95	--	91-158	46-100	42-81	--	49-115	92-119	--	--	84-100	104-156	--	--	
SD FL	9.8	--	18.5	9.5	7.8	--	12.9	10.3	--	--	4.1	8.4	--	--	
%empty	2.2	--	22.2	4.0	5.3		14.3	0.0	--	--	20.0	4.4	--	--	
							August								
n	--	--	76	11	24	--	34	41	--	--	--	--	--	--	186
mean FL	--	--	127	100	73	--	155	142	--	--	--	--	--	--	
range FL	--	--	65-197	80-110	39-91	--	110-212	108-169	--	--	--	--	--	--	
SD FL	--	--	43.0	9.5	10.3	--	31.3	12.9	--	--	--	--	--	--	
%empty	--	--	10.5	18.2	4.2		8.8	4.9	--	--	--	--	--	--	
							September								
n	13	--	480	14	198	--	36	121	--	--	--	12	--	--	874
mean FL	92	--	123	100	92	--	132	148	--	--	--	88	--	--	
range FL	80-109	--	48-200	75-123	43-200	--	94-171	85-182	--	--	--	75-128	--	--	
SD FL	9.5	--	30.8	13.6	24.4	--	23.0	18.6	--	--	--	18.6	--	--	
%empty	7.7	--	14.2	14.3	20.3	--	0.0	10.7	--	--	--	0.0	--	--	
APEX 94-96 data															
							November, 1994								
n	--	--	50	--	30	--	--	--	--	10	--	--	--	--	90
mean FL	--	--	133	--	107	--	--	--	--	84	--	--	--	--	
range FL	--	--	73-234	--	88-118	--	--	--	--	72-93	--	--	--	--	
SD FL	--	--	52.8	--	8.5	--	--	--	--	7.4	--	--	--	--	
%empty	--	--	60.0	--	23.3	--	--	--	--	80.0	--	--	--	--	

Table 1, continued.

Forage Species Species code	Pacific cod (110)	Prow-fish (197)	Pacific Herring (233)	Pacific Tomcod (250)	Walleye Pollock (270)	Sockeye Salmon (420)	Pink Salmon (440)	Chum Salmon (450)	Smooth-tongue (509)	Eulachon (511)	Capelin (516)	Sand-lance (517)	Stickle-back (660)	Sand-fish (699)	Total n per month
July, 1995															
n	--	15	70	10	160	--	22	2	--	--	89	31	--	--	399
mean FL	--	94	100	163	73	--	96	109	--	--	52	81	--	--	
range FL	--	50-134	28-159	139-186	40-197	--	67-136	87-131	--	--	19-143	56-100	--	--	
SD FL	--	22.1	40.4	14.4	42.1	--	22.6	31.1	--	--	45.8	15.2	--	--	
%empty	--	0.0	22.9	0.0	20.6	--	0.0	0.0	--	--	98.9	12.9	--	--	
October, 1995															
n	--	1	40	--	100	--	--	--	--	20	40	--	--	--	201
mean FL	--	133	100	--	135	--	--	--	--	72	29	--	--	--	
range FL	--	0	64-152	--	71-239	--	--	--	--	33-115	17-44	--	--	--	
SD FL	--		24.2	--	48.4	--	--	--	--	34.9	8.0	--	--	--	
%empty	--	0.0	25.0	--	21.0	--	--	--	--	55.0	87.5	--	--	--	
July, 1996															
n	--	--	178	30	--	--	100	10	--	--	--	189	--	11	518
mean FL	--	--	75	71	--	--	94	137	--	--	--	84	--	84	
range FL	--	--	26-211	53-86	--	--	58-137	117-151	--	--	--	49-144	--	74-92	
SD FL	--	--	45.3	8.4	--	--	18.3	10.6	--	--	--	21.0	--	4.9	
%empty	--	--	18.5	16.7	--	--	13.0	0.0	--	--	--	--	--	0.0	
Total n per species	197	16	1467	418	970	181	651	341	55	30	217	476	80	11	5110

Table 2. Grand percent biomass of prey in diets of forage fish from Prince William Sound, 1994-96.

	Forage Species	Pacific cod	Prowfish	Pacific Herring	Pacific Tomcod	Walleye Pollock	Sockeye Salmon	Pink Salmon	Chum Salmon	Smooth-tongue	Eulachon	Capelin	Sandlance	Stickle-back	Sandfish
Year/ Month	Prey Category	(110)	(197)	(233)	(250)	(270)	(420)	(440)	(450)	(509)	(511)	(516)	(517)	(660)	(699)
SEA 1994															
1994	BARNACLE LARVAE	0.0	--	0.1	--	--	--	1.6	0.0	0.4	--	0.0	0.0	0.0	--
May	BIVALVE LARVAE	0.0	--	0.0	--	--	--	0.0	0.0	0.0	--	0.0	0.0	0.0	--
	BRYOZOAN LARVAE	0.0	--	0.0	--	--	--	0.0	0.0	0.0	--	0.0	0.0	0.0	--
	CALANOID, LARGE	97.9	--	48.8	--	--	--	36.1	14.1	44.9	--	13.8	82.0	49.9	--
	CALANOID, SMALL	1.9	--	0.2	--	--	--	7.9	0.1	1.2	--	0.2	11.5	0.3	--
	CHAETOGNATH	0.0	--	0.0	--	--	--	0.0	0.0	0.0	--	0.0	0.0	0.0	--
	CLADOCERA	0.0	--	0.0	--	--	--	0.0	0.0	0.0	--	0.0	0.0	0.0	--
	CNID./CTEN.	0.0	--	0.0	--	--	--	0.0	0.0	0.0	--	0.0	0.0	0.0	--
	DECAPOD	0.0	--	0.6	--	--	--	0.0	0.0	0.0	--	0.3	0.0	0.0	--
	DECAPOD LARVAE	0.1	--	0.1	--	--	--	0.8	0.0	0.0	--	0.6	0.1	0.1	--
	EUPHAUSIID	0.0	--	0.0	--	--	--	23.1	0.1	12.3	--	1.3	0.5	0.0	--
	FISH	0.0	--	4.5	--	--	--	24.0	83.1	16.5	--	60.3	2.5	38.3	--
	GAMMARID	0.0	--	0.0	--	--	--	0.6	0.3	0.0	--	0.4	0.1	0.0	--
	GASTROPOD	0.0	--	0.0	--	--	--	1.1	0.0	0.8	--	1.3	0.0	0.0	--
	HARPACTICOID	0.0	--	0.0	--	--	--	0.9	0.0	0.0	--	0.0	0.0	0.0	--
	HYPERIID	0.0	--	0.9	--	--	--	1.1	0.0	7.8	--	17.5	0.0	8.0	--
	INSECT	0.0	--	0.0	--	--	--	0.0	0.0	0.0	--	0.0	0.0	0.0	--
	INVERT. EGGS	0.1	--	0.0	--	--	--	0.3	0.0	0.0	--	0.0	0.7	0.0	--
	LARVACEA	0.0	--	0.0	--	--	--	0.1	0.4	1.2	--	0.0	0.0	0.1	--
	MALACOSTRACA	0.0	--	44.8	--	--	--	0.0	0.0	7.9	--	4.4	2.6	3.3	--
	OTHER	0.0	--	0.0	--	--	--	0.0	0.0	0.0	--	0.0	0.0	0.0	--
	POLYCHAETE	0.0	--	0.0	--	--	--	0.8	0.1	0.1	--	0.0	0.0	0.0	--
June	BARNACLE LARVAE	0.9	--	0.2	0.7	0.0	0.0	1.3	1.5	--	--	0.0	0.3	--	--
	BIVALVE LARVAE	0.0	--	0.0	0.0	0.0	0.0	0.1	0.1	--	--	0.0	0.0	--	--
	BRYOZOAN LARVAE	0.0	--	0.0	0.0	0.0	0.0	0.0	0.0	--	--	0.0	0.0	--	--
	CALANOID, LARGE	32.0	--	37.1	3.2	54.0	0.2	6.9	5.6	--	--	55.8	6.0	--	--
	CALANOID, SMALL	16.6	--	10.1	7.4	12.9	0.0	17.1	1.6	--	--	5.0	12.7	--	--
	CHAETOGNATH	0.0	--	0.0	0.0	0.0	0.0	0.0	0.0	--	--	0.0	0.0	--	--
	CLADOCERA	1.8	--	0.2	0.4	0.4	0.1	3.2	1.4	--	--	0.1	0.6	--	--
	CNID./CTEN.	0.0	--	0.0	0.0	0.0	0.0	0.0	0.0	--	--	0.0	0.0	--	--
	DECAPOD	2.9	--	0.3	0.3	0.0	0.7	0.4	0.9	--	--	0.0	0.4	--	--
	DECAPOD LARVAE	1.7	--	4.3	1.5	0.9	0.8	0.9	2.0	--	--	3.7	0.2	--	--
	EUPHAUSIID	1.5	--	1.8	0.2	12.3	1.4	9.8	1.2	--	--	5.6	0.5	--	--
	FISH	15.7	--	10.3	75.6	14.5	78.4	28.2	72.2	--	--	24.7	73.2	--	--
	GAMMARID	12.7	--	0.0	6.2	0.1	0.0	0.3	0.2	--	--	0.0	0.0	--	--
	GASTROPOD	5.1	--	4.5	1.5	0.1	17.2	21.2	8.8	--	--	0.2	0.4	--	--
	HARPACTICOID	3.1	--	0.0	0.1	0.0	0.0	0.3	0.0	--	--	0.0	0.0	--	--
	HYPERIID	0.6	--	3.4	0.4	1.3	0.5	0.5	0.4	--	--	1.0	0.3	--	--
	INSECT	0.0	--	0.0	0.0	0.0	0.0	0.0	0.0	--	--	0.0	0.0	--	--
	INVERT. EGGS	0.7	--	1.5	0.3	0.8	0.0	0.6	0.1	--	--	0.1	1.2	--	--
	LARVACEA	0.7	--	1.1	0.7	0.0	0.1	5.4	0.6	--	--	0.0	2.1	--	--
	MALACOSTRACA	2.7	--	25.0	0.3	2.6	0.4	1.7	0.5	--	--	3.8	1.8	--	--
	OTHER	0.7	--	0.2	1.3	0.0	0.2	1.8	2.2	--	--	0.1	0.1	--	--
	POLYCHAETE	0.0	--	0.0	0.0	0.0	0.0	0.0	0.0	--	--	0.0	0.0	--	--

Table 2, continued.

	Forage Species	Pacific cod	Prowfish	Pacific Herring	Pacific Tomcod	Walleye Pollock	Sockeye Salmon	Pink Salmon	Chum Salmon	Smooth-tongue	Eulachon	Capelin	Sandlance	Stickle-back	Sandfish
Year/ Month	**Prey Category**	**(110)**	**(197)**	**(233)**	**(250)**	**(270)**	**(420)**	**(440)**	**(450)**	**(509)**	**(511)**	**(516)**	**(517)**	**(660)**	**(699)**
July	BARNACLE LARVAE	0.6	--	1.1	1.7	0.1	--	0.5	0.0	--	--	0.0	1.8	--	--
	BIVALVE LARVAE	0.0	--	0.0	0.0	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
	BRYOZOAN LARVAE	0.0	--	0.0	0.0	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
	CALANOID, LARGE	18.5	--	36.5	15.4	22.7	--	11.8	0.3	--	--	37.2	16.4	--	--
	CALANOID, SMALL	10.5	--	4.1	16.3	52.6	--	10.0	0.0	--	--	3.8	60.5	--	--
	CHAETOGNATH	0.0	--	0.0	0.0	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
	CLADOCERA	0.1	--	0.0	0.2	0.1	--	0.1	0.0	--	--	0.0	0.3	--	--
	CNID./CTEN.	0.0	--	0.0	0.0	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
	DECAPOD	7.2	--	2.6	3.3	0.3	--	1.0	0.0	--	--	0.0	0.1	--	--
	DECAPOD LARVAE	1.8	--	1.6	3.5	0.6	--	1.3	0.0	--	--	0.0	0.6	--	--
	EUPHAUSIID	9.4	--	13.1	8.6	3.5	--	1.1	0.0	--	--	55.6	0.5	--	--
	FISH	5.1	--	19.9	18.1	3.0	--	32.4	86.5	--	--	0.0	2.2	--	--
	GAMMARID	4.7	--	0.0	0.8	0.0	--	0.1	0.0	--	--	0.0	0.0	--	--
	GASTROPOD	30.2	--	9.5	6.4	0.4	--	28.3	11.0	--	--	0.0	1.4	--	--
	HARPACTICOID	1.2	--	0.0	0.3	0.0	--	0.1	0.0	--	--	0.0	0.0	--	--
	HYPERIID	4.1	--	6.1	8.0	6.5	--	3.2	0.0	--	--	0.0	2.2	--	--
	INSECT	0.0	--	0.0	0.0	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
	INVERT. EGGS	0.4	--	0.1	0.4	3.4	--	0.5	0.0	--	--	0.0	5.4	--	--
	LARVACEA	1.5	--	2.8	5.7	0.7	--	8.3	2.2	--	--	0.1	6.7	--	--
	MALACOSTRACA	2.1	--	0.7	10.8	5.9	--	0.3	0.0	--	--	3.3	1.0	--	--
	OTHER	2.6	--	0.1	0.2	0.1	--	1.0	0.0	--	--	0.0	0.1	--	--
	POLYCHAETE	0.0	--	1.6	0.3	0.0	--	0.1	0.0	--	--	0.0	0.6	--	--
August	BARNACLE LARVAE	--	--	0.0	1.0	0.0	--	0.1	6.6	--	--	--	--	--	--
	BIVALVE LARVAE	--	--	0.0	0.0	0.0	--	0.0	0.0	--	--	--	--	--	--
	BRYOZOAN LARVAE	--	--	0.0	0.0	0.0	--	0.0	0.0	--	--	--	--	--	--
	CALANOID, LARGE	--	--	75.4	1.9	17.5	--	31.1	69.1	--	--	--	--	--	--
	CALANOID, SMALL	--	--	2.8	0.8	22.3	--	0.0	0.3	--	--	--	--	--	--
	CHAETOGNATH	--	--	0.0	0.0	0.0	--	0.0	0.0	--	--	--	--	--	--
	CLADOCERA	--	--	0.0	0.2	0.0	--	0.0	0.1	--	--	--	--	--	--
	CNID./CTEN.	--	--	0.0	0.1	0.0	--	0.1	6.3	--	--	--	--	--	--
	DECAPOD	--	--	0.0	15.7	0.0	--	17.1	0.4	--	--	--	--	--	--
	DECAPOD LARVAE	--	--	0.0	0.0	0.0	--	0.0	0.0	--	--	--	--	--	--
	EUPHAUSIID	--	--	0.0	0.0	1.1	--	3.5	0.0	--	--	--	--	--	--
	FISH	--	--	0.5	46.6	10.1	--	35.6	3.5	--	--	--	--	--	--
	GAMMARID	--	--	0.0	0.2	0.0	--	0.0	0.0	--	--	--	--	--	--
	GASTROPOD	--	--	0.0	0.7	0.5	--	0.1	0.1	--	--	--	--	--	--
	HARPACTICOID	--	--	0.0	0.2	0.0	--	0.0	0.0	--	--	--	--	--	--
	HYPERIID	--	--	13.8	12.1	42.2	--	7.9	2.1	--	--	--	--	--	--
	INSECT	--	--	0.0	0.0	0.0	--	0.0	0.0	--	--	--	--	--	--
	INVERT. EGGS	--	--	0.4	0.0	0.8	--	0.0	0.0	--	--	--	--	--	--
	LARVACEA	--	--	1.1	6.4	0.8	--	3.7	11.0	--	--	--	--	--	--
	MALACOSTRACA	--	--	2.9	9.4	2.4	--	0.6	0.0	--	--	--	--	--	--
	OTHER	--	--	0.0	2.6	0.0	--	0.1	0.0	--	--	--	--	--	--
	POLYCHAETE	--	--	0.0	0.9	0.0	--	0.0	0.0	--	--	--	--	--	--

Table 2, continued.

	Forage Species	Pacific cod	Prowfish	Pacific Herring	Pacific Tomcod	Walleye Pollock	Sockeye Salmon	Pink Salmon	Chum Salmon	Smooth-tongue	Eulachon	Capelin	Sandlance	Stickle-back	Sandfish
Year/ Month	**Prey Category**	**(110)**	**(197)**	**(233)**	**(250)**	**(270)**	**(420)**	**(440)**	**(450)**	**(509)**	**(511)**	**(516)**	**(517)**	**(660)**	**(699)**
September	BARNACLE LARVAE	0.0	--	0.1	0.0	0.1	--	0.3	0.1	--	--	--	0.2	--	--
	BIVALVE LARVAE	0.0	--	0.0	0.0	0.0	--	0.0	0.1	--	--	--	0.7	--	--
	BRYOZOAN LARVAE	0.0	--	0.0	0.0	0.0	--	0.0	0.0	--	--	--	0.0	--	--
	CALANOID, LARGE	0.2	--	14.3	1.5	5.0	--	42.7	12.9	--	--	--	32.1	--	--
	CALANOID, SMALL	0.4	--	29.3	5.4	17.3	--	0.0	0.0	--	--	--	23.0	--	--
	CHAETOGNATH	0.0	--	0.0	0.0	0.0	--	0.0	0.0	--	--	--	0.0	--	--
	CLADOCERA	0.0	--	0.1	0.0	0.0	--	0.0	0.0	--	--	--	0.0	--	--
	CNID./CTEN.	0.0	--	0.0	0.0	0.0	--	0.0	2.7	--	--	--	0.0	--	--
	DECAPOD	1.7	--	2.6	3.1	1.0	--	1.8	2.1	--	--	--	2.4	--	--
	DECAPOD LARVAE	1.6	--	1.2	1.4	0.2	--	0.7	0.1	--	--	--	3.7	--	--
	EUPHAUSIID	35.0	--	13.3	0.0	2.6	--	4.2	7.2	--	--	--	5.0	--	--
	FISH	3.4	--	5.1	61.3	64.1	--	34.3	37.6	--	--	--	0.0	--	--
	GAMMARID	3.1	--	0.0	16.5	0.1	--	0.7	1.2	--	--	--	0.0	--	--
	GASTROPOD	0.0	--	0.6	0.3	0.3	--	0.0	0.1	--	--	--	1.4	--	--
	HARPACTICOID	2.2	--	0.0	0.1	0.0	--	0.0	0.0	--	--	--	0.0	--	--
	HYPERIID	0.6	--	7.5	6.0	2.7	--	11.0	8.4	--	--	--	0.6	--	--
	INSECT	0.0	--	0.0	0.0	0.0	--	0.0	0.0	--	--	--	0.0	--	--
	INVERT. EGGS	0.0	--	1.4	0.2	1.2	--	0.0	1.0	--	--	--	1.4	--	--
	LARVACEA	0.0	--	5.2	2.3	1.8	--	3.1	8.6	--	--	--	2.4	--	--
	MALACOSTRACA	23.1	--	19.3	0.5	3.6	--	0.9	17.9	--	--	--	27.2	--	--
	OTHER	28.5	--	0.1	1.4	0.2	--	0.2	0.1	--	--	--	0.0	--	--
	POLYCHAETE	0.2	--	0.0	0.0	0.0	--	0.0	0.0	--	--	--	0.0	--	--
APEX 1994-96															
1994 November	BARNACLE LARVAE	--	--	0.0	--	0.0	--	--	--	--	0	--	--	--	--
	BIVALVE LARVAE	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--
	BRYOZOAN LARVAE	--	--	0.0	--	0.0	--	--	--	--	0	--	--	--	--
	CALANOID, LARGE	--	--	6.2	--	14.1	--	--	--	--	0.0	--	--	--	--
	CALANOID, SMALL	--	--	17.5	--	5.5	--	--	--	--	0.0	--	--	--	--
	CHAETOGNATH	--	--	0.3	--	0.3	--	--	--	--	0.0	--	--	--	--
	CLADOCERA	--	--	0.0	--	0.0	--	--	--	--	0	--	--	--	--
	CNID./CTEN.	--	--	0.0	--	4.0	--	--	--	--	0.0	--	--	--	--
	DECAPOD	--	--	0.0	--	1.2	--	--	--	--	0.0	--	--	--	--
	DECAPOD LARVAE	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--
	EUPHAUSIID	--	--	51.1	--	45.8	--	--	--	--	46.9	--	--	--	--
	FISH	--	--	0.0	--	0.0	--	--	--	--	0	--	--	--	--
	GAMMARID	--	--	0.1	--	0.3	--	--	--	--	0.0	--	--	--	--
	GASTROPOD	--	--	2.7	--	0.0	--	--	--	--	0.0	--	--	--	--
	HARPACTICOID	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	HYPERIID	--	--	4.7	--	7.9	--	--	--	--	0.0	--	--	--	--
	INSECT	--	--	0.0	--	0.0	--	--	--	--	0	--	--	--	--
	INVERT. EGGS	--	--	0.0	--	0.0	--	--	--	--	0	--	--	--	--
	LARVACEA	--	--	7.8	--	20.9	--	--	--	--	0.0	--	--	--	--
	MALACOSTRACA	--	--	0.2	--	0.0	--	--	--	--	53.1	--	--	--	--
	OTHER	--	--	9.4	--	0.1	--	--	--	--	0.0	--	--	--	--
	POLYCHAETE	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--

Table 2, continued.

	Forage Species	Pacific cod	Prowfish	Pacific Herring	Pacific Tomcod	Walleye Pollock	Sockeye Salmon	Pink Salmon	Chum Salmon	Smooth-tongue	Eulachon	Capelin	Sandlance	Stickle-back	Sandfish
Year/ Month	**Prey Category**	**(110)**	**(197)**	**(233)**	**(250)**	**(270)**	**(420)**	**(440)**	**(450)**	**(509)**	**(511)**	**(516)**	**(517)**	**(660)**	**(699)**
1995	BARNACLE LARVAE	--	0.0	0.1	0.0	0.0	--	0.1	0.0	--	--	0.0	1.3	--	--
July	BIVALVE LARVAE	--	0.0	0.0	0.0	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
	BRYOZOAN LARVAE	--	0.0	0.0	0.0	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
	CALANOID, LARGE	--	0.0	8.4	0.1	17.9	--	13.3	3.8	--	--	0.0	10.8	--	--
	CALANOID, SMALL	--	8.9	80.2	0.0	51.5	--	0.6	0.3	--	--	88.6	62.7	--	--
	CHAETOGNATH	--	0.0	0.0	0.0	1.1	--	4.2	16.4	--	--	0.0	0.0	--	--
	CLADOCERA	--	0.1	0.9	0.0	0.2	--	0.4	0.0	--	--	0.0	0.3	--	--
	CNID./CTEN.	--	0.0	0.0	0.0	0.1	--	0.0	0.0	--	--	0.0	0.0	--	--
	DECAPOD	--	0.0	1.6	0.0	1.6	--	1.3	2.5	--	--	0.0	0.3	--	--
	DECAPOD LARVAE	--	0.0	0.0	0.0	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
	EUPHAUSIID	--	0.0	0.1	0.2	4.4	--	14.9	0.1	--	--	0.0	0.1	--	--
	FISH	--	0.0	0.0	71.5	8.0	--	22.2	29.6	--	--	0.0	0.0	--	--
	GAMMARID	--	0.0	0.0	24.8	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
	GASTROPOD	--	9.2	1.0	0.0	3.2	--	33.7	0.1	--	--	6.7	0.7	--	--
	HARPACTICOID	--	0.0	0.1	0.0	0.0	--	0.1	0.0	--	--	0.0	1.3	--	--
	HYPERIID	--	78.8	0.6	0.0	7.6	--	7.9	41.3	--	--	0.0	0.5	--	--
	INSECT	--	0.0	0.0	0.0	0.0	--	0.1	0.0	--	--	0.0	0.0	--	--
	INVERT. EGGS	--	0.0	0.0	0.0	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
	LARVACEA	--	2.7	1.5	0.0	0.5	--	1.0	5.9	--	--	0.0	18.3	--	--
	MALACOSTRACA	--	0.0	0.3	0.3	0.9	--	0.1	0.0	--	--	0.0	0.0	--	--
	OTHER	--	0.3	5.4	3.2	2.8	--	0.1	0.0	--	--	4.6	4.9	--	--
	POLYCHAETE	--	0.0	0.0	0.0	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
October	BARNACLE LARVAE	--	0.0	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	BIVALVE LARVAE	--	0.0	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	BRYOZOAN LARVAE	--	0.0	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	CALANOID, LARGE	--	0.0	47.7	--	43.4	--	--	--	--	0.0	0.0	--	--	--
	CALANOID, SMALL	--	3.1	8.2	--	1.0	--	--	--	--	0.6	7.0	--	--	--
	CHAETOGNATH	--	0.0	0.4	--	0.7	--	--	--	--	0.0	0.0	--	--	--
	CLADOCERA	--	0.0	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	CNID./CTEN.	--	0.3	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	DECAPOD	--	0.0	0.6	--	0.4	--	--	--	--	0.0	0.0	--	--	--
	DECAPOD LARVAE	--	0.0	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	EUPHAUSIID	--	0.0	13.3	--	44.2	--	--	--	--	97.8	92.6	--	--	--
	FISH	--	0.0	0.0	--	3.1	--	--	--	--	0.0	0.0	--	--	--
	GAMMARID	--	0.0	0.1	--	0.4	--	--	--	--	0.0	0.0	--	--	--
	GASTROPOD	--	0.0	0.3	--	0.0	--	--	--	--	0.5	0.0	--	--	--
	HARPACTICOID	--	0.0	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	HYPERIID	--	94.8	8.6	--	4.8	--	--	--	--	0.0	0.0	--	--	--
	INSECT	--	0.0	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	INVERT. EGGS	--	0.0	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	LARVACEA	--	1.7	16.1	--	0.1	--	--	--	--	0.0	0.0	--	--	--
	MALACOSTRACA	--	0.0	0.8	--	1.4	--	--	--	--	1.1	0.0	--	--	--
	OTHER	--	0.0	3.9	--	0.6	--	--	--	--	0.0	0.4	--	--	--
	POLYCHAETE	--	0.0	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--

Table 2, continued.

	Forage Species	Pacific cod	Prowfish	Pacific Herring	Pacific Tomcod	Walleye Pollock	Sockeye Salmon	Pink Salmon	Chum Salmon	Smooth-tongue	Eulachon	Capelin	Sandlance	Stickle-back	Sandfish
Year/ Month	Prey Category	(110)	(197)	(233)	(250)	(270)	(420)	(440)	(450)	(509)	(511)	(516)	(517)	(660)	(699)
1996	BARNACLE LARVAE	--	--	0.3	1.7	--	--	0.6	12.1	--	--	--	5.8	--	0.0
July	BIVALVE LARVAE	--	--	0.0	0.0	--	--	0.0	0.0	--	--	--	0.0	--	0.0
	BRYOZOAN LARVAE	--	--	0.0	0.0	--	--	0.0	0.0	--	--	--	0.0	--	0.0
	CALANOID, LARGE	--	--	33.3	4.3	--	--	2.7	0.0	--	--	--	12.2	--	0.1
	CALANOID, SMALL	--	--	24.1	20.4	--	--	0.2	0.1	--	--	--	66.7	--	0.3
	CHAETOGNATH	--	--	0.1	0.0	--	--	0.2	0.9	--	--	--	0.0	--	0.0
	CLADOCERA	--	--	0.2	0.2	--	--	0.0	0.0	--	--	--	0.5	--	0.0
	CNID./CTEN.	--	--	0.0	0.0	--	--	0.1	0.0	--	--	--	0.0	--	0.0
	DECAPOD	--	--	20.3	29.4	--	--	4.2	24.8	--	--	--	2.5	--	0.4
	DECAPOD LARVAE	--	--	0.0	0.0	--	--	0.0	0.0	--	--	--	0.0	--	0.0
	EUPHAUSIID	--	--	0.5	0.1	--	--	0.2	0.9	--	--	--	0.1	--	0.6
	FISH	--	--	0.1	0.0	--	--	79.1	12.1	--	--	--	0.7	--	96.9
	GAMMARID	--	--	0.1	0.1	--	--	0.0	0.0	--	--	--	0.1	--	1.6
	GASTROPOD	--	--	0.6	0.9	--	--	0.6	0.0	--	--	--	0.8	--	0.0
	HARPACTICOID	--	--	0.0	0.0	--	--	0.0	0.0	--	--	--	0.0	--	0.0
	HYPERIID	--	--	5.7	0.2	--	--	3.7	41.7	--	--	--	0.2	--	0.0
	INSECT	--	--	0.0	0.9	--	--	1.0	0.5	--	--	--	0.0	--	0.0
	INVERT. EGGS	--	--	0.0	0.0	--	--	0.0	0.0	--	--	--	0.0	--	0.0
	LARVACEA	--	--	11.5	14.8	--	--	6.5	5.4	--	--	--	8.5	--	0.0
	MALACOSTRACA	--	--	3.0	0.0	--	--	0.8	1.0	--	--	--	0.0	--	0.0
	OTHER	--	--	0.4	26.9	--	--	0.2	0.6	--	--	--	2.0	--	0.1
	POLYCHAETE	--	--	0.0	0.0	--	--	0.0	0.0	--	--	--	0.0	--	0.0

Table 3. Grand percent numbers of prey in diets of forage fish from Prince William Sound, 1994-96.

	Forage Species	Pacific cod	Prowfish	Pacific Herring	Pacific Tomcod	Walleye Pollock	Sockeye Salmon	Pink Salmon	Chum Salmon	Smooth-tongue	Eulachon	Capelin	Sandlance	Stickle-back	Sandfish
Year/ Month	Prey Category	(110)	(197)	(233)	(250)	(270)	(420)	(440)	(450)	(509)	(511)	(516)	(517)	(660)	(699)
SEA 1994 data															
1994	BARNACLE LARVAE	0.0	--	0.7	--	--	--	3.0	0.2	1.3	--	0.0	0.1	0.0	--
May	BIVALVE LARVAE	0.0	--	0.0	--	--	--	0.0	0.0	0.0	--	0.2	0.0	0.0	--
	BRYOZOAN LARVAE	0.0	--	0.0	--	--	--	0.0	0.0	0.0	--	0.0	0.0	0.0	--
	CALANOID, LARGE	50.0	--	74.3	--	--	--	8.1	28.3	30.3	--	44.3	17.9	68.0	--
	CALANOID, SMALL	34.7	--	8.8	--	--	--	50.3	3.7	19.5	--	11.5	48.5	10.4	--
	CHAETOGNATH	0.0	--	0.0	--	--	--	0.0	0.0	0.0	--	0.2	0.0	0.0	--
	CLADOCERA	0.0	--	0.0	--	--	--	0.1	0.0	0.8	--	0.0	0.0	0.0	--
	CNID./CTEN.	0.0	--	0.0	--	--	--	0.0	0.0	0.0	--	0.2	0.0	0.0	--
	DECAPOD	0.0	--	0.2	--	--	--	0.0	0.0	0.0	--	0.2	0.0	0.0	--
	DECAPOD LARVAE	1.4	--	0.1	--	--	--	0.1	0.0	0.0	--	1.4	0.0	0.1	--
	EUPHAUSIID	0.0	--	0.0	--	--	--	5.5	1.8	4.2	--	2.5	0.6	0.2	--
	FISH	0.0	--	0.4	--	--	--	0.2	7.6	0.3	--	10.1	0.0	2.3	--
	GAMMARID	0.0	--	0.0	--	--	--	0.3	1.3	0.0	--	0.2	0.0	0.0	--
	GASTROPOD	0.0	--	0.0	--	--	--	3.1	0.4	3.7	--	1.3	0.0	0.0	--
	HARPACTICOID	0.0	--	0.1	--	--	--	4.9	1.1	0.0	--	0.0	0.1	0.0	--
	HYPERIID	0.0	--	0.4	--	--	--	0.1	0.0	0.8	--	19.5	0.0	3.1	--
	INSECT	0.0	--	0.0	--	--	--	0.0	0.0	0.0	--	0.2	0.0	0.0	--
	INVERT. EGGS	13.9	--	1.1	--	--	--	15.0	9.6	2.9	--	0.0	32.6	0.1	--
	LARVACEA	0.0	--	1.3	--	--	--	0.5	21.4	22.9	--	4.1	0.0	14.2	--
	MALACOSTRACA	0.0	--	12.8	--	--	--	0.0	0.0	0.5	--	2.5	0.1	0.8	--
	OTHER	0.0	--	0.1	--	--	--	4.4	21.1	10.8	--	0.0	0.0	0.7	--
	POLYCHAETE	0.0	--	0.0	--	--	--	4.2	3.3	0.8	--	2.2	0.0	0.1	--
June	BARNACLE LARVAE	0.7	--	0.2	1.7	0.1	0.1	0.5	2.7	--	--	0.0	0.4	--	--
	BIVALVE LARVAE	0.2	--	1.5	0.5	0.1	0.7	4.1	10.9	--	--	0.1	0.2	--	--
	BRYOZOAN LARVAE	0.0	--	0.0	0.0	0.0	0.0	0.0	0.0	--	--	0.0	0.0	--	--
	CALANOID, LARGE	4.1	--	4.6	1.3	10.3	0.2	0.5	1.6	--	--	22.4	1.0	--	--
	CALANOID, SMALL	44.2	--	33.8	46.7	51.3	1.0	30.2	9.7	--	--	55.3	36.3	--	--
	CHAETOGNATH	0.0	--	0.0	0.0	0.0	0.0	0.0	0.0	--	--	0.0	0.0	--	--
	CLADOCERA	10.9	--	1.7	6.5	4.3	3.2	12.0	21.8	--	--	1.7	4.4	--	--
	CNID./CTEN.	0.0	--	0.0	0.0	0.0	0.0	0.0	0.0	--	--	0.0	0.0	--	--
	DECAPOD	0.1	--	0.0	0.0	0.0	0.1	0.0	0.1	--	--	0.0	0.0	--	--
	DECAPOD LARVAE	0.2	--	0.4	0.4	0.1	0.6	0.0	0.5	--	--	1.3	0.0	--	--
	EUPHAUSIID	0.3	--	0.4	0.2	0.8	0.3	0.3	0.6	--	--	3.4	0.2	--	--
	FISH	0.1	--	0.1	0.1	0.1	1.7	0.1	0.9	--	--	0.4	0.1	--	--
	GAMMARID	3.4	--	0.0	3.5	0.0	0.0	0.0	0.1	--	--	0.0	0.0	--	--
	GASTROPOD	6.4	--	4.7	4.6	0.2	88.4	17.0	31.2	--	--	0.7	0.6	--	--
	HARPACTICOID	7.9	--	0.0	0.7	0.0	0.0	0.5	0.2	--	--	0.1	0.1	--	--
	HYPERIID	0.0	--	0.1	0.1	0.1	0.1	0.0	0.0	--	--	0.1	0.0	--	--
	INSECT	0.0	--	0.0	0.0	0.0	0.0	0.0	0.0	--	--	0.0	0.0	--	--
	INVERT. EGGS	16.1	--	41.5	18.1	32.1	0.1	9.3	5.0	--	--	5.1	37.8	--	--
	LARVACEA	5.0	--	8.3	14.6	0.3	2.9	23.7	6.9	--	--	0.6	18.4	--	--
	MALACOSTRACA	0.2	--	0.9	0.1	0.1	0.2	0.1	0.1	--	--	8.3	0.1	--	--
	OTHER	0.2	--	1.7	0.8	0.0	0.4	1.6	6.5	--	--	0.1	0.2	--	--
	POLYCHAETE	0.0	--	0.0	0.1	0.0	0.0	0.1	1.3	--	--	0.0	0.2	--	--

Table 3, continued.

	Forage Species	Pacific cod	Prowfish	Pacific Herring	Pacific Tomcod	Walleye Pollock	Sockeye Salmon	Pink Salmon	Chum Salmon	Smooth-tongue	Eulachon	Capelin	Sandlance	Stickle-back	Sandfish
Year/ Month	Prey Category	(110)	(197)	(233)	(250)	(270)	(420)	(440)	(450)	(509)	(511)	(516)	(517)	(660)	(699)
July	BARNACLE LARVAE	0.8	--	2.1	1.5	0.0	--	0.2	0.0	--	--	0.0	0.5	--	--
	BIVALVE LARVAE	0.1	--	1.2	1.2	0.0	--	1.2	0.0	--	--	1.4	0.5	--	--
	BRYOZOAN LARVAE	0.0	--	0.0	0.0	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
	CALANOID, LARGE	4.1	--	10.4	2.0	1.4	--	1.3	0.1	--	--	28.8	0.6	--	--
	CALANOID, SMALL	38.0	--	21.0	34.6	53.4	--	17.9	0.0	--	--	46.0	37.5	--	--
	CHAETOGNATH	0.0	--	0.0	0.0	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
	CLADOCERA	1.2	--	0.2	1.2	0.4	--	0.5	0.0	--	--	0.0	0.7	--	--
	CNID./CTEN.	0.0	--	0.0	0.0	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
	DECAPOD	0.3	--	0.1	0.1	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
	DECAPOD LARVAE	0.3	--	0.3	0.3	0.0	--	0.1	0.0	--	--	0.0	0.0	--	--
	EUPHAUSIID	0.3	--	1.5	0.6	0.6	--	0.2	0.0	--	--	7.9	0.1	--	--
	FISH	0.0	--	0.2	0.0	0.0	--	0.0	0.1	--	--	0.0	0.0	--	--
	GAMMARID	0.6	--	0.0	0.1	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
	GASTROPOD	16.2	--	13.8	8.2	0.3	--	14.7	48.3	--	--	0.0	0.5	--	--
	HARPACTICOID	5.1	--	0.2	0.9	0.0	--	0.2	0.0	--	--	0.0	0.0	--	--
	HYPERIID	0.4	--	1.5	0.3	0.1	--	0.1	0.0	--	--	0.0	0.0	--	--
	INSECT	0.0	--	0.0	0.0	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
	INVERT. EGGS	13.8	--	3.8	9.2	40.9	--	10.9	0.0	--	--	0.7	43.2	--	--
	LARVACEA	17.1	--	42.6	39.0	2.6	--	52.1	51.6	--	--	4.3	16.1	--	--
	MALACOSTRACA	0.7	--	0.4	0.3	0.1	--	0.1	0.0	--	--	10.8	0.1	--	--
	OTHER	0.8	--	0.3	0.4	0.0	--	0.2	0.0	--	--	0.0	0.0	--	--
	POLYCHAETE	0.1	--	0.2	0.0	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
August	BARNACLE LARVAE	--	--	0.0	0.8	0.0	--	0.0	0.5	--	--	--	--	--	--
	BIVALVE LARVAE	--	--	0.0	0.0	0.0	--	0.0	0.0	--	--	--	--	--	--
	BRYOZOAN LARVAE	--	--	0.0	0.0	0.0	--	0.0	0.0	--	--	--	--	--	--
	CALANOID, LARGE	--	--	24.0	1.3	6.2	--	27.8	19.2	--	--	--	--	--	--
	CALANOID, SMALL	--	--	21.3	4.2	62.4	--	0.0	0.8	--	--	--	--	--	--
	CHAETOGNATH	--	--	0.0	0.0	0.0	--	0.0	0.0	--	--	--	--	--	--
	CLADOCERA	--	--	0.2	2.3	0.1	--	0.0	0.5	--	--	--	--	--	--
	CNID./CTEN.	--	--	0.0	0.1	0.0	--	0.1	9.3	--	--	--	--	--	--
	DECAPOD	--	--	0.0	0.5	0.0	--	1.1	0.0	--	--	--	--	--	--
	DECAPOD LARVAE	--	--	0.7	0.1	0.3	--	0.0	0.0	--	--	--	--	--	--
	EUPHAUSIID	--	--	0.1	0.0	0.2	--	0.7	0.1	--	--	--	--	--	--
	FISH	--	--	0.0	0.4	0.1	--	0.3	0.0	--	--	--	--	--	--
	GAMMARID	--	--	0.0	0.1	0.0	--	0.0	0.0	--	--	--	--	--	--
	GASTROPOD	--	--	0.1	1.9	0.8	--	0.0	0.1	--	--	--	--	--	--
	HARPACTICOID	--	--	0.0	1.0	0.0	--	0.0	0.0	--	--	--	--	--	--
	HYPERIID	--	--	1.2	0.7	1.5	--	1.0	0.1	--	--	--	--	--	--
	INSECT	--	--	0.0	0.0	0.0	--	0.0	0.0	--	--	--	--	--	--
	INVERT. EGGS	--	--	28.3	0.5	22.3	--	0.0	0.3	--	--	--	--	--	--
	LARVACEA	--	--	23.3	81.0	6.0	--	68.7	69.1	--	--	--	--	--	--
	MALACOSTRACA	--	--	0.7	0.3	0.1	--	0.0	0.0	--	--	--	--	--	--
	OTHER	--	--	0.0	0.8	0.0	--	0.0	0.0	--	--	--	--	--	--
	POLYCHAETE	--	--	0.0	4.2	0.0	--	0.0	0.0	--	--	--	--	--	--

Table 3, continued.

	Forage Species	Pacific cod	Prowfish	Pacific Herring	Pacific Tomcod	Walleye Pollock	Sockeye Salmon	Pink Salmon	Chum Salmon	Smooth-tongue	Eulachon	Capelin	Sandlance	Stickle-back	Sandfish
Year/ Month	**Prey Category**	**(110)**	**(197)**	**(233)**	**(250)**	**(270)**	**(420)**	**(440)**	**(450)**	**(509)**	**(511)**	**(516)**	**(517)**	**(660)**	**(699)**
September	BARNACLE LARVAE	0.0	--	0.0	0.2	0.1		0.1	0.0	--	--	--	0.2	--	--
	BIVALVE LARVAE	0.8	--	0.0	0.0	0.0	--	0.0	0.0	--	--	--	0.1	--	--
	BRYOZOAN LARVAE	0.0	--	0.0	0.0	0.0	--	0.0	0.0	--	--	--	0.0	--	--
	CALANOID, LARGE	0.3	--	1.4	0.5	0.9	--	19.2	1.1	--	--	--	3.2	--	--
	CALANOID, SMALL	10.1	--	47.6	31.9	47.1	--	0.2	0.1	--	--	--	56.7	--	--
	CHAETOGNATH	0.0	--	0.0	0.0	0.0	--	0.0	0.0	--	--	--	0.0	--	--
	CLADOCERA	0.0	--	0.4	0.6	0.1	--	0.0	0.1	--	--	--	0.1	--	--
	CNID./CTEN.	0.0	--	0.0	0.0	0.0	--	0.0	2.8	--	--	--	0.0	--	--
	DECAPOD	0.3	--	0.0	0.2	0.0	--	0.1	0.0	--	--	--	0.0	--	--
	DECAPOD LARVAE	1.2	--	0.1	0.3	0.0	--	0.2	0.0	--	--	--	0.5	--	--
	EUPHAUSIID	6.6	--	1.0	0.0	0.3	--	0.3	0.5	--	--	--	1.8	--	--
	FISH	0.1	--	0.0	0.6	0.1	--	0.6	0.1	--	--	--	0.0	--	--
	GAMMARID	1.5	--	0.0	6.4	0.0	--	0.2	0.1	--	--	--	0.0	--	--
	GASTROPOD	0.0	--	0.5	1.1	0.5	--	0.1	0.0	--	--	--	1.6	--	--
	HARPACTICOID	69.2	--	0.0	0.8	0.0	--	0.0	0.0	--	--	--	0.0	--	--
	HYPERIID	0.3	--	0.2	0.5	0.1	--	2.4	0.6	--	--	--	0.0	--	--
	INSECT	0.8	--	0.0	0.0	0.0	--	0.0	0.0	--	--	--	0.1	--	--
	INVERT. EGGS	0.0	--	22.3	12.8	34.9	--	0.0	25.7	--	--	--	20.1	--	--
	LARVACEA	0.0	--	25.8	42.3	15.7	--	75.8	68.4	--	--	--	14.2	--	--
	MALACOSTRACA	3.9	--	0.5	0.8	0.1	--	0.2	0.4	--	--	--	1.5	--	--
	OTHER	5.5	--	0.0	0.3	0.0	--	0.3	0.0	--	--	--	0.0	--	--
	POLYCHAETE	0.1	--	0.0	0.0	0.0	--	0.0	0.0	--	--	--	0.0	--	--
APEX 94-96 data															
1994	BARNACLE LARVAE	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--
November	BIVALVE LARVAE	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--
	BRYOZOAN LARVAE	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--
	CALANOID, LARGE	--	--	0.4	--	2.1	--	--	--	--	0.0	--	--	--	--
	CALANOID, SMALL	--	--	24.1	--	8.9	--	--	--	--	0.0	--	--	--	--
	CHAETOGNATH	--	--	0.1	--	0.1	--	--	--	--	0.0	--	--	--	--
	CLADOCERA	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--
	CNID./CTEN.	--	--	0.0	--	0.1	--	--	--	--	0.0	--	--	--	--
	DECAPOD	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--
	DECAPOD LARVAE	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--
	EUPHAUSIID	--	--	0.9	--	0.6	--	--	--	--	50.0	--	--	--	--
	FISH	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--
	GAMMARID	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--
	GASTROPOD	--	--	1.8	--	0.0	--	--	--	--	0.0	--	--	--	--
	HARPACTICOID	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--
	HYPERIID	--	--	0.1	--	0.1	--	--	--	--	0.0	--	--	--	--
	INSECT	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--
	INVERT. EGGS.	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--
	LARVACEA	--	--	26.9	--	87.8	--	--	--	--	0.0	--	--	--	--
	MALACOSTRACA	--	--	0.1	--	0.0	--	--	--	--	50.0	--	--	--	--
	OTHER	--	--	45.6	--	0.3	--	--	--	--	0.0	--	--	--	--
	POLYCHAETE	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--

Table 3, continued.

Year/ Month	Forage Species Prey Category	Pacific cod (110)	Prowfish (197)	Pacific Herring (233)	Pacific Tomcod (250)	Walleye Pollock (270)	Sockeye Salmon (420)	Pink Salmon (440)	Chum Salmon (450)	Smooth-tongue (509)	Eulachon (511)	Capelin (516)	Sandlance (517)	Stickle-back (660)	Sandfish (699)
1995 July	BARNACLE LARVAE	--	0.0	0.0	0.9	0.0	0.0	0.1	0.0	--	--	0.0	--	--	--
	BIVALVE LARVAE	--	0.0	0.0	0.0	0.0	0.0	0.0	0.0	--	--	0.0	--	--	--
	BRYOZOAN LARVAE	--	0.0	0.0	0.0	0.0	0.0	0.0	0.0	--	--	0.0	--	--	--
	CALANOID, LARGE	--	0.0	0.3	0.9	1.6	0.0	5.4	1.0	--	--	0.0	--	--	--
	CALANOID, SMALL	--	47.7	58.3	2.3	57.0	0.0	4.0	1.0	--	--	83.3	--	--	--
	CHAETOGNATH	--	0.0	0.0	0.0	0.3	0.0	6.4	15.6	--	--	0.0	--	--	--
	CLADOCERA	--	0.9	1.6	0.9	0.6	0.0	6.7	0.0	--	--	0.0	--	--	--
	CNID./CTEN.	--	0.1	0.0	0.0	0.0	0.0	0.0	0.0	--	--	0.0	--	--	--
	DECAPOD	--	0.0	0.0	0.0	0.0	0.0	0.3	0.4	--	--	0.0	--	--	--
	DECAPOD LARVAE	--	0.0	0.0	0.0	0.0	0.0	0.0	0.0	--	--	0.0	--	--	--
	EUPHAUSIID	--	0.0	0.0	0.7	0.1	0.0	1.2	0.1	--	--	0.0	--	--	--
	FISH	--	0.0	0.0	0.9	0.0	0.0	0.3	0.2	--	--	0.0	--	--	--
	GAMMARID	--	0.0	0.0	60.1	0.0	0.0	0.0	0.0	--	--	0.0	--	--	--
	GASTROPOD	--	4.6	0.4	0.0	2.3	0.0	48.7	0.4	--	--	2.1	--	--	--
	HARPACTICOID	--	0.0	0.0	0.0	0.0	0.0	0.0	0.0	--	--	0.0	--	--	--
	HYPERIID	--	4.9	0.1	0.0	0.3	0.0	3.2	6.4	--	--	0.0	--	--	--
	INSECT	--	0.0	0.0	0.2	0.0	0.0	0.1	0.0	--	--	0.0	--	--	--
	INVERT. EGGS.	--	0.0	0.0	0.9	0.0	0.0	0.1	0.0	--	--	0.0	--	--	--
	LARVACEA	--	32.1	3.0	0.0	2.1	0.0	20.5	74.8	--	--	0.0	--	--	--
	MALACOSTRACA	--	0.0	0.0	0.5	0.1	0.0	0.3	0.0	--	--	0.0	--	--	--
	OTHER	--	9.6	36.2	32.7	35.4	0.0	2.8	0.0	--	--	14.6	--	--	--
	POLYCHAETE	--	0.0	0.0	0.0	0.0	0.0	0.0	0.0	--	--	0.0	--	--	--
October	BARNACLE LARVAE	--	0.0	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	BIVALVE LARVAE	--	0.0	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	BRYOZOAN LARVAE	--	0.0	0.2	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	CALANOID, LARGE	--	0.0	6.6	--	71.0	--	--	--	--	0.0	0.0	--	--	--
	CALANOID, SMALL	--	42.4	8.3	--	13.1	--	--	--	--	23.1	76.4	--	--	--
	CHAETOGNATH	--	0.0	0.1	--	2.0	--	--	--	--	0.0	0.0	--	--	--
	CLADOCERA	--	0.0	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	CNID./CTEN.	--	1.5	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	DECAPOD	--	0.0	0.0	--	0.1	--	--	--	--	0.0	0.0	--	--	--
	DECAPOD LARVAE	--	0.0	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	EUPHAUSIID	--	0.0	0.3	--	8.0	--	--	--	--	53.8	10.9	--	--	--
	FISH	--	0.0	0.0	--	0.1	--	--	--	--	0.0	0.0	--	--	--
	GAMMARID	--	0.0	0.0	--	0.1	--	--	--	--	0.0	0.0	--	--	--
	GASTROPOD	--	0.0	0.2	--	0.1	--	--	--	--	7.7	0.0	--	--	--
	HARPACTICOID	--	0.0	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	HYPERIID	--	3.0	0.2	--	0.9	--	--	--	--	0.0	0.0	--	--	--
	INSECT	--	0.0	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	INVERT. EGGS	--	0.0	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	LARVACEA	--	50.8	47.5	--	2.5	--	--	--	--	0.0	0.0	--	--	--
	MALACOSTRACA	--	0.0	0.1	--	1.0	--	--	--	--	7.7	0.0	--	--	--
	OTHER	--	2.3	36.5	--	1.0	--	--	--	--	7.7	12.7	--	--	--
	POLYCHAETE	--	0.0	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--

Table 3, continued.

	Forage Species	Pacific cod	Prowfish	Pacific Herring	Pacific Tomcod	Walleye Pollock	Sockeye Salmon	Pink Salmon	Chum Salmon	Smooth-tongue	Eulachon	Capelin	Sandlance	Stickle-back	Sandfish
Year/ Month	Prey Category	(110)	(197)	(233)	(250)	(270)	(420)	(440)	(450)	(509)	(511)	(516)	(517)	(660)	(699)
1996	BARNACLE LARVAE	--	--	0.1	0.6	--	--	0.3	1.5	--	--	--	1.7	--	0.0
July	BIVALVE LARVAE	--	--	0.0	0.0	--	--	0.0	0.0	--	--	--	0.0	--	0.0
	BRYOZOAN LARVAE	--	--	0.0	0.0	--	--	0.0	0.0	--	--	--	0.0	--	0.0
	CALANOID, LARGE	--	--	2.4	0.2	--	--	0.8	0.0	--	--	--	0.5	--	0.7
	CALANOID, SMALL	--	--	48.2	31.1	--	--	1.6	0.5	--	--	--	72.6	--	75.0
	CHAETOGNATH	--	--	0.0	0.0	--	--	0.2	0.9	--	--	--	0.0	--	0.0
	CLADOCERA	--	--	0.7	0.5	--	--	0.2	0.0	--	--	--	0.9	--	1.2
	CNID./CTEN.	--	--	0.0	0.0	--	--	0.1	0.2	--	--	--	0.0	--	0.0
	DECAPOD	--	--	0.7	0.6	--	--	0.6	3.1	--	--	--	0.1	--	0.8
	DECAPOD LARVAE	--	--	0.0	0.0	--	--	0.0	0.0	--	--	--	0.0	--	0.0
	EUPHAUSIID	--	--	0.0	0.0	--	--	0.0	0.1	--	--	--	0.2	--	2.5
	FISH	--	--	0.0	0.0	--	--	0.8	0.1	--	--	--	0.0	--	2.2
	GAMMARID	--	--	0.0	0.0	--	--	0.0	0.0	--	--	--	0.0	--	7.3
	GASTROPOD	--	--	0.5	0.5	--	--	1.1	0.0	--	--	--	0.5	--	0.0
	HARPACTICOID	--	--	0.0	0.0	--	--	0.0	0.0	--	--	--	0.0	--	0.0
	HYPERIID	--	--	0.1	0.1	--	--	0.3	17.2	--	--	--	0.0	--	0.0
	INSECT	--	--	0.0	0.1	--	--	0.5	0.5	--	--	--	0.0	--	0.0
	INVERT. EGGS	--	--	0.0	0.0	--	--	0.0	0.0	--	--	--	0.0	--	0.0
	LARVACEA	--	--	45.5	45.8	--	--	87.6	71.2	--	--	--	18.7	--	0.0
	MALACOSTRACA	--	--	0.0	0.0	--	--	0.2	1.2	--	--	--	0.0	--	0.5
	OTHER	--	--	1.7	20.4	--	--	5.8	3.5	--	--	--	4.7	--	9.8
	POLYCHAETE	--	--	0.0	0.0	--	--	0.0	0.0	--	--	--	0.0	--	0.0

Table 4. Grand percent frequency of occurrence of prey in diets of forage fish from Prince William Sound, 1994-96.

	Forage Species	Pacific cod	Prowfish	Pacific Herring	Pacific Tomcod	Walleye Pollock	Sockeye Salmon	Pink Salmon	Chum Salmon	Smooth-tongue	Eulachon	Capelin	Sandlance	Stickle-back	Sandfish
Year/ Month	Prey Category	(110)	(197)	(233)	(250)	(270)	(420)	(440)	(450)	(509)	(511)	(516)	(517)	(660)	(699)
SEA 1994 data															
1994 May	BARNACLE LARVAE	0.0	--	14.6	--	--	--	34.4	4.0	7.3	--	0.0	14.7	0.0	--
	BIVALVE LARVAE	0.0	--	0.0	--	--	--	0.0	0.0	0.0	--	2.4	0.0	0.0	--
	BRYOZOAN LARVAE	0.0	--	0.0	--	--	--	0.0	0.0	0.0	--	0.0	0.0	0.0	--
	CALANOID, LARGE	100.0	--	51.2	--	--	--	68.9	94.0	54.5	--	80.5	76.5	98.8	--
	CALANOID, SMALL	80.0	--	48.8	--	--	--	96.7	38.0	49.1	--	63.4	100.0	52.5	--
	CHAETOGNATH	0.0	--	0.0	--	--	--	0.0	0.0	0.0	--	0.0	0.0	0.0	--
	CLADOCERA	0.0	--	0.0	--	--	--	6.6	0.0	5.5	--	0.0	0.0	0.0	--
	CNID./CTEN.	0.0	--	0.0	--	--	--	0.0	0.0	0.0	--	2.4	0.0	0.0	--
	DECAPOD	0.0	--	2.4	--	--	--	0.0	0.0	0.0	--	2.4	0.0	0.0	--
	DECAPOD LARVAE	10.0	--	2.4	--	--	--	3.3	0.0	0.0	--	12.2	5.9	1.3	--
	EUPHAUSIID	0.0	--	0.0	--	--	--	52.5	16.0	21.8	--	22.0	76.5	2.5	--
	FISH	0.0	--	17.1	--	--	--	3.3	34.0	1.8	--	48.8	8.8	25.0	--
	GAMMARID	0.0	--	0.0	--	--	--	8.2	10.0	0.0	--	2.4	17.6	0.0	--
	GASTROPOD	0.0	--	0.0	--	--	--	29.5	8.0	21.8	--	7.3	0.0	0.0	--
	HARPACTICOID	0.0	--	2.4	--	--	--	49.2	16.0	0.0	--	0.0	17.6	0.0	--
	HYPERIID	0.0	--	0.0	--	--	--	0.0	0.0	5.5	--	58.5	0.0	21.3	--
	INSECT	0.0	--	0.0	--	--	--	0.0	0.0	0.0	--	0.0	0.0	0.0	--
	INVERT. EGGS	10.0	--	4.9	--	--	--	34.4	8.0	3.6	--	0.0	73.5	1.3	--
	LARVACEA	0.0	--	19.5	--	--	--	13.1	42.0	41.8	--	17.1	5.9	58.8	--
	MALACOSTRACA	0.0	--	41.5	--	--	--	0.0	0.0	3.6	--	24.4	35.3	11.3	--
	OTHER	0.0	--	2.4	--	--	--	29.5	48.0	41.8	--	0.0	11.8	6.3	--
	POLYCHAETE	0.0	--	0.0	--	--	--	19.7	16.0	5.5	--	7.3	20.6	1.3	--
June	BARNACLE LARVAE	22.6	--	22.6	24.0	5.2	9.9	35.7	39.6	--	--	0.0	47.5	--	--
	BIVALVE LARVAE	17.9	--	35.1	25.3	5.6	20.4	58.6	47.7	--	--	3.1	42.5	--	--
	BRYOZOAN LARVAE	0.0	--	0.0	0.0	0.0	0.0	0.0	0.0	--	--	0.0	0.0	--	--
	CALANOID, LARGE	54.8	--	34.1	48.1	55.2	12.7	32.0	43.2	--	--	65.6	85.8	--	--
	CALANOID, SMALL	92.9	--	45.6	87.0	88.5	28.2	80.7	55.0	--	--	78.1	99.2	--	--
	CHAETOGNATH	0.0	--	0.0	0.0	0.0	0.0	0.0	0.0	--	--	0.0	0.0	--	--
	CLADOCERA	63.1	--	33.3	67.5	50.4	45.3	68.4	63.1	--	--	25.0	79.2	--	--
	CNID./CTEN.	0.0	--	0.0	0.0	0.0	0.0	0.0	0.0	--	--	0.0	0.0	--	--
	DECAPOD	9.5	--	2.4	3.9	0.0	12.2	0.8	3.6	--	--	0.0	5.0	--	--
	DECAPOD LARVAE	17.9	--	18.7	27.9	4.0	27.1	8.6	22.5	--	--	12.5	30.0	--	--
	EUPHAUSIID	22.6	--	13.7	22.1	21.4	10.5	20.9	18.9	--	--	31.3	69.2	--	--
	FISH	7.1	--	8.7	19.5	2.0	43.6	10.7	25.2	--	--	3.1	33.3	--	--
	GAMMARID	35.7	--	0.4	10.4	0.8	0.0	5.7	9.9	--	--	0.0	17.5	--	--
	GASTROPOD	53.6	--	40.1	46.1	5.2	81.8	78.3	77.5	--	--	3.1	65.8	--	--
	HARPACTICOID	58.3	--	4.2	20.8	1.2	3.9	25.8	9.0	--	--	3.1	38.3	--	--
	HYPERIID	6.0	·	11.3	7.8	2.4	7.2	3.3	3.6	--	--	3.1	4.2	--	--
	INSECT	0.0	--	0.0	0.0	0.0	0.0	0.0	0.0	--	--	0.0	0.0	--	--
	INVERT. EGGS	46.4	--	18.3	58.4	57.9	5.0	36.5	22.5	--	--	25.0	90.0	--	--
	LARVACEA	19.0	--	24.4	37.7	4.8	22.7	63.9	39.6	--	--	3.1	72.5	--	--
	MALACOSTRACA	15.5	--	18.7	17.5	5.2	9.9	5.7	4.5	--	--	21.9	27.5	--	--
	OTHER	17.9	--	27.4	20.1	1.2	17.7	53.7	68.5	--	--	3.1	65.0	--	--
	POLYCHAETE	4.8	--	0.6	3.9	0.0	2.8	10.7	21.6	--	--	0.0	53.3	--	--

Table 4, continued.

	Forage Species	Pacific cod	Prowfish	Pacific Herring	Pacific Tomcod	Walleye Pollock	Sockeye Salmon	Pink Salmon	Chum Salmon	Smooth-tongue	Eulachon	Capelin	Sandlance	Stickle-back	Sandfish
Year/ Month	Prey Category	(110)	(197)	(233)	(250)	(270)	(420)	(440)	(450)	(509)	(511)	(516)	(517)	(660)	(699)
July	BARNACLE LARVAE	31.1	--	30.6	40.5	6.3	--	30.5	0.0	--	--	0.0	71.1	--	--
	BIVALVE LARVAE	11.1	--	16.7	22.5	3.9	--	37.7	0.0	--	--	13.3	70.0	--	--
	BRYOZOAN LARVAE	0.0	--	0.0	0.0	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
	CALANOID, LARGE	70.0	--	22.2	63.5	57.8	--	46.1	16.7	--	--	60.0	87.8	--	--
	CALANOID, SMALL	88.9	--	38.9	91.5	79.1	--	79.9	0.0	--	--	66.7	98.9	--	--
	CHAETOGNATH	0.0	--	0.0	0.0	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
	CLADOCERA	40.0	--	8.3	43.0	22.8	--	46.8	0.0	--	--	0.0	73.3	--	--
	CNID./CTEN.	2.2	--	0.0	0.0	0.5	--	0.0	0.0	--	--	0.0	0.0	--	--
	DECAPOD	18.9	--	8.3	11.0	0.5	--	3.2	0.0	--	--	0.0	3.3	--	--
	DECAPOD LARVAE	25.6	--	19.4	28.0	5.8	--	17.5	0.0	--	--	0.0	23.3	--	--
	EUPHAUSIID	20.0	--	19.4	33.0	36.9	--	22.7	0.0	--	--	53.3	43.3	--	--
	FISH	3.3	--	8.3	9.5	1.0	--	5.2	16.7	--	--	0.0	8.9	--	--
	GAMMARID	41.1	--	0.0	15.5	1.5	--	3.2	0.0	--	--	0.0	2.2	--	--
	GASTROPOD	70.0	--	30.6	66.0	17.5	--	68.8	83.3	--	--	0.0	83.3	--	--
	HARPACTICOID	80.0	--	16.7	28.0	6.8	--	13.6	0.0	--	--	0.0	23.3	--	--
	HYPERIID	17.8	--	13.9	26.5	12.6	--	17.5	0.0	--	--	0.0	16.7	--	--
	INSECT	0.0	--	0.0	0.0	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
	INVERT. EGGS	42.2	--	13.9	36.5	65.0	--	36.4	0.0	--	--	6.7	90.0	--	--
	LARVACEA	17.8	--	19.4	74.0	32.0	--	90.3	100.0	--	--	20.0	97.8	--	--
	MALACOSTRACA	44.4	--	16.7	34.0	16.5	--	18.2	0.0	--	--	46.7	33.3	--	--
	OTHER	42.2	--	13.9	15.0	6.3	--	26.6	0.0	--	--	0.0	35.6	--	--
	POLYCHAETE	7.8	--	2.8	5.5	1.9	--	4.5	0.0	--	--	0.0	17.8	--	--
August	BARNACLE LARVAE	--	--	2.6	37.5	4.2	0.0	8.8	22.0	--	--	0.0	0.0	--	--
	BIVALVE LARVAE	--	--	5.3	0.0	0.0	0.0	2.9	0.0	--	--	0.0	0.0	--	--
	BRYOZOAN LARVAE	--	--	0.0	0.0	0.0	0.0	0.0	0.0	--	--	--	--	--	--
	CALANOID, LARGE	--	--	43.4	18.8	66.7	0.0	47.1	46.3	--	--	--	--	--	--
	CALANOID, SMALL	--	--	44.7	25.0	100.0	0.0	11.8	39.0	--	--	--	--	--	--
	CHAETOGNATH	--	--	0.0	0.0	0.0	0.0	0.0	0.0	--	--	--	--	--	--
	CLADOCERA	--	--	28.9	50.0	12.5	0.0	14.7	31.7	--	--	--	--	--	--
	CNID./CTEN.	--	--	0.0	6.3	0.0	0.0	20.6	82.9	--	--	--	--	--	--
	DECAPOD	--	--	0.0	12.5	0.0	0.0	44.1	4.9	--	--	--	--	--	--
	DECAPOD LARVAE	--	--	32.9	12.5	33.3	0.0	11.8	4.9	--	--	--	--	--	--
	EUPHAUSIID	--	--	14.5	0.0	33.3	0.0	8.8	7.3	--	--	--	--	--	--
	FISH	--	--	5.3	25.0	8.3	0.0	11.8	7.3	--	--	--	--	--	--
	GAMMARID	--	--	1.3	6.3	0.0	0.0	0.0	0.0	--	--	--	--	--	--
	GASTROPOD	--	--	14.5	18.8	25.0	0.0	11.8	22.0	--	--	--	--	--	--
	HARPACTICOID	--	--	3.9	37.5	0.0	0.0	2.9	0.0	--	--	--	--	--	--
	HYPERIID	--	--	36.8	25.0	50.0	0.0	58.8	24.4	--	--	--	--	--	--
	INSECT	--	--	0.0	0.0	0.0	0.0	0.0	0.0	--	--	--	--	--	--
	INVERT. EGGS	--	--	13.2	12.5	58.3	0.0	0.0	4.9	--	--	--	--	--	--
	LARVACEA	--	--	42.1	50.0	50.0	0.0	73.5	46.3	--	--	--	--	--	--
	MALACOSTRACA	--	--	19.7	12.5	8.3	0.0	17.6	2.4	--	--	--	--	--	--
	OTHER	--	--	10.5	37.5	4.2	0.0	14.7	12.2	--	--	--	--	--	--
	POLYCHAETE	--	--	1.3	43.8	4.2	0.0	0.0	0.0	--	--	--	--	--	--

Table 4, continued.

	Forage Species	Pacific cod	Prowfish	Pacific Herring	Pacific Tomcod	Walleye Pollock	Sockeye Salmon	Pink Salmon	Chum Salmon	Smooth-tongue	Eulachon	Capelin	Sandlance	Stickle-back	Sandfish
Year/ Month	Prey Category	(110)	(197)	(233)	(250)	(270)	(420)	(440)	(450)	(509)	(511)	(516)	(517)	(660)	(699)
September	BARNACLE LARVAE	0.0	--	10.8	7.1	11.1	--	11.1	5.8	--	--	--	58.3	--	--
	BIVALVE LARVAE	30.8	--	11.0	0.0	1.0	--	0.0	0.8	--	--	--	41.7	--	--
	BRYOZOAN LARVAE	0.0	--	0.0	0.0	0.0	--	0.0	0.0	--	--	--	0.0	--	--
	CALANOID, LARGE	7.7	--	42.9	21.4	46.5	--	80.6	22.3	--	--	--	66.7	--	--
	CALANOID, SMALL	46.2	--	56.0	42.9	74.2	--	30.6	24.0	--	--	--	100.0	--	--
	CHAETOGNATH	0.0	--	0.0	0.0	0.0	--	0.0	0.0	--	--	--	0.0	--	--
	CLADOCERA	0.0	--	25.6	7.1	10.6	--	5.6	15.7	--	--	--	41.7	--	--
	CNID./CTEN.	0.0	--	1.7	0.0	0.5	--	8.3	81.8	--	--	--	0.0	--	--
	DECAPOD	7.7	--	5.2	7.1	5.1	--	27.8	9.1	--	--	--	8.3	--	--
	DECAPOD LARVAE	30.8	--	20.8	14.3	5.1	--	44.4	4.1	--	--	--	75.0	--	--
	EUPHAUSIID	38.5	--	38.8	0.0	33.8	--	44.4	17.4	--	--	--	100.0	--	--
	FISH	7.7	--	2.7	21.4	6.1	--	61.1	14.0	--	--	--	0.0	--	--
	GAMMARID	38.5	--	0.6	71.4	2.0	--	11.1	3.3	--	--	--	8.3	--	--
	GASTROPOD	0.0	--	27.1	21.4	27.3	--	13.9	5.0	--	--	--	66.7	--	--
	HARPACTICOID	53.8	--	6.5	21.4	4.5	--	0.0	0.0	--	--	--	8.3	--	--
	HYPERIID	15.4	--	25.8	14.3	20.7	--	55.6	23.1	--	--	--	16.7	--	--
	INSECT	0.0	--	0.0	0.0	0.0	--	0.0	0.0	--	--	--	0.0	--	--
	INVERT. EGGS	0.0	--	23.1	21.4	36.4	--	0.0	5.8	--	--	--	83.3	--	--
	LARVACEA	0.0	--	51.3	64.3	54.0	--	52.8	24.8	--	--	--	100.0	--	--
	MALACOSTRACA	30.8	--	31.7	14.3	21.7	--	27.8	12.4	--	--	--	91.7	--	--
	OTHER	38.5	--	6.9	14.3	7.1	--	38.9	10.7	--	--	--	8.3	--	--
	POLYCHAETE	7.7	--	3.1	0.0	1.0	--	2.8	0.0	--	--	--	0.0	--	--
APEX 94-96 data															
1994	BARNACLE LARVAE	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--
November	BIVALVE LARVAE	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--
	BRYOZOAN LARVAE	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--
	CALANOID, LARGE	--	--	18.0	--	56.7	--	--	--	--	0.0	--	--	--	--
	CALANOID, SMALL	--	--	76.0	--	70.0	--	--	--	--	0.0	--	--	--	--
	CHAETOGNATH	--	--	8.0	--	16.7	--	--	--	--	0.0	--	--	--	--
	CLADOCERA	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--
	CNID./CTEN.	--	--	0.0	--	13.3	--	--	--	--	0.0	--	--	--	--
	DECAPOD	--	--	0.0	--	6.7	--	--	--	--	0.0	--	--	--	--
	DECAPOD LARVAE	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--
	EUPHAUSIID	--	--	30.0	--	53.3	--	--	--	--	10.0	--	--	--	--
	FISH	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--
	GAMMARID	--	--	2.0	--	6.7	--	--	--	--	0.0	--	--	--	--
	GASTROPOD	--	--	32.0	--	6.7	--	--	--	--	0.0	--	--	--	--
	HARPACTICOID	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--
	HYPERIID	--	--	8.0	--	23.3	--	--	--	--	0.0	--	--	--	--
	INSECT	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--
	INVERT. EGGS	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--
	LARVACEA	--	--	58.0	--	83.3	--	--	--	--	0.0	--	--	--	--
	MALACOSTRACA	--	--	6.0	--	0.0	--	--	--	--	10.0	--	--	--	--
	OTHER	--	--	46.0	--	36.7	--	--	--	--	0.0	--	--	--	--
	POLYCHAETE	--	--	0.0	--	0.0	--	--	--	--	0.0	--	--	--	--

Table 4, continued.

	Forage Species	Pacific cod	Prowfish	Pacific Herring	Pacific Tomcod	Walleye Pollock	Sockeye Salmon	Pink Salmon	Chum Salmon	Smooth-tongue	Eulachon	Capelin	Sandlance	Stickle-back	Sandfish
Year/ Month	Prey Category	(110)	(197)	(233)	(250)	(270)	(420)	(440)	(450)	(509)	(511)	(516)	(517)	(660)	(699)
1995	BARNACLE LARVAE	--	6.7	25.7	10.0	2.5	--	13.6	0.0	--	--	0.0	48.4	--	--
July	BIVALVE LARVAE	--	0.0	0.0	0.0	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
	BRYOZOAN LARVAE	--	0.0	1.4	0.0	0.0	--	9.1	0.0	--	--	0.0	0.0	--	--
	CALANOID, LARGE	--	0.0	37.1	40.0	45.0	--	95.5	50.0	--	--	0.0	58.1	--	--
	CALANOID, SMALL	--	93.3	80.0	70.0	79.4	--	95.5	100.0	--	--	24.7	64.5	--	--
	CHAETOGNATH	--	6.7	0.0	0.0	17.5	--	40.9	100.0	--	--	0.0	0.0	--	--
	CLADOCERA	--	46.7	52.9	30.0	11.9	--	18.2	0.0	--	--	0.0	45.2	--	--
	CNID./CTEN.	--	20.0	0.0	0.0	0.6	--	0.0	0.0	--	--	0.0	0.0	--	--
	DECAPOD	--	0.0	48.6	0.0	4.4	--	50.0	50.0	--	--	0.0	3.2	--	--
	DECAPOD LARVAE	--	0.0	0.0	0.0	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
	EUPHAUSIID	--	0.0	35.7	20.0	15.0	--	63.6	50.0	--	--	0.0	9.7	--	--
	FISH	--	0.0	1.4	30.0	2.5	--	50.0	50.0	--	--	0.0	0.0	--	--
	GAMMARID	--	0.0	0.0	100.0	0.6	--	4.5	0.0	--	--	0.0	0.0	--	--
	GASTROPOD	--	66.7	50.0	0.0	40.0	--	90.9	100.0	--	--	1.1	22.6	--	--
	HARPACTICOID	--	0.0	0.0	0.0	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
	HYPERIID	--	93.3	58.6	0.0	34.4	--	77.3	100.0	--	--	0.0	3.2	--	--
	INSECT	--	0.0	0.0	10.0	0.0	--	22.7	0.0	--	--	0.0	0.0	--	--
	INVERT. EGGS	--	0.0	0.0	0.0	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
	LARVACEA	--	86.7	31.4	0.0	57.5	--	36.4	100.0	--	--	0.0	48.4	--	--
	MALACOSTRACA	--	6.7	28.6	20.0	15.0	--	22.7	0.0	--	--	0.0	0.0	--	--
	OTHER	--	53.3	68.6	100.0	49.4	--	36.4	0.0	--	--	4.5	64.5	--	--
	POLYCHAETE	--	0.0	0.0	0.0	0.0	--	0.0	0.0	--	--	0.0	0.0	--	--
October	BARNACLE LARVAE	--	0.0	0.0	--	1.0	--	--	--	--	0.0	0.0	--	--	--
	BIVALVE LARVAE	--	0.0	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	BRYOZOAN LARVAE	--	0.0	12.5	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	CALANOID, LARGE	--	0.0	50.0	--	75.0	--	--	--	--	0.0	0.0	--	--	--
	CALANOID, SMALL	--	100.0	82.5	--	62.0	--	--	--	--	5.0	17.5	--	--	--
	CHAETOGNATH	--	0.0	25.0	--	26.0	--	--	--	--	0.0	0.0	--	--	--
	CLADOCERA	--	0.0	2.5	--	2.0	--	--	--	--	0.0	0.0	--	--	--
	CNID./CTEN.	--	100.0	0.0	--	1.0	--	--	--	--	0.0	0.0	--	--	--
	DECAPOD	--	0.0	5.0	--	3.0	--	--	--	--	0.0	0.0	--	--	--
	DECAPOD LARVAE	--	0.0	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	EUPHAUSIID	--	0.0	35.0	--	47.0	--	--	--	--	35.0	10.0	--	--	--
	FISH	--	0.0	0.0	--	3.0	--	--	--	--	0.0	0.0	--	--	--
	GAMMARID	--	0.0	2.5	--	7.0	--	--	--	--	0.0	0.0	--	--	--
	GASTROPOD	--	0.0	25.0	--	4.0	--	--	--	--	5.0	0.0	--	--	--
	HARPACTCOID	--	0.0	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	HYPERIID	--	100.0	37.5	--	28.0	--	--	--	--	0.0	0.0	--	--	--
	INSECT	--	0.0	2.5	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	INVERT. EGGS	--	0.0	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--
	LARVACEA	--	100.0	70.0	--	26.0	--	--	--	--	0.0	0.0	--	--	--
	MALACOSTRACA	--	0.0	25.0	--	17.0	--	--	--	--	5.0	0.0	--	--	--
	OTHER	--	100.0	67.5	--	31.0	--	--	--	--	5.0	5.0	--	--	--
	POLYCHAETE	--	0.0	0.0	--	0.0	--	--	--	--	0.0	0.0	--	--	--

Table 4, continued.

	Forage Species	Pacific cod	Prowfish	Pacific Herring	Pacific Tomcod	Walleye Pollock	Sockeye Salmon	Pink Salmon	Chum Salmon	Smooth-tongue	Eulachon	Capelin	Sandlance	Stickle-back	Sandfish
Year/ Month	Prey Category	(110)	(197)	(233)	(250)	(270)	(420)	(440)	(450)	(509)	(511)	(516)	(517)	(660)	(699)
1996	BARNACLE LARVAE	--	--	22.5	30.0	--	--	11.0	10.0	--	--	--	54.5	--	0.0
July	BIVALVE LARVAE	--	--	0.0	0.0	--	--	0.0	0.0	--	--	--	0.0	--	0.0
	BRYOZOAN LARVAE	--	--	0.6	3.3	--	--	0.0	0.0	--	--	--	0.5	--	0.0
	CALANOID, LARGE	--	--	18.0	26.7	--	--	33.0	0.0	--	--	--	16.4	--	9.1
	CALANOID, SMALL	--	--	87.6	73.3	--	--	53.0	30.0	--	--	--	77.8	--	27.3
	CHAETOGNATH	--	--	6.2	0.0	--	--	22.0	50.0	--	--	--	0.5	--	0.0
	CLADOCERA	--	--	52.8	33.3	--	--	19.0	0.0	--	--	--	45.5	--	9.1
	CNID./CTEN.	--	--	0.6	0.0	--	--	7.0	20.0	--	--	--	0.0	--	0.0
	DECAPOD	--	--	24.2	23.3	--	--	21.0	40.0	--	--	--	5.3	--	27.3
	DECAPOD LARVAE	--	--	0.0	0.0	--	--	0.0	0.0	--	--	--	0.0	--	0.0
	EUPHAUSIID	--	--	9.0	6.7	--	--	8.0	10.0	--	--	--	7.4	--	18.2
	FISH	--	--	0.6	0.0	--	--	25.0	10.0	--	--	--	2.1	--	100.0
	GAMMARID	--	--	2.2	3.3	--	--	3.0	0.0	--	--	--	3.2	--	45.5
	GASTROPOD	--	--	43.8	40.0	--	--	41.0	0.0	--	--	--	39.2	--	0.0
	HARPACTICOID	--	--	0.0	0.0	--	--	0.0	0.0	--	--	--	0.0	--	0.0
	HYPERIID	--	--	12.4	10.0	--	--	23.0	60.0	--	--	--	1.1	--	0.0
	INSECT	--	--	0.0	10.0	--	--	20.0	50.0	--	--	--	1.1	--	0.0
	INVERT. EGGS	--	--	0.0	0.0	--	--	0.0	0.0	--	--	--	0.0	--	0.0
	LARVACEA	--	--	71.9	93.3	--	--	83.0	50.0	--	--	--	55.6	--	0.0
	MALACOSTRACA	--	--	7.3	0.0	--	--	11.0	30.0	--	--	--	0.0	--	9.1
	OTHER	--	--	61.8	73.3	--	--	45.0	20.0	--	--	--	69.3	--	36.4
	POLYCHAETE	--	--	0.0	0.0	--	--	0.0	0.0	--	--	--	0.0	--	0.0

Table 5. Diet overlap (PSI) between forage fish species in Prince William Sound, Alaska, by month in 1994. Values are based on pooled biomass of prey categories for each forage species. An 'x' represents no data available.

May, 1994

	Pacific cod	Pacific Herring	Pacific Tomcod	Pollock	Sockeye Salmon	Pinks Salmon	Chum Salmon	Smooth-tongue	Eulachon	Capelin	Sandlance	Stickle-back
Pacific cod	--	49	X	X	X	38	14	46	X	14	84	50
Pacific Herring		--	X	X	X	42	19	59	X	24	54	58
Pacific Tomcod			--	X	X	X	X	X	X	X	X	X
Pollock				--	X	X	X	X	X	X	X	X
Sockeye Salmon					--	X	X	X	X	X	X	X
Pink Salmon						--	39	69	X	43	47	62
Chum Salmon							--	31	X	75	17	53
Smoothtongue								--	X	45	52	73
Eulachon									--	X	X	X
Capelin										--	20	64
Sandlance											--	55
Stickleback												--

June, 1994

	Pacific cod	Pacific Herring	Pacific Tomcod	Pollock	Sockeye Salmon	Pinks Salmon	Chum Salmon	Smooth-tongue	Eulachon	Capelin	Sandlance	Stickle-back
Pacific cod	--	66	39	66	25	54	36	X	X	60	41	X
Pacific Herring		--	27	65	19	39	28	X	X	63	33	X
Pacific Tomcod			--	28	80	46	85	X	X	36	87	X
Pollock				--	18	49	26	X	X	84	37	X
Sockeye Salmon					--	49	85	X	X	28	76	X
Pink Salmon						--	53	X	X	46	54	X
Chum Salmon							--	X	X	37	84	X
Smoothtongue								--	X	X	X	X
Eulachon									--	X	X	X
Capelin										--	39	X
Sandlance											--	X
Stickleback												--

July, 1994

	Pacific cod	Pacific Herring	Pacific Tomcod	Pollock	Sockeye Salmon	Pinks Salmon	Chum Salmon	Smooth-tongue	Eulachon	Capelin	Sandlance	Stickle-back
Pacific cod	--	57	61	44	X	65	18	X	X	34	37	X
Pacific Herring		--	68	42	X	56	32	X	X	54	33	X
Pacific Tomcod			--	53	X	60	27	X	X	31	48	X
Pollock				--	X	32	4	X	X	33	81	X
Sockeye Salmon					--	X	X	X	X	X	X	X
Pink Salmon						--	46	X	X	17	37	X
Chum Salmon							--	X	X	0	6	X
Smoothtongue								--	X	X	X	X
Eulachon									--	X	X	X
Capelin										--	22	X
Sandlance											--	X
Stickleback												--

Table 5, continued.

August, 1994

	Pacific cod	Pacific Herring	Pacific Tomcod	Pollock	Sockeye Salmon	Pinks Salmon	Chum Salmon	Smooth-tongue	Eulachon	Capelin	Sandlance	Stickle-back
Pacific cod	--	X	X	X	X	X	X	X	X	X	X	X
Pacific Herring		--	19	38	X	41	73	X	X	X	X	X
Pacific Tomcod			--	29	X	66	16	X	X	X	X	X
Pollock				--	X	38	24	X	X	X	X	X
Sockeye Salmon					--	X	X	X	X	X	X	X
Pink Salmon						--	41	X	X	X	X	X
Chum Salmon							--	X	X	X	X	X
Smoothtongue								--	X	X	X	X
Eulachon									--	X	X	X
Capelin										--	X	X
Sandlance											--	X
Stickle--back												--

September, 1994

	Pacific cod	Pacific Herring	Pacific Tomcod	Pollock	Sockeye Salmon	Pinks Salmon	Chum Salmon	Smooth-tongue	Eulachon	Capelin	Sandlance	Stickle-back
Pacific cod	--	40	13	12	X	13	32	X	X	X	33	X
Pacific Herring		--	25	41	X	38	59	X	X	X	70	X
Pacific Tomcod			--	75	X	48	52	X	X	X	15	X
Pollock				--	X	49	56	X	X	X	34	X
Sockeye Salmon					--	X	X	X	X	X	X	X
Pink Salmon						--	67	X	X	X	43	X
Chum Salmon							--	X	X	X	42	X
Smoothtongue								--	X	X	X	X
Eulachon									--	X	X	X
Capelin										--	X	X
Sandlance											--	X
Stickleback												--

November, 1994

	Pacific cod	Pacific Herring	Pacific Tomcod	Pollock	Sockeye Salmon	Pinks Salmon	Chum Salmon	Smooth-tongue	Eulachon	Capelin	Sandlance	Stickle-back
Pacific cod	--	X	X	X	X	X	X	X	X	X	X	X
Pacific Herring		--	X	71	X	X	X	X	47	X	X	X
Pacific Tomcod			--	X	X	X	X	X	X	X	X	X
Pollock				--	X	X	X	X	46	X	X	X
Sockeye Salmon					--	X	X	X	X	X	X	X
Pink Salmon						--	X	X	X	X	X	X
Chum Salmon							--	X	X	X	X	X
Smoothtongue								--	X	X	X	X
Eulachon									--	X	X	X
Capelin										--	X	X
Sandlance											--	X
Stickleback												--

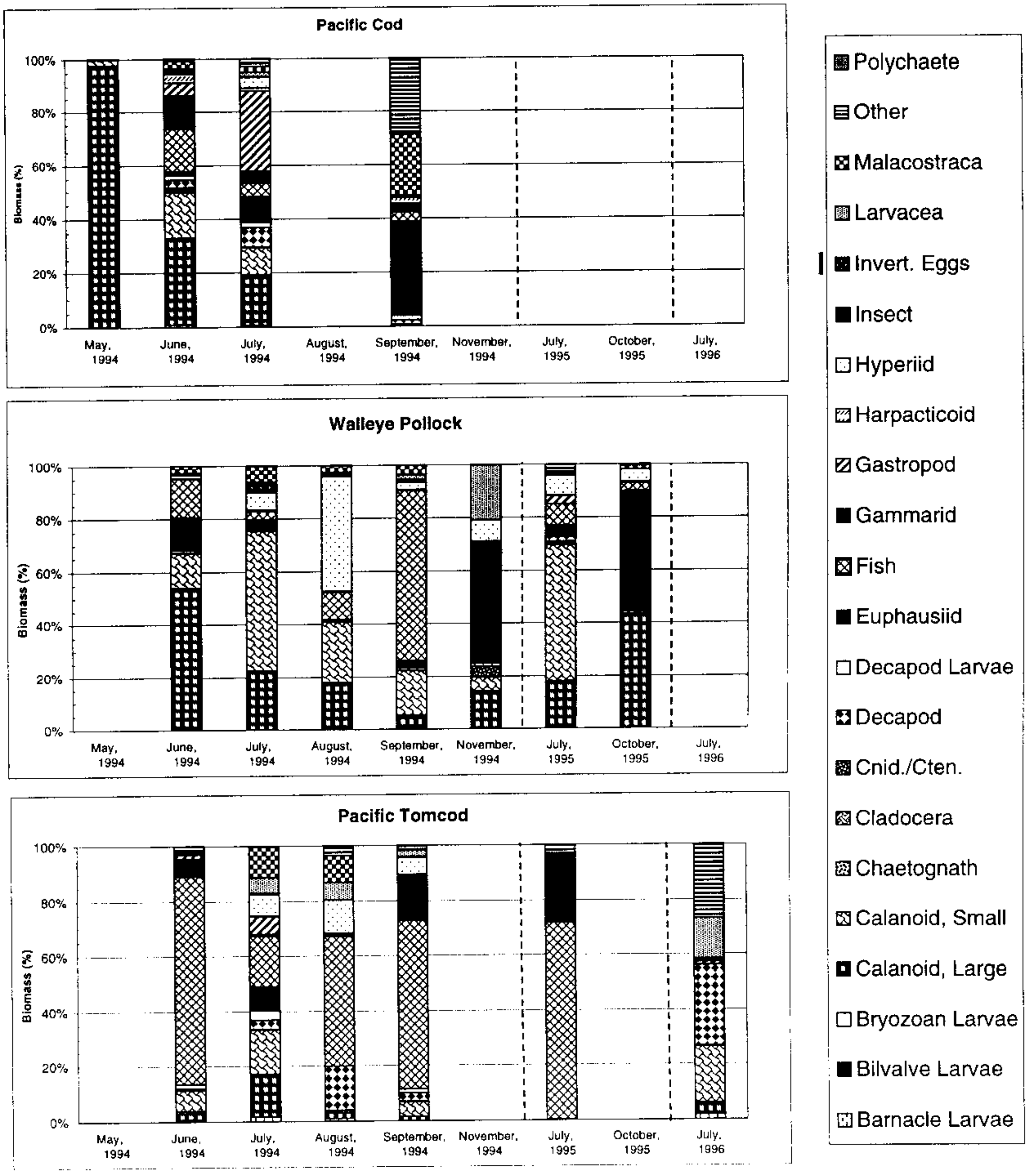

Figure 1. Monthly diet composition (grand percent biomass of prey categories) of forage species in PWS, 1994-1996. Legend is the same for all graphics. Dashed lines separate the years. See also Tables 1-4.

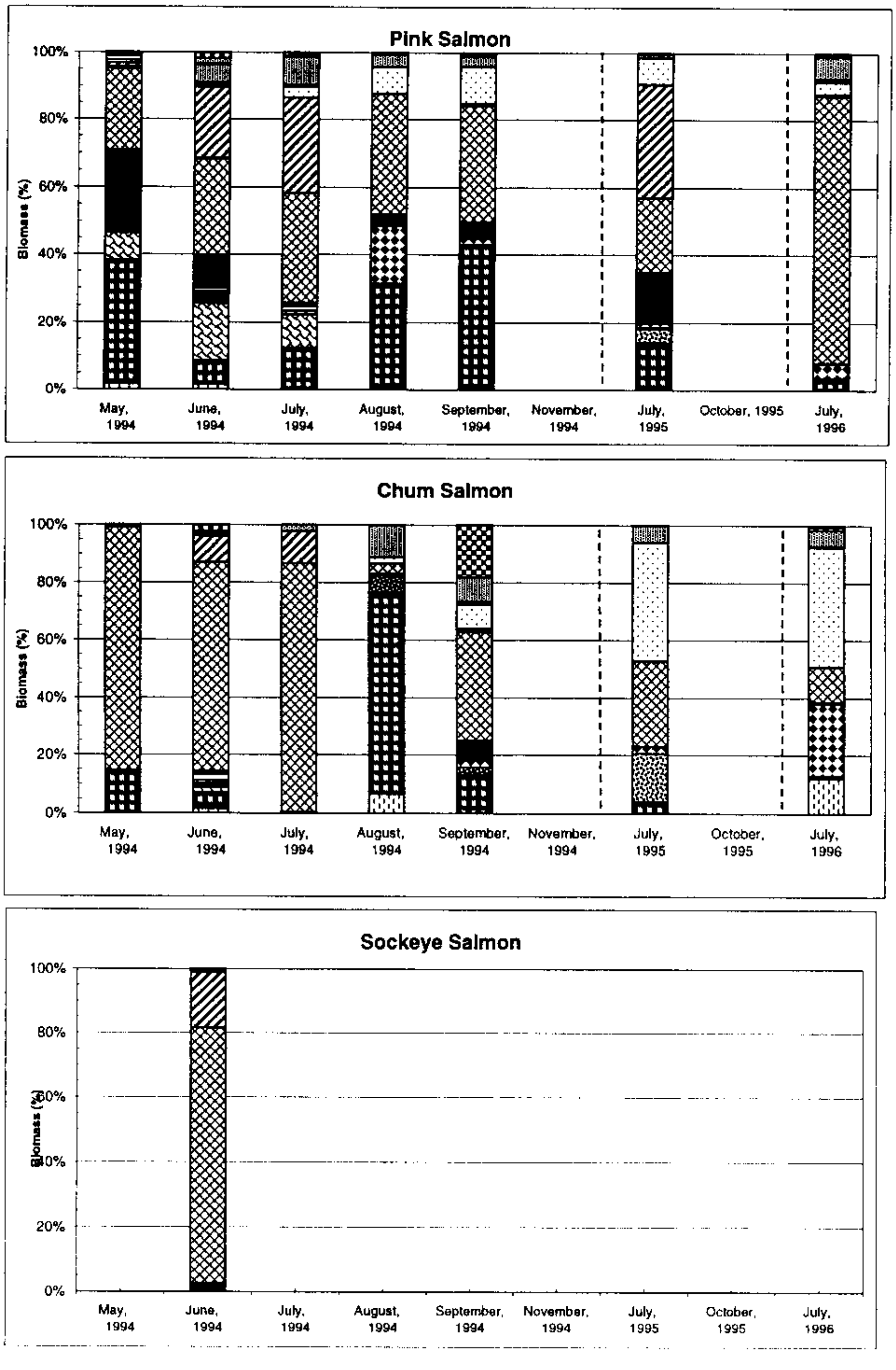

Figure 1, continued.

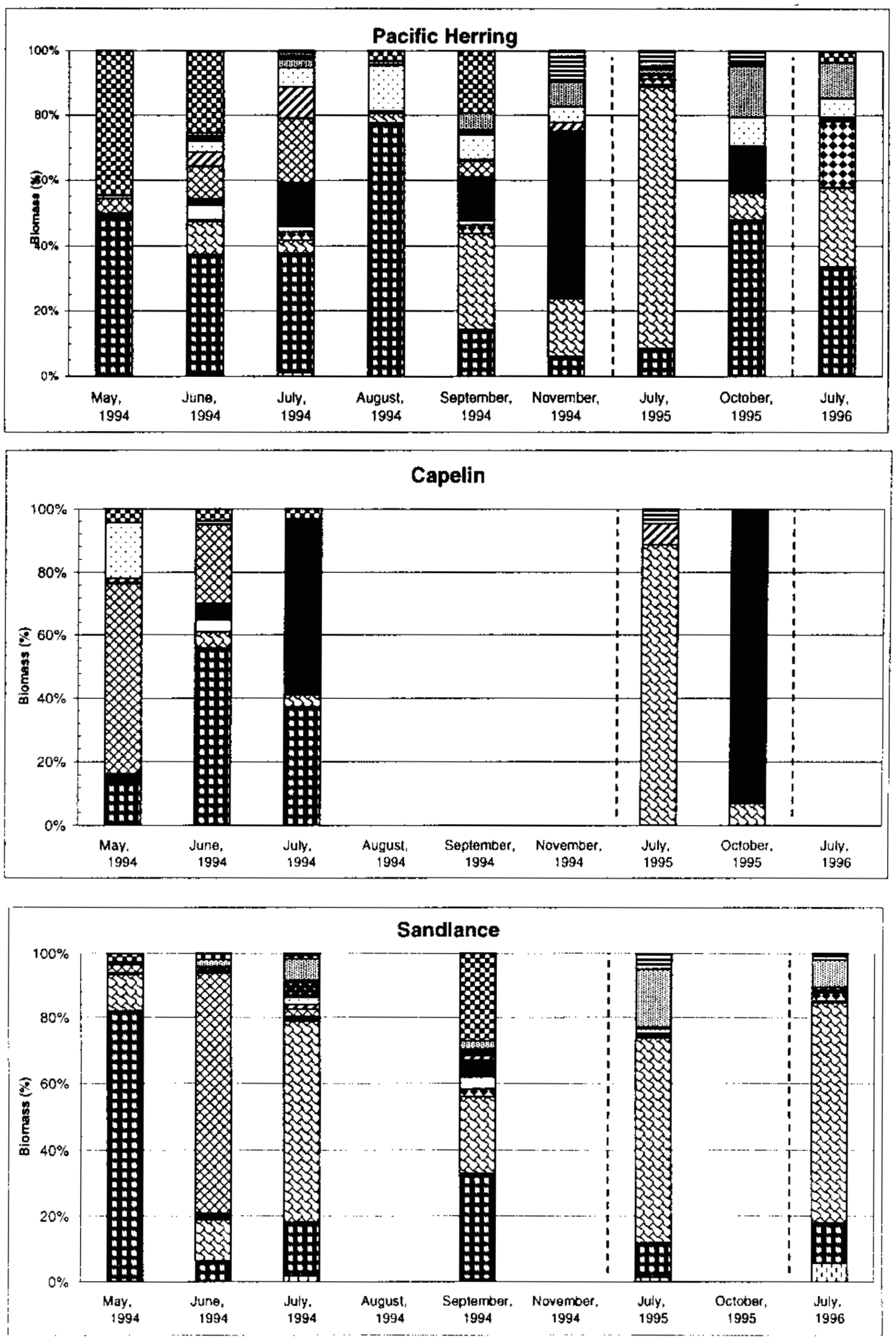

Figure 1, continued.

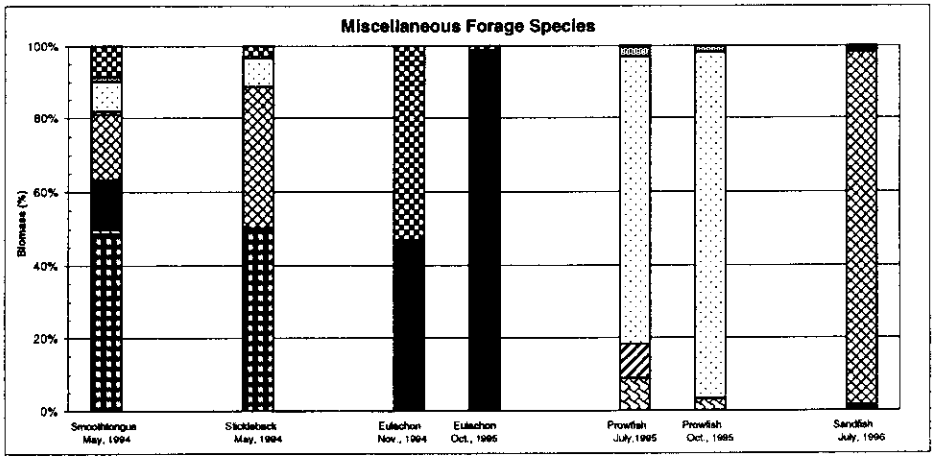

Figure 1, continued.

Chapter 2. Feeding, Prey Fields and Potential Competition of Young-of-the-Year Walleye Pollock (*Theragra chalcogramma*) and Pacific Herring (*Clupea harengus*) in Prince William Sound, Alaska in Summer and Autumn

Authors: Molly V. Sturdevant, Audra L. J. Brase, and Leland B. Hulbert

Abstract - Chapter 2

Diets of young-of-the-year (YOY) walleye pollock (*Theragra chalcogramma*) and Pacific herring (*Clupea pallasi*) were compared between summer, early autumn and late autumn seasons and between autumn allopatric and sympatric fish aggregations in Prince William Sound (PWS), Alaska. Stomach samples were collected principally by mid-water trawl in the northeastern, central and southwestern regions of the sound during July 20-August 12, 1995, October 5-14, 1995 and November 7-13, 1994. Zooplankton samples were collected concurrently in vertical tows (303 μm mesh in summer and 243 μm mesh in early autumn) to characterize seasonal changes in prey fields and to assess prey selection.

Diets of YOY pollock and herring were principally composed of small calanoids in summer and of large calanoids, larvaceans and euphausiids in autumn. The seasonal diet shift to larger prey coincided with larger fish size and with decreased abundance and proportions of the principal zooplankter, small calanoids, and increased abundance and proportions of large calanoids and larvaceans in zooplankton tows. This change in prey was accompanied by trends toward decreased feeding in autumn compared to summer. All measures of food quantity declined for herring from early to late autumn and %BW declined for pollock from summer to late autumn. Herring and pollock in summer allopatric aggregations exhibited a high degree of diet overlap ($R_o > 0.76$). Diet overlap between sympatric species was higher and more consistent in late autumn ($R_o \leq 0.94$) than in early autumn ($R_o \leq 0.69$), when the quantity of food consumed was significantly greater (ANOVA, $p < 0.05$) for both species. Differences in prey selection between allopatric and sympatric herring could have been related to sampling time, depth or diel feeding rhythms, but could not be attributed to size or sympatry alone. The similarity in diets of both allopatric and sympatric YOY pollock and herring, which are important in commercial fisheries and as forage for marine birds and mammals, indicate potential for competitive interactions that may have contributed to changes in their population structures and changes in rates of predation on them observed since the late 1970's.

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Table 1. Characteristics of summer and autumn sampling stations where YOY Pacific herring and walleye pollock were collected in 1994 and 1995 from Prince William Sound, Alaska. Abbreviations: T = Trawl, D = Dipnet, B = beach seine, NE = Northeast, C = Central, SW = Southwest. Ten fish per species were examined from each station. Zooplankton were collected at most fishing stations only in 1995; numbers in parentheses indicate adjacent stations substituted when zooplankton were not collected.

Table 2. Size and feeding attributes for allopatric and sympatric YOY walleye pollock and Pacific herring (n = 10 each) from PWS stations in summer, 1995 and autumns, 1994-1995. Standard error of the means (SE) in parentheses. Abbreviations as in Table 1.

Table 3. Seasonal fish size and feeding attributes (mean and SE) of YOY walleye pollock and Pacific herring from Prince William Sound in 1994-1995. Measures for autumn allopatric (Allo.) and sympatric (Symp.) subgroups are shown for each species.

Table 4. Horn's Overlap Index values for total numbers and biomass of prey consumed by YOY walleye pollock and Pacific herring caught separately in summer and together in early and late autumn in Prince William Sound, 1994-1995. No summer sympatric fish were available and autumn allopatric fish were not caught in the same year. Overlap greater than 0.60 indicates similar diets (see text).

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Introduction - Chapter 2

"Forage fishes are abundant, schooling fishes preyed upon by many species of seabirds, marine mammals, and other fish species. They provide important ecosystem functions by transferring energy from primary or secondary producers to higher trophic levels," (Springer and Speckman, 1997). Walleye Pollock (*Theragra chalcogramma*) and Pacific herring (*Clupea pallasi*) are two members of forage fish communities inhabiting the northeastern Pacific Ocean rim. The roles of these and other species have been studied in the course of damage assessment and ecosystem investigations in Prince William Sound in the years since the March, 1989 *Exxon Valdez* oil spill (Brown et. al, 1996). Although a number of planktivorous species inhabit PWS, pollock and herring are conspicuous for several reasons. Both species support important commercial fisheries as recruited adults in various areas of the Gulf of Alaska, both are important components of marine bird and mammal diets, and historical data show dramatic changes in both their populations (Springer, 1992; Anderson et. al, 1997; Bechtol, 1997). Young-of-the-year (YOY) walleye pollock and YOY Pacific herring are found at the same depths and locations during at least part of the year (Brodeur and Wilson, 1996; Willette et al., 1997; Stokesbury et al., 1998) and both consume zooplankton as their primary prey (Boldt, 1997; Willette at al., 1997; Foy and Norcross, 1998). Because of these similarities and because the frequency and nature of species interactions may be affected as fish populations shift, an investigation of the potential for competition between these two species is important.

The species composition of forage fish populations in the Gulf of Alaska and Prince William Sound (PWS) has undergone a dramatic shift in recent decades. Prior to the late 1970's, the forage fish community was dominated by capelin, *Mallotus villosus* (Anderson et al., 1994; Bechtol, 1997). Environmental variations such as an ENSO event in 1976, followed by increased water temperatures (Niebauer, 1983; Royer, 1993; Bailey et. al, 1995; Piatt and Anderson, 1996), induced changes in the forage fish biota of PWS. Included among these changes were increases in the number of walleye pollock and other demersal fish, a 75% decline in the spawning population of Pacific herring by 1993 (Brown et. al, 1996), and a 50% decrease in overall fish biomass (Piatt and Anderson, 1996). Such dramatic shifts in the composition and abundance of forage fish populations may have cascading effects in marine food webs (Springer and Speckman, 1997; Livingston, 1993).

Decreases in the marine bird and mammal populations of PWS may be related to these changes in fish population structure (Piatt and Anderson, 1996; Oakley and Kuletz, 1996; Iverson et. al, 1997). Apparently, fewer high quality forage fish have been available, and the species composition has changed to one in which the predominant genera (Gadidae) are less energetically valuable prey for marine birds and mammals (Piatt and Anderson, 1996; Anthony and Roby, 1997). This decrease in prey quality may force predators to expend more energy in capturing sufficient resources for successful breeding (Roby et. al 1998).

The ecosystem of Prince William Sound has been the focus of intense research since the *Exxon Valdez* (EVOS) oil spill Natural Resource Damage Assessment (NRDA) studies. This report stems from the Alaska Predator Ecosystem Experiment (APEX), a multi-disciplinary study which attempted to link current knowledge about the forage fish of PWS with their seabird predators. We describe the feeding of allopatric (single species) and sympatric (multi-species) aggregations of YOY walleye pollock and YOY Pacific herring collected in summer and autumn by trawl in PWS and speculate on their potential for feeding competition. Evidence for competition between YOY fish may support the hypothesis that pollock are supplanting herring as the primary forage fish resource available in PWS.

Materials and Methods - Chapter 2

Field Methods

Fish stomach and zooplankton samples were collected during APEX forage fish population surveys in central, northeastern and southwestern PWS (Figure 1; Haldorson, 1995; Haldorson et. al., 1996). In a pilot study in 1994, we sampled November 7-13 (late autumn) aboard the Alaska Department of Fish and Game R/V *Medeia*; in 1995, we sampled July 20-August 12 (summer) aboard the charter F/V *Caravelle* and October 5-14 (early autumn) aboard the R/V *Medeia*. Hydroacoustic surveys were conducted offshore along a grid of parallel transects spaced at two-mile intervals and ending as near shore as possible. The grid was surveyed twice in summer and once, partially, in the each autumn. Acoustic gear consisted of a 420 kHz Biosonics Model 120-121 echo-integration system, with transducers towed alongside the vessel. Where fish were detected, the vessel either interrupted the survey or returned after the transect was completed to fish with a research scale, mid-water beam trawl. The net was generally fished 20-35 minutes each time. The trawl's effective mouth opening was 50 m^2, with net mesh sizes diminishing from 5 cm (2") in the wings to 1 cm (3/8") in the cod end. Additionally, a 0.3 cm (1/8") mesh liner was sewn into the cod end, which terminated in a plankton bucket having 500 μm nytex mesh. In summer, beach seine and dipnet samples occasionally supplemented the trawl catches.

Subsamples of forage species from hauls that caught fish were retained for diet studies. Specimens (n = 10 to 15) were preserved in a 10% buffered formalin-seawater solution on board the vessels for later stomach analysis in the laboratory. In 1995, the zooplankton prey spectrum was assessed from dual vertical hauls at each station, using conical nets 0.5 m in diameter with 303 μm mesh in summer and 243 μm mesh in autumn. We towed the nets from a standard of 20 m depth or to the depth at which fish were caught. Zooplankton samples were usually collected within two hours of fish catches. Two ancillary investigations of zooplankton were conducted to examine differences in fish prey resources. In the first, we conducted mesh trials using 105μm , 243μm , and 303μm mesh nets at three stations in summer to test for a mesh size-related difference in density of summer zooplankton. This was done because related studies had employed each of these nets (Willette et. al, 1997; SEA; Sturdevant et. al, 1996) and because we anticipated changing to a smaller standard mesh size in autumn. Secondly, we collected samples to compare zooplankton densities at shallow (< 25 m) and deeper (25 < m < 100) depths at seven stations in summer (95-1-53 to 95-1-62 and 95-1-112) and one station in early autumn (95-2-7; Table 1). Hydrographic profile data were collected with a Seabird SEACAT CTD to depths down to 200 m (Haldorson, 1995; Haldorson et. al, 1996).

Laboratory Methods

After a minimum of 6 weeks in formalin solution, fish samples were transferred to 50%

isopropanol for at least 10 days before stomach analysis was performed. Ten specimens of each species and size class were measured (mm standard fork length, FL; mg wet weight) and the stomachs examined. Size was used to develop age-class categories for the walleye pollock and Pacific herring diet samples; age estimates were corroborated with length frequency plots of all catch data (Haldorson et. al 1997; Smith, 1981). Walleye pollock 20 to 120 mm FL and Pacific herring 60 to 120 mm FL were classified as YOY or age-class 0. Stomachs were excised, weighed and the contents removed. The weight of prey contents was recorded as the difference between full and empty stomach weights. Fish were considered to be feeding if their stomachs contained more than a trace of food. Relative stomach fullness was recorded as integers (1-7) representing 25% increments on a scale from empty to distended. State of digestion was recorded as 1 = partially-digested contents, 2 = mostly-digested contents, and 3 = empty stomachs. Stomach contents and zooplankton samples were identified with a binocular microscope to the highest taxonomic resolution possible and enumerated. We subsampled all zooplankton samples, and stomach samples when practical, using a Folsom splitter to achieve a minimum count of approximately 200 of the predominant taxon. Numbers were expanded and total prey weights were determined by multiplying the number observed by the mean weight per individual taxon (data on file, Auke Bay Laboratory and University of Alaska Fairbanks, Institute of Marine Science).

Analytical Methods

Forage fish were considered to occur in allopatric aggregations if only one species and age-class was caught in a net haul. They were considered to be sympatric if at least two species or two age-classes of the same species (≥ 10 fish each) were caught in the trawl. For this study, we restricted analyses to YOY pollock and herring that were allopatric or that co-occurred only with each other to limit the complexity of trophic interactions. We examined the size of forage fish and their feeding attributes. Size included FL and wet weight. Feeding attributes included five measures of the quantity of food consumed (mean total number and total weight of prey, mean stomach fullness index (rounded to nearest 25%), and prey percent body weight (%BW) expressed as ratios of wet stomach content weight or total prey weight to fish body weight), two measures of feeding frequency (the proportions of feeding fish to non-feeding fish and the proportions of partially- to mostly-digested stomach contents), and prey composition by percent number and percent biomass of prey categories. Zooplankton density per cubic meter (D) was calculated for species, principal prey taxa, and total organisms in each vertical tow using the expanded organism count, X, divided by the volume, V, of a cylinder having 0.5 m diameter and height, h, equal to the depth of the tow:

$$D = \frac{X}{V} = \frac{X}{\pi \times r^2 \times h}$$

Analysis of variance (ANOVA) was the principal tool used to examine for both intraspecific and interspecific differences in YOY pollock and YOY herring size and feeding attributes and in zooplankton density. We compared data between seasons, between allopatric and sympatric aggregation categories, and between sympatric species. For fish size, we tested FL and wet weight. For fish diets, we tested all five measures of food quantity. Chi-square tests were used to test the feeding frequency measures for association between species, seasons or time of day. For time of day tests, we classified samples collected between 08:00 and 20:00 as "day" and those between 20:01 and 07:59 as "night." Prey composition and selection were assessed graphically. For zooplankton, we also used ANOVA to test for differences in densities and proportional densities of principal taxa between seasons (summer and early autumn, 1995), between mesh sizes, and between depths sampled. Data were transformed (ln x+1, rank or square root) in order to meet the assumptions of ANOVA. Post hoc Student-Newman-Keuls (SNK) comparisons were performed when significant differences were indicated ($p < 0.05$) in order to determine where they occurred. We present the means of raw data, even when tests were performed on transformed data.

Feeding selectivity of allopatric and sympatric aggregations of pollock and herring was calculated for summer and early autumn, 1995, when zooplankton were collected concurrently at the fish sampling stations. Occasionally, in summer, zooplankton samples from adjacent stations were substituted for those fishing stations without explicit prey samples (Table 1). We used Strauss' Linear Selection Index, L_o (Strauss, 1979), a measure varying from -1 to +1. Negative values indicate no preference and positive values indicate preference:

$$L_o = r_i - p_i$$

where r_i = percentage of prey resource I in the diet, and p_i = percentage of prey resource I in the environment. Prey resources for selection were defined as the species, stages and sizes of prey pooled into principal taxa.

Feeding overlap between species and within species between fish in allopatric and sympatric aggregations was described using Horn's Overlap Index (Horn, 1966; Krebs, 1989; Smith and Zaret, 1982). This index minimizes bias due to changing numbers of resource categories and resource evenness. Overlap was computed at two levels, with prey resources defined at the lowest level (species, stage and size) and at a pooled level (principal taxa). Horn's Overlap Index values, R_o, are expressed from 0 (no overlap) to 1 (total overlap) for predator species j and k:

$$R_o = \frac{\sum (p_{ij}+p_{ik}) \log (p_{ij}+p_{ik}) - \sum p_{ij} \log p_{ij} - \sum p_{ik} \log p_{ik}}{2 \log 2}$$

where p_{ij} = proportion resource I is of the total resources utilized by species j, and p_{ik} = proportion resource I is of the total resources utilized by species k. We considered R_o values > 0.60 to indicate similar use of resources and $R_o > 0.75$ to indicate very similar use of resources.

Results - Chapter 2

Seasonal differences in the aggregations of YOY walleye pollock and Pacific herring sampled from PWS were apparent. Fish were not collected from both allopatric and sympatric aggregations in all seasons (Table 1). In summer, 1995, when 62 total trawl hauls were made, no sympatric YOY pollock and YOY herring were caught in the 18 hauls catching sufficient samples of either one. Allopatric YOY pollock were collected at 12 summer stations (n = 120 diet samples) in the central region and allopatric YOY herring were collected at one central and one northeastern station (n = 20 diet samples; Figure 1). In four additional summer hauls, YOY pollock or herring were caught with other age classes or species (Pacific sandlance, capelin, Pacific tomcod). However, in early autumn (October, 1995, 11 trawl hauls) and late autumn (November, 1994, 14 trawl hauls), these species were caught both allopatrically and sympatrically. Sympatric YOY pollock and herring were caught in 36% of 11 autumn hauls catching YOY of these species, at two stations in the northeastern region of PWS in both early and late autumn (n = 20 diet samples per species and season). Allopatric fish were collected in different autumn months, the allopatric pollock (n = 10) in late autumn (southwestern region) and the allopatric herring (n = 10) in early autumn (central region). Additional hauls caught YOY pollock and herring that we excluded from this study because of our restricted definitions of allopatric and sympatric and our objective to examine only YOY pollock-herring trophic interactions. In early autumn, four additional hauls caught YOY pollock and herring, three as co-occurring species, but other age classes and either capelin or eulachon were also caught; in late autumn, one haul caught co-occurring YOY pollock and herring with eulachon.

In addition to species composition, other qualities of the catches varied, including numbers caught, relative species composition, sampling time and sampling depth. In summer, the number of pollock caught in trawls varied by two orders of magnitude between stations, from 22-1689 per haul. Herring catches could not be compared to trawl catches because they were collected by dipnet or beach seine. In autumn, between 14 and 4156 of each species was caught at a station, but YOY pollock and herring numbers were not consistently partitioned among sympatric catches. Similar numbers of each species were caught at some stations, while, at others, an order of magnitude greater number of one species was caught (Table 1). Samples were collected during different periods of the day and at different depths in summer and in autumn. In summer, most samples were collected by early evening. Summer pollock were mostly caught offshore at 50-80 m trawl depths ($\bar{x}$ = 60 m), while herring were caught in alternative gear at the surface and nearshore (Table 1). In autumn, most samples were collected shortly before midnight, at a mean depth of 30 m, in bays. The autumn allopatric samples were collected earlier in the day and deeper than the autumn sympatric samples.

Seasonal Comparisons

YOY pollock were generally larger than YOY herring during a season (Figure 2), but intraspecific patterns of size across seasons differed (2-way ANOVA interaction, $p < 0.05$). Although both species FLs and weights were significantly greater in early or late autumn than in summer (1-way ANOVA, SNK multiple comparisons, $p < 0.05$), only pollock size differed between early and late autumn. Mean FLs of both species were approximately 60% longer in autumn than in summer (Tables 2 and 3; Figure 2). In late autumn compared to early autumn, pollock FL was approximately 14 mm greater, while wet weight was approximately 50% greater ($p < 0.05$). For herring, neither lengths nor weights differed between early autumn and late autumn ($p > 0.05$).

Seasonal patterns in feeding attributes differed consistently for the two species. The stomachs of the majority of YOY pollock and herring examined did contain food, but full stomachs (mean fullness of 100%) were not common for either species (Table 2). For pollock, the proportion of non-feeding individuals was not associated with season (χ^2 test, $p = 0.2296$), but for herring, it was associated with season (χ^2 test, $p = 0.0004$). Herring in late autumn were the only group with a higher proportion of non-feeding fish than feeding fish (Table 3). Pollock and herring had very similar proportions of feeders in summer and early autumn ($\geq 80\%$), but in late autumn, the proportion of non-feeding herring was more than twice the proportion of non-feeding pollock.

Interspecific differences in seasonal feeding were also evident from tests on stomach fullness index, both %BW ratios, and total numbers and weights of prey (2-way ANOVA interactions, $p \leq 0.0276$). Among pollock, only two significant differences were found across seasons, both between summer and late autumn. Prey %BW and content %BW were both above 1% in summer and below 1% in the autumn months, but only the late autumn values were significantly lower than the summer values (SNK multiple comparisons, $p < 0.05$; Table 3). No differences between summer and early autumn or between early and late autumn feeding attributes were significant for pollock. Pollock stomachs were approximately half full in each season and the total number and biomass of prey consumed did not differ (Figure 3). Pollock prey numbers were highly variable and prey weights were similar in each month. Mean prey number ranged from a high of approximately 294 in summer to a low of 63 in early autumn, while mean prey weight ranged from approximately 34 to 39 mg.

Among herring, trends toward lowest feeding in late autumn were significant, but trends toward lower feeding in early autumn compared to summer were not significant. All five food quantity measures were significantly lower in late autumn compared to summer and in late autumn compared to early autumn, but did not differ between summer and early autumn (SNK multiple comparisons, $p < 0.05$). Herring stomachs were fullest in summer (75%), were half full in early autumn, but contained only trace amounts of food in late autumn. Herring %BW measures were also greatest in summer ($\geq 1.9\%$) and least in late autumn ($\leq 0.3\%$). Similarly, mean total numbers and weights of prey decreased seasonally for herring, from 3011 prey weighing 271.1 mg in summer, to 528 items weighing 82.2 mg in early autumn and 23 items weighing 13.2 mg in late autumn (Figure 3; Table 3).

Individual fish digestion data were pooled across seasons to test for differences in diel feeding patterns. The condition of stomach contents differed significantly between the species by time of day. Pollock had greater proportions of mostly-digested contents during the day compared to the night (χ^2 test, 2 d.f., $p = 0.0033$). Conversely, herring had marginally greater proportions of mostly-digested contents during the night compared to the day (χ^2 test, 2 d.f., $p = 0.0670$). However, the proportions of feeding and non-feeding fish were not different by day and night for either species (χ^2 test, 2 d.f., $p = 0.7877$).

Allopatric/Sympatric Comparisons

Patterns in size and feeding of fish in autumn allopatric and sympatric aggregations varied with species. We did not pool sympatric fish from early and late autumn for comparison to allopatric groups because of the intraspecific differences in size and feeding measures between these seasons. For late autumn pollock, FLs of allopatric and sympatric fish were not different (t-test, $p > 0.05$), but fish were approximately 1.5 g lighter ($p = 0.0494$) in sympatric aggregations compared to fish in allopatric aggregations. For early autumn herring, no differences were observed between the sizes of allopatric and sympatric fish ($p > 0.05$; Figure 2; Table 3).

We also found differences in feeding between the allopatric and sympatric pollock from late autumn but not between the allopatric and sympatric herring from early autumn. Among pollock, the late autumn allopatric fish consumed the greatest numbers and biomass of prey of all autumn pollock (Figure 3; Table 3). All other feeding measures were also consistently greatest among the allopatric pollock. Feeding measures for late autumn sympatric pollock were significantly lower than values for both the late autumn allopatric and the early autumn sympatric pollock (1-way ANOVA, $p < 0.0002$). With one exception, the late autumn allopatric values were not significantly different from the early autumn sympatric values ($p > 0.05$). Prey numbers were the only measure of these allopatric pollock that differed significantly (greater, $p < 0.05$) from prey numbers of early autumn sympatric pollock (Figures 4 and 5). The late autumn allopatric pollock consumed more than 700 prey items (71 mg), while late autumn sympatric pollock consumed 13 prey items (16 mg) and early autumn sympatric pollock consumed 63 prey items (39 mg). The late autumn allopatric pollock and the early autumn sympatric pollock had stomachs that were more full ($\geq 75\%$) and mean %BW values that were higher ($\geq 0.8\%$BW) than these measures for late autumn sympatric fish (25% full, $\leq 0.4\%$ BW; Table 3).

The allopatric-sympatric feeding pattern was different for herring than for pollock. The early autumn allopatric herring consumed the greatest prey biomass, but not prey numbers, among all the autumn herring (Figure 3; Table 3). The allopatric and sympatric values from early autumn were not significantly different from each other, but both of these values were greater than the late autumn sympatric values ($p < 0.0001$). Content %BW was the only significantly different measure between allopatric and sympatric herring in early autumn. In early autumn, herring stomachs were $\geq 50\%$ full whether allopatric or sympatric, while in late autumn, sympatric herring stomachs were less than 25% full. Allopatric herring consumed 386 prey items (103 mg), while sympatric herring consumed 599 prey items (~72 mg), in early autumn. In late autumn, sympatric herring consumed ~23 prey items (13 mg). Herring mean %BW (either value) was also lower for late autumn sympatric fish (= 0.3% BW) than for the other groups (> 0.9% BW).

In tests restricted to sympatric fish, we again found strong seasonal differences, but few interspecific differences in feeding between the pollock and herring; no season-species interaction term was significant for sympatric fish (2-way ANOVA, $p > 0.05$). All five measures of food quantity were significantly greater among early autumn sympatric fish than among late autumn sympatric fish ($p < 0.0001$), but only the fullness index differed between species. Pollock stomachs were slightly (< 25%), but significantly more full in sympatric aggregations than herring stomachs ($p = 0.0377$). The proportion of non-feeding sympatric individuals was not associated with species (χ^2 test, $p = 0.2039$), and no interspecific differences were found for prey numbers or biomass, or prey %BW (ANOVA, $p > 0.05$).

Young-of-the-year pollock and herring prey compositions were similar in both summer and autumn (Figures 4 and 5), but prey composition differed between seasons. Small prey predominated in summer and larger prey in autumn, especially in terms of biomass composition. In summer, small calanoid copepods (*Pseudocalanus* spp., *Centropages abdominalis, Acartia longiremis*) dominated the diets both numerically and in terms of prey biomass. Among pollock, small calanoids comprised 55% by number and 57% by weight. By number, most of the remainder of summer pollock diet was comprised of invertebrate eggs (39%); by weight, the remainder was large calanoids (principally *Calanus pacificus*, *C. marshallae* and *Metridia pacifica*), fish, hyperiid amphipods and euphausiids (both larvae and older stages, including *Thysannoessa* sp.). Small amounts of other prey, including larvaceans, gastropods, and chaetognaths, were also commonly consumed by pollock. Among summer herring, small calanoids comprised proportionally more of the diet than among pollock. Overall, small calanoids made up 77% by number and 88% by weight of herring diet; they were the sole taxon consumed by the YOY herring at Eleanor Island station 110 (Table 2). Other small prey (cladocerans, bivalve larvae, and invertebrate eggs) formed most of the rest of the herring diet, with minor contributions of decapod larvae, gastropods, hyperiids, and euphausiid larvae consumed. We could not compare allopatric and sympatric diets in summer because of lack of samples.

In early autumn (1995) and late autumn (1994), pollock and herring fed from the same prey categories. Larvaceans and large calanoid copepods numerically dominated the autumn diets of both species, comprising 57-91% of prey. Euphausiids and large calanoids dominated the autumn diets in terms of biomass proportions (Figs. 4 and 5). Compared to these prey taxa, small calanoids comprised smaller proportions of the diet (up to 37% of prey number and 9% of prey biomass), and hyperiids occasionally contributed up to 11% biomass. Euphausiids included *Thysanoessa raschii*, *T. spinifera* and unidentified juveniles and adults, but no larvae. Large calanoids included the same species present in summer diets, as well as *M. ohkotensis* and *Neocalanus* spp., while small calanoids included *Pseudocalanus* spp., *Acartia longiremis*, and *Oithona similis*. Invertebrate eggs (the majority of "other") were present less frequently in autumn diets than in summer diets. Some differences in diet composition between early and late autumn did exist, however. Early autumn diets included proportionally more biomass from large calanoids, while late autumn diets included proportionally more biomass from euphausiids; larvacean numbers tended to be less prominent in early autumn than in late autumn.

Substantial interspecific and intraspecific diet overlap was observed for YOY pollock and herring in both early autumn (1995) and late autumn (1994). Higher values of Horn's Overlap Index were indicated when prey species were grouped into principal taxa (Table 4). In summer, Horn's Overlap Index indicated very similar diets ($R_o > 0.76$) between allopatric species in terms of numbers and weights of prey species or principal prey taxa. In early autumn, no numeric overlap between sympatric pollock and herring was observed ($R_o < 0.60$). In late autumn, diets of sympatric species were similar ($R_o > 0.69$) at both stations where they co-occurred based on numbers of prey consumed from principal taxa. Mean numeric overlap for the late autumn sympatric species was approximately twice that of the early autumn sympatric species ($R_o = 0.97$ versus 0.43). Based on biomass of the prey items consumed from principal taxa, significant diet overlap was observed between sympatric species at both early autumn stations and one late autumn station. Overall, diets of sympatric pollock and herring overlapped less in terms of biomass in early autumn ($R_o = 0.69$) than in late autumn ($R_o = 0.95$). Diet overlap between allopatric and sympatric pollock or herring collected in the same season was extensive at the principal taxon level for herring in early autumn in terms of biomass ($R_o = 0.93$) and for pollock in late autumn in terms of prey number ($R_o = 0.91$).

Zooplankton Composition

The densities per cubic meter and the composition of zooplankton present in the water column were compared between summer (303μm mesh) and early autumn (243μm mesh), but no data were available for late autumn. Total zooplankton density (ln-transformed) was not different (1-way ANOVA, $p = 0.1685$) between summer (n = 37) and autumn (n = 8). Mean total densities were 1184 ± 138 organisms*m^{-3} in summer and 1414 ± 185 in early autumn (Figure 6). Taxa were less diverse in summer than in autumn, but small calanoids predominated in both seasons. Small calanoids were a significantly ($p < 0.0001$) greater proportion of the total in summer than in early autumn (84% vs. 58%), although their absolute density did not differ between seasons (1018 ± 133 vs. 828 ± 130 organisms*m^{-3}; $p < 0.05$). Gastropods (*Limacina helicina*) were second most abundant in summer, but followed large calanoids and bryozoan cyphonautes larvae in abundance in autumn. No other taxon contributed more than 5% in summer. Gastropods numbered 60 ± 10*m^{-3} (5.8% total) in summer and 96 ± 19*m^{-3} (6.8%) in early autumn; neither density nor proportional density of gastropods differed between seasons ($p > 0.05$). Large calanoids were an order of magnitude less abundant in summer than in early autumn ($p < 0.0001$), when they formed 13% of total zooplankton (204 ± 60). Larvacean density and percent density were each approximately three times lower in summer (14 ± 4 organisms*m^{-3}) compared to early autumn (45 ± 11 organisms*m^{-3}; $p < 0.0194$). Cladocera were present only in summer (approximately 5% total) and cyphonautes were present only in early autumn (~16% total, 205 ± 50 organisms*m^{-3}). Hyperiid amphipods, euphausiid larvae, chaetognaths, and barnacle and decapod larvae were sometimes present in low numbers (< 2 organisms*m^{-3}).

Mesh size-related differences in zooplankton density were observed in summer. Total density estimates decreased significantly (1-way ANOVA, n = 11, $p = 0.0008$), by an order of magnitude, from the smaller mesh nets to the larger mesh nets; all pairs of estimates were different (SNK, $p < 0.05$). Mean total densities decreased from approximately 41,000 organisms*m^{-3} estimated from 105 μm mesh to 11,000 organisms*m^{-3} estimated from 243 μm mesh to 2,300 organisms*m^{-3} estimated from 303 μm mesh. Small calanoids were always the most abundant organisms. Among all taxa, net size-selectivity was observed only for small calanoids and for "other"; declines in density estimates with increasing mesh size were highly significant ($p = 0.0001$) for small calanoids and marginally significant ($p = 0.0711$) for "other". Small calanoid density estimates decreased 4x between successive mesh sizes. However, relative zooplankton composition was the same for all mesh sizes, with small calanoids contributing 79-90% of total organisms ($p = 0.2886$). For all other principal zooplankton taxa (large calanoids, larvaceans, cladocerans, and gastropods), neither the percentage contribution nor absolute density differed between the three mesh sizes (1-way ANOVA, $p > 0.05$).

The depth of the water column sampled also impacted the zooplankton density estimates in each season. At the seven summer stations and one autumn station where a shallow (20-25m) pair of zooplankton tows was followed by another pair of tows to the depth where fish were sampled (50-100 m), mean total densities were always greater in the shallower water column, and lesser in the deeper water column. In summer, the total density per cubic meter estimated from shallow hauls was more than twice the estimate from deep hauls (1371 ± 191 vs. 645 ± 91 organisms*m^{-3}; 2-way ANOVA, $p < 0.0001$). In early autumn, total densities at shallow depths (25 m) were marginally greater (t-test, $n = 4$, $p = 0.1098$) than at deeper depths (1299 ± 64 vs. 1064 ± 56 organisms*m^{-3}). Differences in the abundance, but not the percentage composition, of principal taxa with depth were also observed. In summer, small calanoid abundance was twice as high nearer the surface (1175 ± 181 vs. 550 ± 87 organisms*m^{-3}; $p = 0.0002$); small calanoids comprised approximately 84% of total zooplankters at each depth (ANOVA, $p = 0.7365$), however. In early autumn, both the absolute density and the proportion of small calanoids were at least marginally greater nearer the surface ($p < 0.0530$); small calanoid densities were 685 ± 48 (53%) and 426 ± 40 (40%) organisms*m^{-3} in shallow and deep water, respectively. Large calanoids exhibited the reverse pattern in early autumn, but not in summer. In summer, the abundance and proportion of large calanoids did not differ ($p > 0.05$) between depths, density being 36.9 ± 6.7 (3.3%) in shallow water and 27.6 ± 56 (4.7%) organisms*m^{-3} in deep water. In early autumn, the abundance of large calanoids was significantly ($p = 0.0036$) greater in deep water than in shallow water (176 ± 3 vs. 104 ± 3 organisms*m^{-3}); the proportional density of large calanoids was also significantly ($p = 0.0099$) greater in deeper water in autumn (16.6% vs. 8.1% of the total). Gastropods were the only other taxon that comprised more than 10% of the total zooplankton in either season. Gastropod numbers were greater ($p < 0.0136$) in both seasons nearer the surface, but proportions did not differ with depth ($p > 0.05$). Gastropod densities in shallow and deep water were 99.4 ± 22.8 vs. 36 ± 5.3 organisms*m^{-3}, respectively, in summer, compared to 141.4 ± 4 vs. 84 ± 5.3 organisms*m^{-3} in autumn. Larvaceans showed no biologically meaningful, significant differences between depths for either absolute or proportional density in either season ($p > 0.05$). Cladoceran density was marginally greater ($p = 0.0329$) near the surface compared to deeper water in summer (24.9 ± 8.9 vs. 6.0 ± 1.3 organisms*m^{-3}, but proportional density was not different ($p > 0.05$); cladocerans were absent in autumn. Cyphonautes larvae were present only in autumn and showed no differential abundance by depth (approximately 300 organisms*m^{-3}; $p > 0.05$).

We also compared densities of important prey taxa among stations within seasons as a measure of prey patchiness. Summer stations spanned the central sound from Applegate Rocks to Storey Island; autumn stations were in the northeastern region. Total zooplankton density differed significantly (2-way ANOVA, $p = 0.0088$) among summer stations, but no interaction existed between station and depth ($p = 0.2448$). Zooplankton densities at East Eleanor Island (station 62) were higher ($p > 0.05$) than at all stations except Montague Point (station 53). Density of small calanoids at station 62 was significantly higher (> 2x) than at all others except station 53 (2-way ANOVA, $p = 0.0049$). Inter-station differences in density of large calanoids and gastropods also existed ($p < 0.0005$), but the patterns were more complex. For large calanoids, an interaction between station and depth was found ($p = 0.0057$). At stations 54 and 62, density of large calanoids was higher at deep locations than at shallow depths, the reverse of the pattern at the remaining summer stations. Large calanoid density at station 56 was higher than at all other summer stations, while it was lower at station 62 than at all stations except station 58. For gastropods, densities at stations 54 and 57 were lower than at three stations (56, 58, and 62). Larvacean density did not differ significantly ($p = 0.1712$) between stations. No other consistent pattern of differences between summer stations was observed. Among early autumn stations, sampling depths ranged from 25 m to 80 m. Total density at one sympatric station, Galena Bay, was significantly (ANOVA, $p < 0.05$) greater (~2x) than at either of the other two stations. This pattern was repeated for large calanoids (~4x) and small calanoids (~2x; $p < 0.0149$), but no difference existed for larvaceans ($p = 0.4462$).

Selection by pollock and herring from among the zooplankton taxa present in 20 m zooplankton tows was noted in both summer and early autumn, 1995 (Figure 5). Summer pollock avoided small calanoids and moderately selected for large calanoids, gastropods and larvaceans. Nonetheless, pollock diet was made up of > 50% small calanoids. Summer herring were not strongly selective of any prey category. Their predominant prey, small calanoids, was consumed in close proportion to its availability. In early autumn, pollock strongly selected for large calanoid copepods and herring strongly selected for larvaceans, the largest components of their diets. Small calanoids were avoided by both species. Allopatric herring were more selective of large calanoids than were sympatric herring in early autumn, while selection for larvaceans was similar for both groups. A strong trend towards selectivity or avoidance was not observed for any other prey category, but pollock consumed hyperiids more frequently than euphausiids in summer and both pollock and herring consumed euphausiids more frequently than hyperiids in autumn.

Discussion - Chapter 2

In the summer of 1995, diets of YOY walleye pollock and Pacific herring in allopatric aggregations were very similar. Prey of both species were predominantly composed of small calanoids, with smaller proportions of a variety of organisms. These results are supported by other work from PWS in 1994-1996 and by additional, widespread, studies. Calanoids were the dominant prey of both YOY pollock and herring by percent numbers, weight and frequency of occurrence in late summer, 1994, in PWS, and were the basis for high diet overlap between the species (Willette et. al, 1997). Elsewhere, pollock 30-70 mm in length caught during spring and summer in Japanese waters consumed virtually all types and sizes of calanoid copepods inhabiting the area, as well as larval euphausiids and a variety of other small prey (Kamba, 1977). In late summer, pollock 60-93 mm caught in the Kodiak Island-Alaska Peninsula region of the eastern North Pacific had diets in which small calanoids comprised over 75% of prey numbers, but euphausiids were already more than 75% of prey biomass (Livingston, 1985). Similarly, small calanoids were the principal prey (percent number or volume) of YOY pollock 33-97 mm in length in southeastern Alaska between August-October, with one species, *Acartia clausi*, particularly important (Krieger, 1985).

YOY herring also depend on small calanoid prey. Small calanoids comprised the greatest dietary biomass of fish from four bays in PWS in summer, although spatial differences in the diets were observed (Foy et. al, 1998). In another PWS study, most of the diet of beach seined YOY herring was made up of small calanoids, but larvaceans were selected in greater proportions than they were present in zooplankton samples (Sturdevant et. al, 1999). In the Strait of Georgia in early summer, calanoid copepods predominated (> 80% occurrence) in YOY herring diets; other principal prey included amphipods, invertebrate eggs and euphausiids, plus barnacle larvae later in summer (Haegele, 1997). Depending on the habitat occupied, early YOY herring diet may include epibenthic prey, such as harpacticoid copepods and gammarid amphipods, as well as pelagic prey, such as calanoid copepods, cladocerans and oikopleurans

(Blaxter and Hunter, 1982; Lassuy, 1989). In southern B.C., age-0 herring consumed whatever plankters were readily available (Wailes, 1936), with calanoids and barnacle larvae being most important.

Despite the similarity of their summer diets in PWS, we observed some differences in prey selection between the YOY pollock and herring. Some of these probably relate to diel vertical distributions of predator and prey. The summer herring were located at the surface where densities of small calanoids, their main prey, were twice as high as deeper in the water column. Higher concentrations of zooplankton were also observed below the surface off the Oregon Coast (Petersen and Miller, 1970). Both herring and pollock perform diel vertical migrations, but the time of day and depth of feeding of juveniles are not well known (Willette et. al, 1997; Merati and Brodeur, 1996). Herring are primarily visual feeders requiring minimum light levels to feed (Blaxter, 1982). Young herring vertical distribution varies widely in both day and night, and they respond to prey distributions that may be correlated with thermocline depth (e.g.., Fossum and Johannessen, 1979, in Munk et. al, 1989). For example, when prey were distributed throughout the water column, herring larvae migrated up to depths of optimal light intensity for feeding; when their copepod food source was concentrated at 40 m, the fish migrated down to this depth only at noon, when light levels were sufficient for feeding (Munk et. al, 1989). In our study, herring were located in more dense prey patches and where light for feeding was most intense, compared to the deeper pollock. The herring fed non-selectively--small calanoids were present in their diets in similar proportions as they were present in the environment. Smaller individuals' diets were limited to this taxon, while larger individuals' diets were more diverse. Judging by the relatively less-digested condition of herring stomach contents by day compared to night, these surface aggregations occurred at the principal time of feeding.

The summer depth of pollock in our study contrasted with that of herring and may relate to different feeding rhythms and prey preferences. Pollock were located in relatively deep water where all of the taxa they consumed were less abundant than at the surface. Similar to herring, small calanoids made up the largest single dietary component of pollock, but these prey were avoided relative to their availability. Pollock sometimes selected large calanoids, but these prey were not more abundant at depths where the fish were located. Abundance of the other prey selected by pollock was either no different (larvaceans) or was lower (gastropods) at depths where the fish were located. Just as for herring, feeding conditions can affect the vertical distribution of juvenile pollock, along with other factors such as predator presence, light, turbidity, and pressure (Olla et. al, 1996). In the Bering Sea, juvenile pollock were located between the thermocline and neustonic layer, a preference partly regulated by temperature. Vertical movement though a thermocline depended on relative availability of food and was less likely to be performed by the smaller juveniles (Bailey, 1989; Olla and Davis, 1990; Sogard and Olla, 1996; Olla et al, 1996). Avoidance of light increased and avoidance of cold water decreased with growth, especially under conditions of low zooplankton. Pollock prey preferences, zooplankton distribution at the time of sampling, and the mostly-digested condition of their prey suggested that pollock in our study were not feeding principally during the day; instead, they may have fed the night before.

Changes in zooplankton composition from summer to early autumn were reflected in fish diets. Although they were highly abundant in both seasons, small calanoids were not selected, but were eaten randomly or avoided by both fish species. The proportional density of small calanoids in the zooplankton declined by nearly 30% from summer to early autumn, and the proportion consumed by fish was likewise much reduced. In contrast, both large calanoids and larvaceans were more abundant in zooplankton samples in early autumn than in summer and, along with euphausiids, formed larger dietary components at that time. Large calanoid copepods were selected for by both species in autumn, especially by pollock. Larvaceans were selected by pollock in summer and by herring in autumn. These species continue to exhibit similar prey requirements and minimal prey partitioning during seasonal changes in the available prey suite.

The changes in diet that we observed from summer to early autumn may also relate to the seasonal increase in fish size and energy requirements, as well as to changes in zooplankton prey spectrum. The autumn prey composition of pollock that we observed is very similar to the September diet of YOY pollock in the Gulf of Alaska (Merati and Brodeur, 1996). In that study, increased fish size was correlated with decreased predation on copepods and increased predation on larvaceans and euphausiids, and geographic differences in diet were pronounced. In southeastern Alaska, larvaceans were consumed frequently by pollock only in September, and were never a high percentage of numbers or volume of prey; large calanoids (numbers) and euphausiids (volume) were more substantial in late autumn-winter juvenile pollock diets (Krieger, 1985). By winter, epibenthic prey, including mysids, shrimps, cumaceans and chaetognaths, may also be incorporated in the diet as vertical distributions of the fish change and pelagic prey become scarce (Krieger, 1985; Merati and Brodeur, 1996). For YOY herring, predation on calanoids by younger fish and on euphausiids by older fish is also often reported (Lassuy, 1989; Haegele, 1997; Wailes, 1936). The predominant prey biomass of YOY herring in other PWS studies changed from small calanoids in June to larvaceans in October (Foy et. al, 1998), while euphausiids were minor dietary components (Foy et. al, 1998). Malacostracans (including mysids and euphausiids) formed larger portions of the prey biomass in November (Foy and Paul, 1999). A common pattern of diet transition in early autumn or with larger size was observed in the above studies of herring and pollock as well as ours: small calanoids were supplanted by larger calanoids, larvaceans and larger crustaceans.

Differences in the species' diets could also have been related to specific prey attributes, such as size, life history stage or vertical distribution, and to regional or habitat differences the prey available within PWS. Both the fish and many of their invertebrate prey undergo diel vertical migration (DVM). Other studies have correlated size-related differences in the vertical distribution of herring larvae with shifts to larger prey that had different migration patterns (Fortier and Leggett, 1983 in Munk et. al, 1989). During both summer and autumn in our study, pollock and herring consumed a variety of calanoid species with varied life history patterns and whose sizes assigned them to both small and large size classes (< 2.5 mm and > 2.5 mm total length, TL, respectively). Both large and small calanoids can alter their migration patterns in response to environmental conditions, including predator presence (e.g., Bollens et. al, 1992; Frost and Bollens, 1992). Migration patterns of calanoids can also vary between species or life history stages (e.g., Hattori, 1989; Bollens and Frost, 1991; Neill, 1992) and within species in response to food levels (Dagg, 1985; Dagg et. al, 1997). Among two commonly-consumed large calanoids, *Metridia lucens* was found deeper than *Calanus pacificus* during both day and night; *M. lucens* migrated in a consistent pattern, and was not found at the surface during the day as *C.*

pacificus sometimes was. Juvenile herring preferred *Calanus*, but predator-avoidance was not thought to be the factor controlling the distribution of *M. lucens* (Bollens et. al, 1993). Among small calanoids, conversely, the diverse behavioral repertoire of *Pseudocalanus newmani* (Frost and Bollens, 1992) and the strength of DVM of *Acartia hudsonica* (Bollens et. al, 1992) were thought to be avoidance responses to teleost and invertebrate predators, not responses to light or food. These variations in behavior suggest that a complex array of interactions between predator and prey, as well as between potentially-competing predators, can influence fish diets.

Other characteristics besides density and size influence the selection of prey taxa. Larvaceans are a highly visible taxon (Bailey et. al, 1975) that is relatively small when without their mucous houses. Although they are gelatinous, their caloric value per unit weight is closer to that of euphausiids, hyperiids, calanoids, and gastropods (*Limacina helicina*) than to cnidarians or ctenophores (Davis et al., 1998), possibly because they concentrate phytoplankton prey (Knoechel and Steel-Flynn, 1989). Individual larvacean weight is on the order of 10-100x lighter than a large calanoid copepod and 2x lighter than a small calanoid (data on file, Auke Bay Laboratory). Therefore, many more larvaceans must be consumed to accumulate the equivalent calories obtained from the crustaceans. Larvaceans may appear to be selected for if fish have fed in a front or other hydrographic feature that can maintain prey aggregations (Alldredge, 1982). Conversely, fish may avoid the predominant prey available if other, less abundant taxa are more attractive or if the energy expended to consume sufficient calories as small calanoids exceeds that expended to capture less motile prey, such as larvaceans, or larger, highly motile prey, such as large calanoids. Visual feeders may also feed opportunistically on dense organisms in the dark (Batty et. al, 1986). The presence of high numbers of minute prey that escaped our plankton nets (e.g., bivalve larvae and invertebrate eggs < 100 μm in diameter), is an often-noted (Krieger, 1985; Grover, 1990, 1991; Merati and Brodeur 1996; Haegele, 1997) example of opportunistic feeding by filtration rather than by selection (Batty et al., 1986). Foy et. al (1998) hypothesized that herring could achieve greater energy intake by selective feeding during periods of low prey diversity and high prey density, compared to periods of high prey diversity and low prey density, even if stomachs were not as full.

Besides calanoid mesozooplankton, two macrozooplankters which perform diel vertical migrations, euphausiids and hyperiid amphipods, appeared in the diets of pollock and herring in all seasons (Figures 4 and 5). Little is known about these macrozooplankters in PWS, and our qualitative data do not allow us to calculate selection. One would expect to observe different size classes of these taxa in fish diets during much of the year, however, since a variety of euphausiid and amphipod species produce multiple broods annually (Wing, 1976; Tanasichuk, 1998a). They were not a substantial biomass component of the summer diets because the small, early stages were consumed most often; the larger stages contributed more prey biomass in autumn. The early stages of euphausiids and hyperiids were captured in low numbers in plankton nets and older specimens were captured in trawls and NIO nets in both seasons. They were patchily distributed and a regional distribution gradient was exhibited by euphausiid species (Paul, 1995; Dr. T. C. Shirley, personal communication). Adult (15-25 mm TL) *Euphausia pacifica* and four species of *Thysanoessa* were captured in all seasons (Haldorson et. al, 1996). Hyperiids were not identified and were only enumerated from late autumn trawls (Paul, 1996).

Since sampling time of day differed between seasons, diel period may partially account for seasonal differences in the appearance of euphausiids and other prey in the diet. In summer, sampling coincided with an unlikely time for predation to occur: during daylight, when the distributions of vertically migrating predator and prey did not overlap. In summer, euphausiids were captured in only 7 out of 62 trawls (11%). These were collected below the mean depth of our pollock catches, 60 m. Euphausiids were present in both the northeastern and southwestern regions of the sound, but were not caught in the central region or at any of our fish stations. Summer fish may have been too small to feed on juvenile and adult euphausiids, and/or they may not occupy the same habitat during the day.

Autumn fish were larger than summer fish and the small calanoids that were their former principal prey were not only proportionally less abundant but were probably no longer an appropriate size to sustain them (Parsons and LeBrasseur, 1973). In early autumn, all groups of both species avoided small calanoids, and all groups of herring selected larvaceans. However, feeding and selection patterns differed between aggregations within species. The deeper, allopatric herring collected in daytime were the only ones that strongly selected for large calanoids, although these prey were less abundant at the allopatric station than at the sympatric stations. The proportion of large calanoids in the allopatric and sympatric herring diets was not different, however.

We found little indication that one species fed poorly compared to the other when they co-occurred. We observed the same frequency of feeders for pollock as for herring in sympatric aggregations and diets overlapped extensively. The two species' diets were also similar when they occurred allopatrically, in either summer or autumn. Diet composition changed little in the presence of a potential competitor, but a few differences between early autumn diets of the two sympatric species existed. In contrast to herring, the sympatric pollock did select large calanoids, especially at Galena Bay, where this prey taxon was most abundant and where catches of YOY pollock were the highest. We also observed that *Metridia* spp. were selected more strongly by pollock than by herring, possibly indicating a difference in feeding time or habitat utilization between the species. Sympatric pollock also consumed proportionally more euphausiid biomass than the sympatric herring. Large calanoids and euphausiids could have been consumed at different feedings, particularly if their vertical distributions overlapped with the fish vertical distributions at different times. Changes in prey composition with time of day have been noted previously for YOY pollock (Merati and Brodeur, 1996). No differences were apparent in the species or size of euphausiids consumed by different aggregations of fish. These observations suggest that, for the sympatric juvenile herring, interspecific interactions may limit predation on large calanoids, but predation on euphausiids may be limited by fish size.

Euphausiids were a principal prey in terms of biomass, particularly for autumn pollock. Some of the fish in all autumn aggregations consumed euphausiids, the largest and most energy-dense taxon, especially when large calanoid consumption declined in November. Euphausiids may also have been more available in autumn compared to summer. They were caught in trawls much more often in autumn, at four of seven trawl stations in early autumn (57%), and at five of 14 stations in late autumn (36%). They were not caught in the southwestern region in early autumn, but were present in all three regions in late autumn. Among the early autumn stations for which we have fish diet data, euphausiids were not collected at East Naked Island, but the allopatric herring there consumed juvenile euphausiids and amphipods more frequently than three out of the four sets of sympatric fish from Galena Bay and Landlocked Bay, where euphausiids were collected. Overall, despite these prey "advantages," the allopatric herring had very similar prey composition, did not consume greater quantity of food, and the fish were not larger compared to sympatric herring.

In late autumn, allopatric pollock caught in daytime in deep water had much higher feeding measures than sympatric pollock caught at night in shallow water. Among late autumn stations, amphipods, but not euphausiids, were collected at Icy Bay, yet the allopatric pollock there ate euphausiids and amphipods more frequently than any of the sympatric groups at Galena Bay and Port Gravina, where both amphipods and euphausiids were collected. They ate euphausiids and large calanoids more frequently than sympatric fish, but overall, proportionally less of their prey biomass was euphausiids. Euphausiids made up less than 30% of prey biomass in these allopatric pollock, while in the sympatric pollock and herring, euphausiids comprised approximately 80% of the prey biomass. Fish in all aggregations ate a variety of sizes of juvenile-adult euphausiids (*Thysannoessa raschii* and unidentifiable euphausiids) and amphipods (*Themisto pacifica, Primno macropa* and *Hyperia* sp.). Even though the allopatric fish presumably expended more energy to consume the high numbers of small prey that constituted more prey biomass than the sympatric pollock, they were in better condition than the sympatric pollock. Nonetheless, the smaller sympatric pollock were not less inclined to prey on the energetically advantageous prey than sympatric herring; both species had low feeding measures and ate similar proportions of euphausiids. Given the apparent differences in euphausiid availability, continued predation on euphausiids by pollock and herring in areas where they were not collected suggests strong selectivity for this taxon. Euphausiids could have been consumed at night near the surface or during the day near the bottom (Krieger, 1985; Pearcy et. al, 1979). Also, the larger autumn fish may be better able to prey on late stage euphausiids than the smaller summer fish (Merati and Brodeur, 1996; Kamba, 1977; Haegele, 1997). Whether the differences in diet between fish in allopatric and sympatric aggregations are due to regional spatial differences in prey available, to time of day and depth, or to the species composition of the foraging aggregation remains unclear.

If competition occurs between sympatric species, one would expect that, given similar prey fields, the quantity or quality of prey consumed would improve when fish are allopatric compared to when they are sympatric. Spatial variation in diet of YOY herring from four bays in PWS (Foy et. al, 1998) and for YOY pollock in three areas of the western Gulf of Alaska (Merati and Brodeur, 1996) have been reported previously. Our small sample sizes make it difficult to distinguish between diet characteristics that may relate to aggregation type (allopatric/sympatric) versus time of day, habitat, or region. The allopatric and sympatric herring in early autumn and the allopatric and sympatric pollock in late autumn consumed different proportions of the same taxa. Allopatric and sympatric fish may exhibit different behaviors that affect their distributions and therefore affect predation on euphausiids or other strong migrators. They might also partition the available prey to avoid competition, but our finding that less quantity of food was eaten by sympatric fish compared to allopatric fish suggests that competition was occurring. Alternatively, the sympatric herring and pollock could have had less full stomachs than the allopatric fish because of sampling time, if they had not been feeding actively near the surface where food was more abundant long enough to fill their stomachs.

We found high intraspecific diet overlap between allopatric and sympatric fish for both herring and pollock in autumn. Lack of intraspecific comparisons of allopatric and sympatric fish in each season is unfortunate, however, since differences in prey composition and the lower overlap observed between sympatric pollock and herring in October compared to November suggests that some prey partitioning does occur when resources are sufficiently abundant. Stomachs of sympatric pollock contained less food and fish were in poorer condition compared to allopatric pollock in late autumn, but these differences were not found for early autumn herring. These findings suggest that a combination of interference competition and seasonal or diel prey declines occurred. In another study, compared to allopatric herring, herring sympatric with sandlance that had similar diets shifted prey and ate less food, but they also shifted prey and ate less when sympatric with pink salmon that had different diets; these diet shifts and declines in food consumption were attributed to prey partitioning, predator size, and possibly to lower prey density (Sturdevant et. al, 1999). Boldt (1997) analyzed a subset of the pollock data included here, and speculated that differences in summer diet between pollock at different stations in central PWS might relate to differences in fish density that could lead to intraspecific competition, since pollock density was lowest at the only station of five where fish consumed large calanoids. However, we did not observe a clear pattern linking selection of any prey to lower fish density.

Although we could detect few differences in the quality of prey selected by fish in allopatric and sympatric aggregations, we did find differences in the quantity consumed by the two species. Trends toward decreased feeding from summer to late autumn were stronger for herring than for pollock, despite the fact that the early autumn and late autumn fish were not from the same cohorts. For herring, all feeding attributes declined from summer to late autumn. For pollock, fewer feeding declines were observed, and only for late autumn relative to summer. By late autumn, interspecific differences were also observed: proportionally fewer herring were feeding than pollock. Reduced total feeding and prey diversity, as well as increased diet overlap, could reflect declines in the numbers and types of prey available and a constriction in feeding for all fish. These factors could also indicate a density dependent convergence of the diets. Unfortunately, we have no zooplankton data for late autumn, but others have shown a steady decline in zooplankton biomass and macrozooplankters over the winter (Foy and Paul, 1999) or longer time scales (Tanasichuk, 1998a and b). In British Columbia during several years that encompassed the period of our study, adult abundance of *Thysanoessa spinifera* declined steadily due to warmer than usual conditions (Tanasichuk, 1998a), while production of *Euphausia pacifica* was higher in years of strong upwelling (Tanasichuk, 1998b). If the environmental changes in the Gulf of Alaska that have resulted in forage fish population shifts have also affected prey taxa such as euphausiids, then the trophic relationships and energy flows in PWS could be drastically altered. Unfortunately, long-term population data do not exist for most of these trophic levels.

Some of our results suggest that the seasonal decline in feeding occurs at the same time that total zooplankton in early autumn declines from summer high values. We estimated zooplankton densities in summer and early autumn of approximately 1.2 - 1.4 organisms per liter using different nets. However, results of our summer mesh trials suggested that zooplankton abundance estimates would have been greater had we used the same small-mesh net employed in autumn; if so, trends toward more intensive feeding in summer were supported by a food supply of small calanoids that was 4x greater than in early autumn that year, and was similar to densities measured the next summer with the small-mesh net (Sturdevant and Hulbert, 1999). Nonetheless, a decline in zooplankton density from summer to autumn does not change our conclusions because the fish switched away from small calanoids to larger prey which were not differentially selected by the two plankton nets. Even if our density estimates are not directly comparable between summer and autumn, our finding that the percentage composition of the zooplankton did not vary with mesh size allows valid comparisons of seasonal prey selection, since the selection index we used is calculated with percentages.

The similarity of dietary requirements between YOY pollock and herring could induce competition when these fish co-occur during periods or in places of low food availability, such as late autumn-winter. Seasonal movement of juvenile pollock and herring into small bays may maximize food resources at the same time it induces density dependent interactions, because stormy conditions and spring tides that mix different water masses may concentrate the prey remaining in autumn, such as larvaceans (Alldredge, 1982). We found significant diet overlap based on either numbers or biomass of prey in both the summer and autumn, even though these species may occur sympatrically only in the autumn. Significant overlap values were also calculated by Willette et. al. (1997), who found that diet composition and the degree of diet overlap changed over a 24-hour diel sampling event in late summer. Diets of pollock and herring from sympatric sites also overlapped by more than two times the diets of fish at allopatric sites (Willette et. al, 1997).

Other evidence suggests that seasonal changes in prey availability affect feeding and diet more than sympatry does. Willette et. al (1997) found highly similar diets between juvenile pollock and herring in late summer in PWS, based on small calanoids, including *Pseudocalanus* spp., and malacostracan prey. In October, we observed fewer non-feeders and guts that were more full than in November. Furthermore, diet overlap was considerably lower among the sympatric aggregations of pollock and herring from early autumn than those from late autumn. This low overlap resulted from the early autumn sympatric pollock being more selective of large calanoids and eating proportionally more euphausiids, while the herring selected larvaceans. A diversity of available prey enhances the likelihood of partitioning between species, decreasing diet overlap. In late autumn, euphausiids were prominent in the diets of both species in sympatric aggregations, more so than in the early autumn diets. Decreased density and diversity of prey increases the potential for diet overlap.

Although the diets of allopatric pollock and herring in our study overlapped extensively in summer, the vertical distributions of these species did not overlap, at least during the day. The summer pollock were captured in deep water (≥ 60m) during the day, when we expected less active feeding than for autumn fish captured nearer the surface (15-20 m depth) at night, but just as much food quantity was consumed. Similarly, the summer herring caught at the surface during the day consumed just as much prey as the early autumn herring caught slightly deeper at night. Similar prey could have been consumed by the two species at different times. Even if their vertical distributions did overlap at night (we had too few night samples to compare), having different principal times of day for feeding could result in highly similar diets without suggesting direct competition, since predation on the same prey resources would be temporally separated. Different feeding periodicities could result in indirect competition if prey resources are limited, however.

These feeding contrasts suggest that the two species' diel rhythms change between seasons or that they feed throughout the day. Our comparisons of day-night condition of prey also suggest that daily time of peak feeding could differ for the two species. Digestion indices indicated that pollock fed principally at night, while herring apparently fed principally during the day. Diel studies reported similar patterns of feeding for pollock (Merati and Brodeur, 1996; Brodeur and Wilson, 1996) and herring (Willette et. al, 1997; Blaxter and Hunter, 1982; DeSilva, 1972). Therefore, some of the seasonal differences in feeding we have demonstrated may actually be diel differences. However, they do not explain the lack of differences between summer and early autumn feeding for both species or the existence of differences between early autumn and late autumn feeding for herring. Similarly, since the autumn allopatric samples were collected earlier in the day than the sympatric samples, the fact that allopatric pollock stomachs were more full than sympatric stomachs in late autumn might be related to feeding time rather than trophic interactions such as interference competition, particularly since euphausiids (prey with a strong DVM pattern) were a smaller proportion of the diet by number and biomass. However, the fact that allopatric herring stomachs were no more full than sympatric stomachs in early autumn at a time of day when the state of digestion indicates that they should have been feeding more suggests that a factor other than sympatry is involved. Unfortunately, our samples were not extensive enough to demonstrate a seasonal diel feeding or depth-related pattern that might occur with a changing light regime and our allopatric-sympatric comparisons are based on small sample sizes. However, Krieger (1985) speculated that YOY pollock switch from feeding principally during the day in summer to feeding at night in autumn based on a change in digestion of prey with time of day.

Trends toward greater size in late autumn were stronger for pollock than for herring. Both pollock and herring were larger in early autumn than in summer, but only pollock were larger in late autumn than in early autumn. Pollock also appeared to be in better condition than herring, since only their weight increased from early to late autumn. Such growth is advantageous for survival through the extreme conditions of coming winter. Juvenile pollock tested between the temperatures of 3° C to 7.5° C exhibited a linear increase in consumption (%BW/day) with temperature, but grew more rapidly at colder temperatures under conditions of low food. The maintenance ration for these fish was also lower at the colder temperature (Smith et. al, 1986). The pollock in our study consumed well above this maintenance ration in all seasons, but the low prey %BW of herring in late autumn could indicate starvation.

For pollock, the larger size in November compared to October, along with the smaller size of sympatric fish compared to allopatric fish in November, suggests that pollock continue to feed in late autumn but could be at a competitive disadvantage when they co-occur with herring. For herring, the similar size of both allopatric and sympatric fish in October along with unchanged sympatric size in November suggests that seasonal feeding declines are more important than sympatry. These species may have different strategies for overwintering, as suggested by differences reported for feeding success. Among YOY herring, the proportion of empty stomachs peaked in December (Foy and Paul, 1999), but among YOY pollock, no empty stomachs were observed in any period (Krieger, 1985). In terms of avian predation, not only was there a major difference in the nutritional quality between these fish species--pollock lipid content was low compared to herring--but lipid content also varied in opposite directions with age (Anthony and Roby, 1997). Herring lipid content increased with age and pollock lipid content decreased with age. Therefore, the feeding differences we observed support the ideas that herring are dependent on stored energy to survive, while pollock allocate energy from year round feeding for somatic growth.

The larger size of the November pollock should have been accompanied by consumption of greater prey biomass compared to the smaller October pollock, but only the allopatric pollock ate more. Sympatric pollock were larger but did not consume more prey. We observed decreases in prey numbers from early to late autumn that are compatible with changes from small to larger prey of similar caloric density. However, the seasonal increase in predation on large prey by both species did not coincide with size increases for both species. Only the late autumn pollock were larger than their early autumn conspecifics. A size no larger among late autumn herring than either early autumn herring group is consistent with our finding that they fed less in late autumn than in early autumn, but larger size of the pollock is not consistent with our finding that these fish also fed less in late autumn than in early autumn. Herring were apparently affected by diminished prey resources sooner than pollock were. If herring do enter the winter lagging even a month behind pollock in the accumulation of winter energy stores, the edge gained by pollock could enhance their potential to supplant herring in PWS. However, our findings could relate to interannual differences instead of seasonal differences. Regardless of the source of the differences, the pattern for pollock differs from the pattern for herring. Foy and Paul (1999) found that herring whole body energy content increased from October to November, then declined through the winter. A steady decline in zooplankton biomass between the months of October and February in their study coincided with feeding decline and reliance on stored energy. Krieger (1985) observed pollock feeding throughout the year, with stomach fullness highest in July (100%) and lowest in December (50%). He also observed declining feeding rates in October compared to August and September, not only in terms of stomachs fullness, but in relation to prey numbers because of the switch from small prey to larger prey.

One explanation for the continued growth of pollock in late autumn is lower energetic requirements. Energy can be conserved during times of reduced prey by altering behaviors to decrease metabolic costs, such as restricting movement or residing in regions of colder ambient temperature, for example deeper water (Sogard and Olla, 1996). If environmental temperatures drop after October in PWS, growth could continue under lower food conditions (Smith and Paul, 1986). Although it is reasonable to assume that zooplankton becomes less available during this period of transition to winter, we do not have zooplankton data from November, 1994 to compare availability of the numerically prominent prey in the diets at that time, large calanoids and larvaceans.

The seasonal distributions of YOY pollock and herring are partially determined by adult life history traits. Herring spawn nearshore, inter- and subtidally; their adhesive eggs are retained upon algae and benthic structure. After hatching and through the juvenile stage, larval herring may be transported away from spawning areas or may remain in the nearshore bays (Lassuy, 1989; Stokesbury et al., 1998). The onset of schooling behavior occurs at metamorphosis at 25-40 mm, at approximately 10 weeks of age (Lassuy, 1989; Gallego and Heath, 1994). In contrast, pollock broadcast spawn their eggs in deep water offshore (Smith, 1981); the demersal eggs may be carried throughout PWS by advective currents. Pollock larvae may hatch in a nearshore retention area or in the more open areas of the sound, and therefore be exposed to different rates of predation, cannibalism and advection. Large numbers of YOY pollock have been observed in nearshore bays, which may be important nursery areas (Smith et al., 1984; Brodeur and Wilson, 1996; Wilson, 1997).

For sympatry to occur, the distribution of juvenile walleye pollock and Pacific herring must overlap in three dimensions: time (seasonal and diel), and both horizontal and vertical space. Since both species' patterns of movement change ontogenetically in each of these dimensions, their behaviors suggest that utilization of similar habitats could occur at different times and the degree of spatial overlap is likely to vary. In general, juvenile herring school near the bottom along shore during the day, then move up to the surface at dusk and disperse (Blaxter and Hunter, 1982; Lassuy, 1989; Haegele, 1997). Early YOY pollock stayed principally in surface water above the thermocline, performed a DVM, and dispersed or moved inshore at night; depth distribution increased from summer to autumn (Bailey, 1989; Brodeur and Wilson, 1996; Olla et al, 1996). In Auke Bay in southeastern Alaska, demersal YOY pollock inhabited nearshore waters beginning in July, remaining until October at a size of 92 mm. These nearshore juvenile pollock were caught in summer at 10-20 m depths during the day, in early autumn at 10-40 m depths mainly during the day, but in late autumn at 40-60 m depths (near bottom) mainly at night (Krieger, 1985). Observations of YOY pollock at some of these same sites in Auke Bay were consistently made over 22 years of diving, confirming non-random habitat utilization (Carlson, 1995). Herring and pollock in PWS were depth stratified in July, October, and March, with herring occupying the upper 30 m of the water column and pollock associated with the bottom (Stokesbury et al., 1998). Both species aggregated in bays in July and October, with herring in tighter schools than pollock. Perhaps summer growth allows both species to reach an early autumn size great enough to promote volitional migration into common nearshore areas. The summer-autumn difference of 30-40 mm in mean FL that we observed in both pollock and herring could serve this function. Some authors have suggested the two species simply have an affinity for the same habitats, rather than a strong species association (Brodeur and Wilson, 1996). Yet at least some of the population occurs sympatrically in summer and autumn (Haldorson et. al, 1996; Willette et. al, 1997). Sympatry may be limited in spring and early summer because of different hatching habitats, time to metamorphosis, and differential rates or timing of migration into common areas. Unpublished seasonal data from SEA, 1994 (M. Willette, pers. comm.) showed that, of the monthly sets catching herring or pollock from April to September, after May, > 50% of herring sets also caught pollock, and after July, > 50% of pollock sets also caught herring. This pattern suggests that sympatry increases seasonally, with highest rates of co-occurrence in the autumn. However, fishing gear and duration of the tows are unknown components that may mask any micro-scale spatial segregation of the species.

Pollock migration follows both diel and ontogenetic rhythms on horizontal, vertical and seasonal scales (Brodeur and Wilson, 1996). In the laboratory, Pacific herring feeding response decreased in October-November through February-March, when they again began to put on fat and condition (Stacy and Houston, 1982, in Lassuy, 1989). In this study, surface temperatures where fish were located were lower in late autumn than in early autumn. Surface temperatures were approximately 12°C in summer, 10°C in early autumn, and 7-8°C in late autumn (Boldt, 1997). The thermocline, when present, tended to be slightly deeper in late autumn, progressing from 40-50 m in July-August to 50-60 m in November; temperatures below the thermocline remained at 5-6°C in each season. The vertical distribution of YOY pollock and herring coincided with the temperature maximum in November (Haldorson, 1995). If this pattern of water column conditions is typical, then movement from cool, deeper offshore locations in summer to shallow water in bays in autumn achieved little change in the temperature quality of habitat occupied between summer and autumn. Differences in other qualities may be more important. For example, food production may continue later into the autumn in bays that are warmer and more nutrient-rich than offshore, or the little food produced late in the year may be concentrated in bays by hydrographic features. In July and October, surface waters of PWS bays were colder than outside the bays; the pattern reversed in March (Stokesbury et. al, 1998). In combination with better feeding conditions and favorable hydrographic conditions, movement into the bays by autumn could prolong seasonal feeding.}}

It is clear from acoustic estimates of biomass that pollock and herring populations vary interannually and seasonally. In a review of the distributions and species associations of pollock in NMFS historical bottom trawl surveys in the Gulf of Alaska, Shima et al (1996) reported a lower association of YOY pollock with herring after 1980. In contrast to 1995, the APEX July, 1996 surveys caught only two sets of YOY pollock sympatric with other species; they were seined nearshore and were sympatric with species other than herring (Haldorson et al., 1997; Sturdevant et al., 1999). This fits in with the timing of inshore movement documented by Krieger (1985). The APEX project has shown that pollock and herring frequently associate with other species (Haldorson 1995, 1996, 1997).

It seems clear that, with an affinity for similar habitats and similar food requirements, juvenile pollock and herring distributions will overlap. If schools are less tightly aggregated during food searching, which expands the total volume occupied while decreasing competition between individuals, two schools have a greater tendency to overlap. YOY pollock forage in socially interactive groups when food occurs in ephemeral patches (Ryer and Olla, 1992; 1995) and the activity of feeding in schools attracts other fish. With dispersed food, they ignore others' behavior and feed more independently, but may be more aggressive toward intruders. Hunger stimulated increasingly active searches for food. Laboratory studies also showed that smaller individuals formed less cohesive schools and were less active than larger individuals. More studies comparing the spatial and temporal patterns of distribution are needed to clarify the extent and frequency of YOY pollock and herring interactions in Prince William Sound and elsewhere.

The potential for food competition between pollock and herring appears to be greater in the autumn, particularly late autumn, than in the summer. Clearly, both pollock and herring consumed the same types of food in different proportions in each season, whether allopatric or sympatric. Although their diets are very similar in all three seasons, the synergistic effects of increased rates of sympatry and declining zooplankton stocks in autumn may cause both feeding declines for these species and higher diet overlap between them in late autumn. This occurs at the same time that approaching winter hydrography creates more metabolically demanding conditions. Previous studies have shown that stored energy is used extensively by herring of all ages to survive the winter; autumn may be the most important for YOY herring, which frequently had too little fat stored to persist through lean times (Paul, 1997; Paul et. al, 1998; Paul and Paul, 1998; Foy and Paul, 1999). Large-scale changes in the environment, such as ENSO events which cause changes in water temperatures and current patterns, may have greater effects on some fish populations than dramatic, one-time events such as the *Exxon Valdez* oil spill. If walleye pollock have a competitive advantage over Pacific herring in the critical autumn period, dramatic negative effects on the PWS marine bird and mammal populations which rely on these forage fish resources could occur. However, increasing numbers of another energy-dense forage species, the sandlance *Ammodytes hexapterus*, have been reported in PWS recently (Brown et al., 1997??; Kuletz et al.??). The trophic interactions between sandlance and walleye pollock, if any exist, are unknown. Additional and changing species interactions are likely to occur with such community changes, and result in unknown ecosystem impacts. Therefore, long-term monitoring is essential to improve understanding of the PWS ecosystem. Continued studies in PWS will expand our understanding of interactions between pollock, herring, and other forage species.

Acknowledgments - Chapter 2

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Table 1. Characteristics of summer and autumn sampling stations where YOY Pacific herring and walleye pollock were collected in 1994 and 1995 from Prince William Sound, Alaska. Abbreviations: T = Trawl, D = Dipnet, B = beach seine, NE = Northeast, C = Central, SW = Southwest. Ten fish per species were examined from each station. Zooplankton were collected at most fishing stations only in 1995; numbers in parentheses indicate adjacent stations substituted when zooplankton were not collected.

year-cruise-station-gear	region and location	bottom depth (m)	gear depth (m)	number caught	sample day	start time
		SUMMER				
Allopatric Pacific Herring						
95-1-27D (22)	NE, Port Fidalgo	6	0	271	26-Jul-95	19:30
95-1-110B (112)	C, Southeast Eleanor	3	1	??	09-Aug-95	15:30
Allopatric Walleye Pollock						
95-1-3T	C, Applegate Rocks	162	60	74	22-Jul-95	12:33
95-1-5T	C, Seal Island	174	50-60	31	22-Jul-95	17:04
95-1-19T (84)	C, Lilhengren Passage	70-130	50	139	27-Jul-95	15:37
95-1-53-1T	C, Montague Point	110	50-60	??	01-Aug-95	9:17
95-1-53-2T	C, Montague Point	110	20	694	01-Aug-95	9:55
95-1-54T	C, East Knight Island	130-160	60	1056	01-Aug-95	12:14
95-1-56T	C, Seal Island	200	80	1689	01-Aug-95	15:27
95-1-57T	C, Seal Island	160	75-80	386	01-Aug-95	17:30
95-1-58T	C, North Knight Island	170	75-80	843	02-Aug-95	9:25
95-1-62-2T	C, East Eleanor Island	70-120	50-60	293	02-Aug-95	15:16
95-1-108T (107)	C, Southeast Knight Is.	25-50	10-20	22	08-Aug-95	21:57
95-1-112T	C, South Naked Island	80-140	80	504	10-Aug-95	13:13
		EARLY AUTUMN				
Allopatric Pacific Herring						
95-2-5T	C, East Naked Island	50-90	45-65	89	13-Oct-95	11:31
Sympatric Walleye Pollock/Pacific Herring						
95-2-6T	NE, Galena Bay	220	10-15	4156/425	13-Oct-95	21:43
95-2-7T	NE, LandlockedBay	95-106	10-20	535/592	14-Oct-95	21:58
		LATE AUTUMN				
Allopatric Walleye Pollock						
94-2-5T	SW, Icy Bay	110-150	35-50	61	08-Nov-94	15:32
Sympatric Walleye Pollock/Pacific Herring						
94-2-6T	NE, Galena Bay	100-150	15-20	145 / 26	10-Nov-94	22:42
94-2-7T	NE, Port Gravina	118	15-21	14/398	12-Nov-94	22:33

Table 2. Size and feeding attributes for allopatric and sympatric YOY walleye pollock and Pacific herring (n = 10 each) from PWS stations in summer, 1995 and autumns, 1994-1995. Standard error of the means (SE) in parentheses. Abbreviations as in Table 1.

year-cruise-stn-gear	FL (mm)	% feeders	% fullness index	content %BW	prey %BW	total number of prey	total weight of prey (mg)
SUMMER							
Allopatric Pacific Herring							
95-1-27D	76 (2.0)	100	100	3.8 (0.4)	23.8 (3.3)	5968.7 (604.3)	540.71 (62.8)
95-1-110B	30 (0.3)	60	25	0.0 (0.0)	1.3 (0.5)	52.6 (28.6)	1.55 (0.7)
Allopatric Walleye Pollock							
95-1-3T	59 (1.5)	60	25	0.7 (0.2)	2.1 (1.4)	171.0 (113.0)	14.25 (7.5)
95-1-5T	54 (1.2)	60	50	1.2 (0.3)	3.2 (1.3)	37.1 (14.1)	27.27 (12.0)
95-1-19T	58 (1.7)	80	50	1.8 (0.5)	1.1 (0.4)	12.4 (3.6)	12.11 (5.0)
95-1-53-1T	56 (1.1)	100	75	1.1 (0.1)	1.6 (0.3)	154.1 (27.5)	13.35 (2.4)
95-1-53-2T	62 (1.3)	100	75	1.2 (0.2)	3.0 (0.7)	261.5 (38.9)	34.84 (5.7)
95-1-54T	54 (1.6)	60	25	1.3 (0.3)	0.7 (0.3)	53.5 (30.2)	4.68 (2.2)
95-1-56T	58 (1.8)	50	25	0.7 (0.2)	0.4 (0.2)	21.8 (10.5)	4.86 (2.1)
95-1-57T	58 (2.6)	80	50	1.4 (0.5)	3.1 (2.0)	45.0 (19.6)	38.59 (26.0)
95-1-58T	56 (2.1)	100	100	2.2 (0.4)	3.5 (1.1)	242.0 (84.8)	33.70 (9.6)
95-1-62-2T	53 (1.1)	90	50	1.4 (0.2)	1.7 (0.8)	17.2 (4.3)	15.99 (7.8)
95-1-108T	66 (1.4)	100	100	2.7 (0.4)	13.8 (2.3)	2489.5 (351.1)	193.24 (24.6)
95-1-112T	65 (2.8)	90	50	0.9 (0.1)	0.9 (0.3)	20.6 (4.5)	14.79 (5.0)
EARLY AUTUMN							
Allopatric Pacific Herring							
95-2-5T	92 (1.4)	100	50	1.4 (0.1)	1.6 (0.3)	385.9 (89.5)	103.36 (19.5)
Sympatric Pacific Herring							
95-2-6T	84 (4.3)	90	75	1.2 (0.2)	1.4 (0.4)	927.1 (303.6)	58.63 (11.4)
95-2-7T	95 (3.3)	90	50	0.5 (0.1)	0.8 (0.5)	271.1 (103.7)	84.50 (62.3)
Sympatric Walleye Pollock							
95-2-6T	93 (2.8)	100	100	1.2 (0.2)	1.2 (0.2)	78.3 (14.2)	61.26 (14.4)
95-2-7T	90 (2.4)	90	50	0.5 (0.1)	0.4 (0.1)	46.8 (15.0)	16.79 (3.9)
LATE AUTUMN							
Allopatric Walleye Pollock							
94-2-5T	111 (1.6)	100	100	1.8 (0.4)	0.8 (0.2)	722.6 (156.2)	71.62 (11.4)
Sympatric Pacific Herring							
94-2-6T	93 (4.1)	20	10	0.1 (0.0)	0.0 (0.0)	13.8 (9.0)	0.78 (0.5)
94-2-7T	97 (4.2)	70	25	0.5 (0.2)	0.4 (0.2)	31.8 (14.7)	25.64 (12.7)
Sympatric Walleye Pollock							
94-2-6T	100 (3.1)	70	50	0.5 (0.5)	0.2 (0.1)	18.5 (5.1)	18.29 (9.2)
94-2-7T	111 (1.7)	60	25	0.4 (0.1)	0.2 (0.1)	6.4 (1.9)	14.56 (7.5)

Table 3. *Seasonal fish size and feeding attributes (mean and SE) of YOY walleye pollock and Pacific herring from Prince William Sound in 1994-1995. Measures for autumn allopatric (Allo.) and sympatric (Symp.) subgroups are shown for each species.*

	n	FL	wet weight (g)	% non-feeders	% fullness index	content % BW	prey %BW	total number of prey	total weight of prey (mg)
Walleye Pollock									
Summer (Allo.)	12	58.0 (1.0)	1.1 (0.1)	19	50 (5)	1.4 (0.1)	2.9 (0.4)	294 (68)	34.0 (5.6)
Early autumn (Symp.)	20	91.5 (2.4)	5.0 (0.3)	5	75 (10)	0.8 (0.3)	0.8 (0.1)	63 (11)	39.0 (8.9)
Late autumn	30	107.2 (2.0)	8.1 (0.3)	23	50 (10)	0.9 (0.2)	0.4 (0.1)	249 (80)	34.8 (7.2)
Allopatric	10	111.0 (1.6)	9.1 (0.4)	0	100 (5)	1.8 (0.4)	0.8 (0.2)	723 (156)	71.6 (11.4)
Sympatric	20	105.4 (2.1)	7.6 (0.5)	35	25 (10)	0.4 (0.1)	0.2 (0.1)	13 (3)	16.4 (5.8)
Pacific Herring									
Summer (Allo.)	20	52.7 (2.4)	1.5 (0.3)	20	75 (10)	1.9 (0.5)	12.6 (3.1)	3011 (739)	271.1 (69.0)
Early autumn	30	90.2 (2.0)	6.6 (0.3)	7	50 (5)	1.0 (0.1)	1.3 (0.2)	528 (119)	82.2 (21.6)
Allopatric	10	91.6 (1.4)	6.8 (0.4)	0	50 (10)	1.4 (0.1)	1.2 (0.1)	386 (90)	103.4 (19.5)
Sympatric	20	89.5 (3.0)	6.5 (0.6)	10	75 (10)	0.9 (0.1)	0.9 (0.1)	599 (173)	71.6 (31.0)
Late autumn (Symp.)	20	94.6 (2.4)	6.9 (0.3)	55	10 (10)	0.3 (0.1)	0.2 (0.1)	23 (9)	13.2 (6.8)

Table 4. Horn's Overlap Index values for total numbers and biomass of prey consumed by YOY walleye pollock and Pacific herring caught separately in summer and together in early and late autumn in Prince William Sound, 1994-1995. No summer sympatric fish were available and autumn allopatric fish were not caught in the same year. Overlap greater than 0.60 indicates similar diets (see text).

		Overlap in Number		Overlap in Biomass	
Year-Station	Region	by prey species	by prey category	by prey species	by prey category
Summer Allopatric Fish					
95	C[1]	0.79	0.82	0.76	0.83
Early Autumn Sympatric Fish					
95-6	NE	0.16	0.22	0.44	0.64
95-7	NE	0.43	0.48	0.53	0.69
average	NE	0.31	0.43	0.55	0.69
Late Autumn Sympatric Fish					
94-6	NE	0.69	0.94	0.08	0.39
94-7	NE	0.86	0.91	0.88	0.91
average	NE	0.87	0.97	0.88	0.95
Allopatric-Sympatric fish					
Early Autumn Herring		0.51	0.89	0.56	0.93
Late Autumn Pollock		0.87	0.91	0.56	0.73

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[1] One set of herring was caught in the NE region.

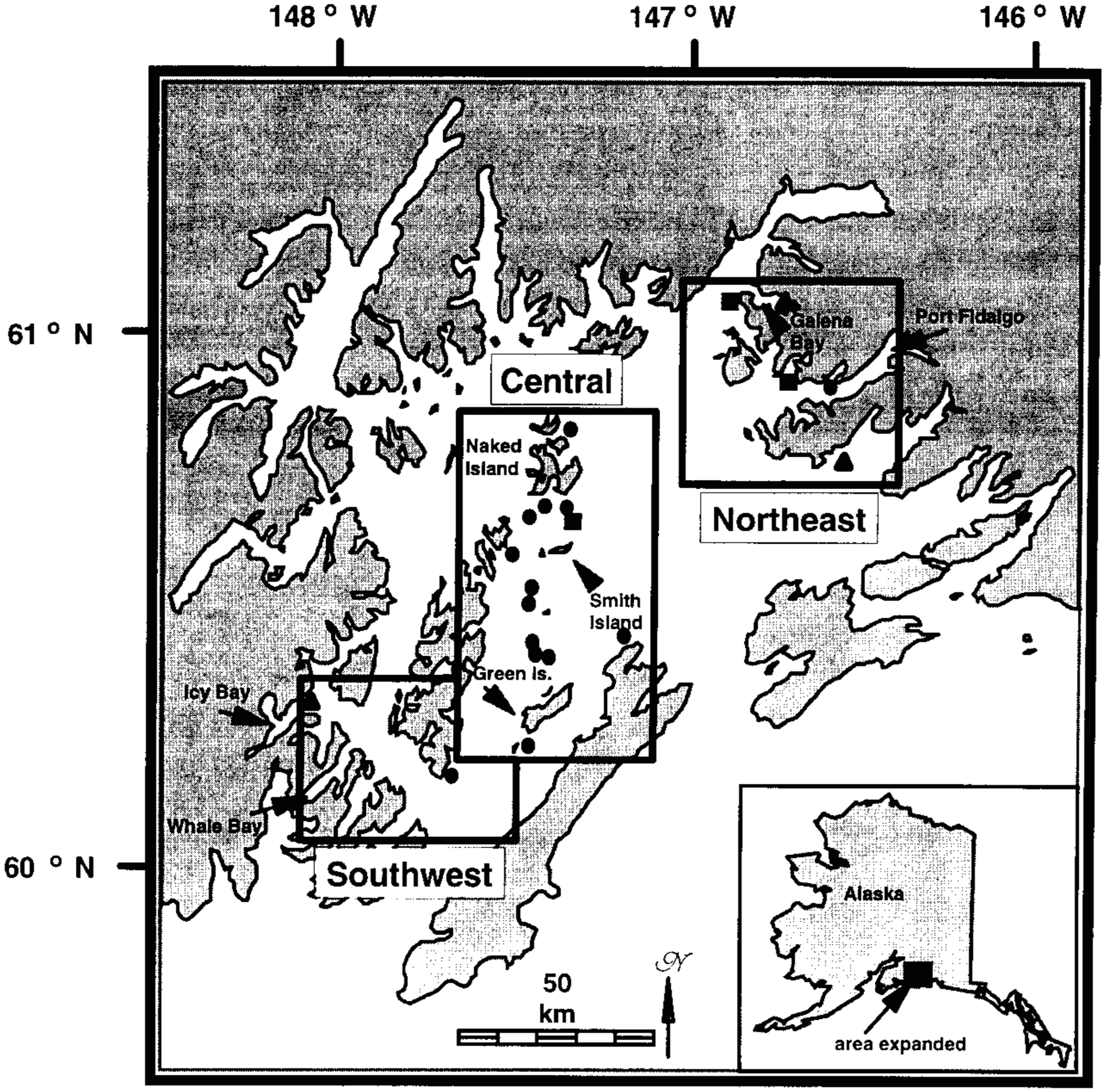

Figure 1. Sampling regions and stations for YOY walleye pollock and Pacific herring diet samples collected in Prince William Sound, Alaska. Circles: July-August, 1995; squares: October, 1995; triangles: November, 1994.

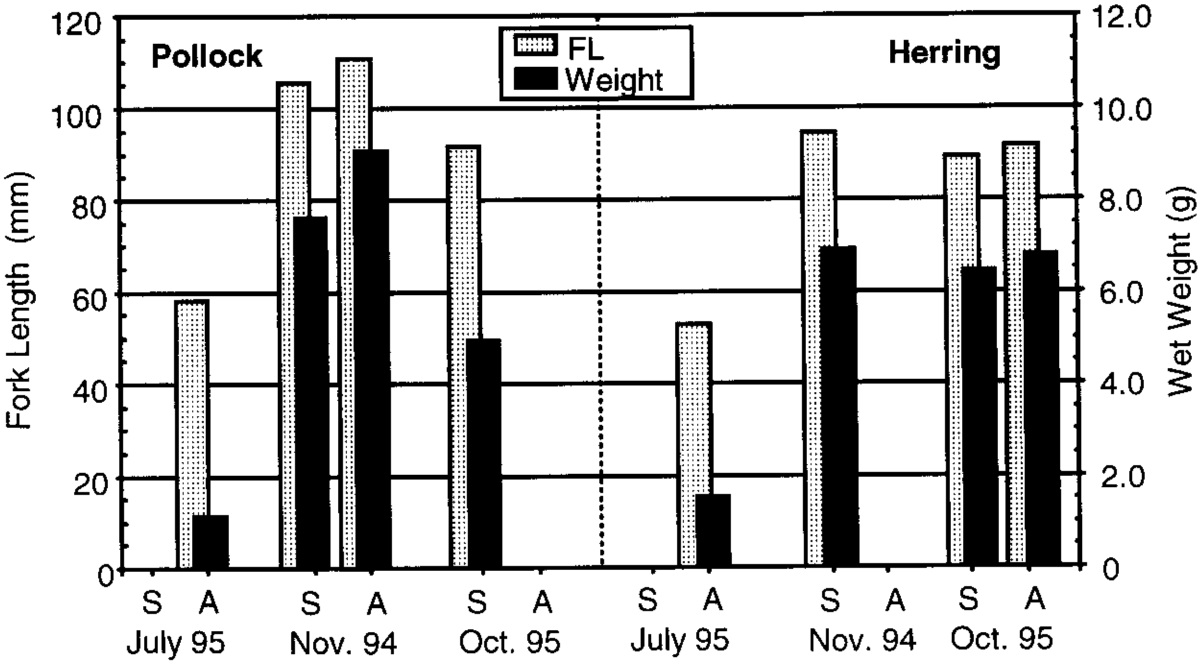

Figure 2. Size of YOY walleye pollock and Pacific herring collected seasonally in PWS from sympatric (S) and allopatric (A) aggregations.

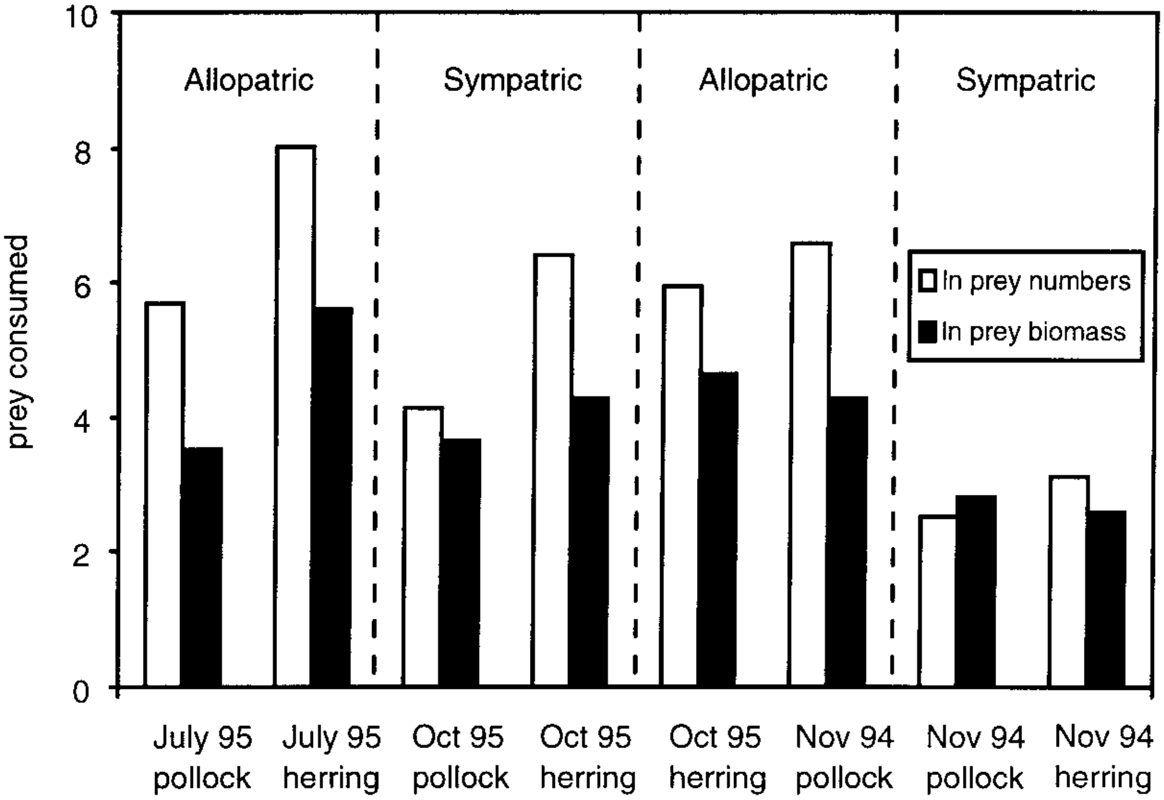

Figure 3. Total number and total biomass of prey (ln-transformed means) consumed by allopatric and sympatric YOY walleye pollock and YOY Pacific herring from Prince William Sound, Alaska in summer and early autumn, 1995, and late autumn, 1994.

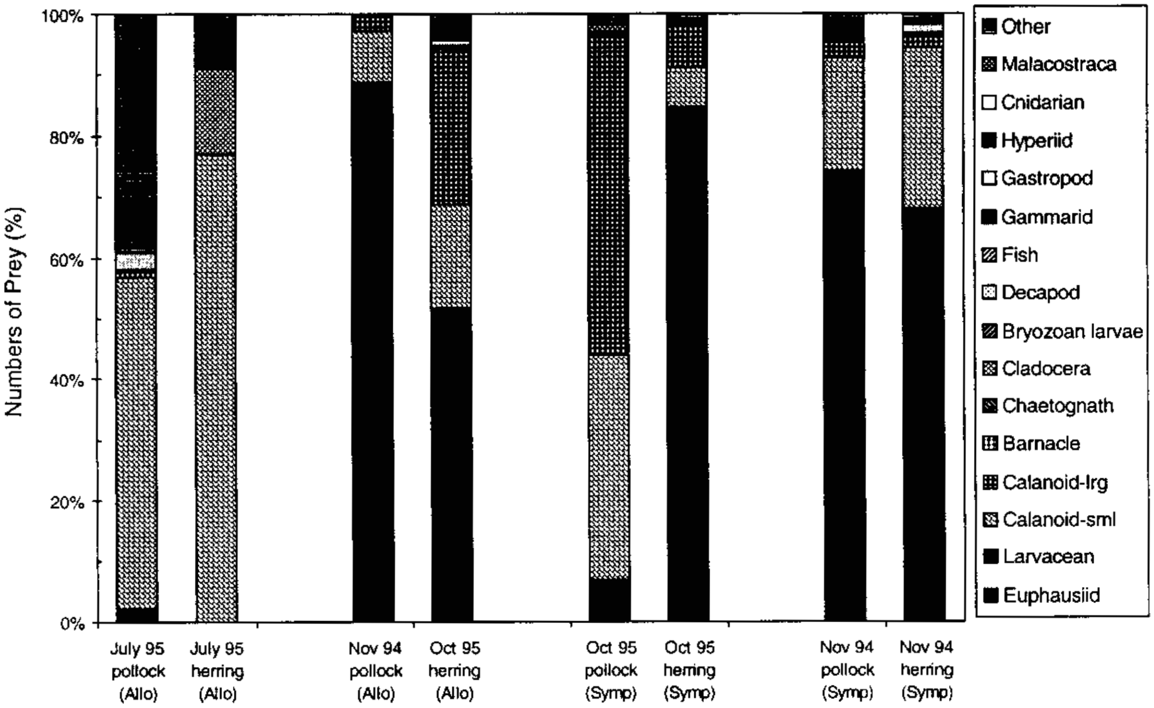

Figure 4. Percent total number of prey consumed by YOY walleye pollock and Pacific herring from sympatric and allopatric aggregations in Prince Willam Sound, Alaska, in July-August, 1995, October, 1995 and November, 1994.

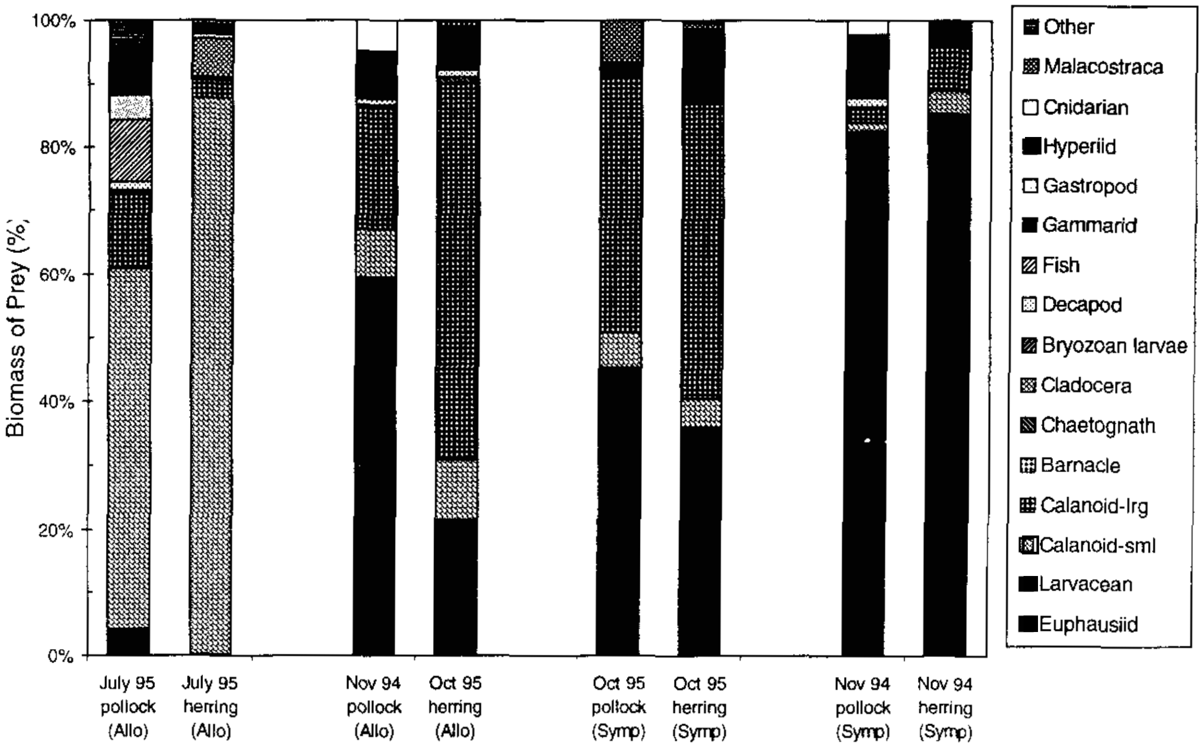

Figure 5. Percent total biomass of prey consumed by YOY walleye pollock and Pacific herring from sympatric and allopatric aggregations in Prince Willam Sound, Alaska, in July-August, 1995, October, 1995 and November, 1994.

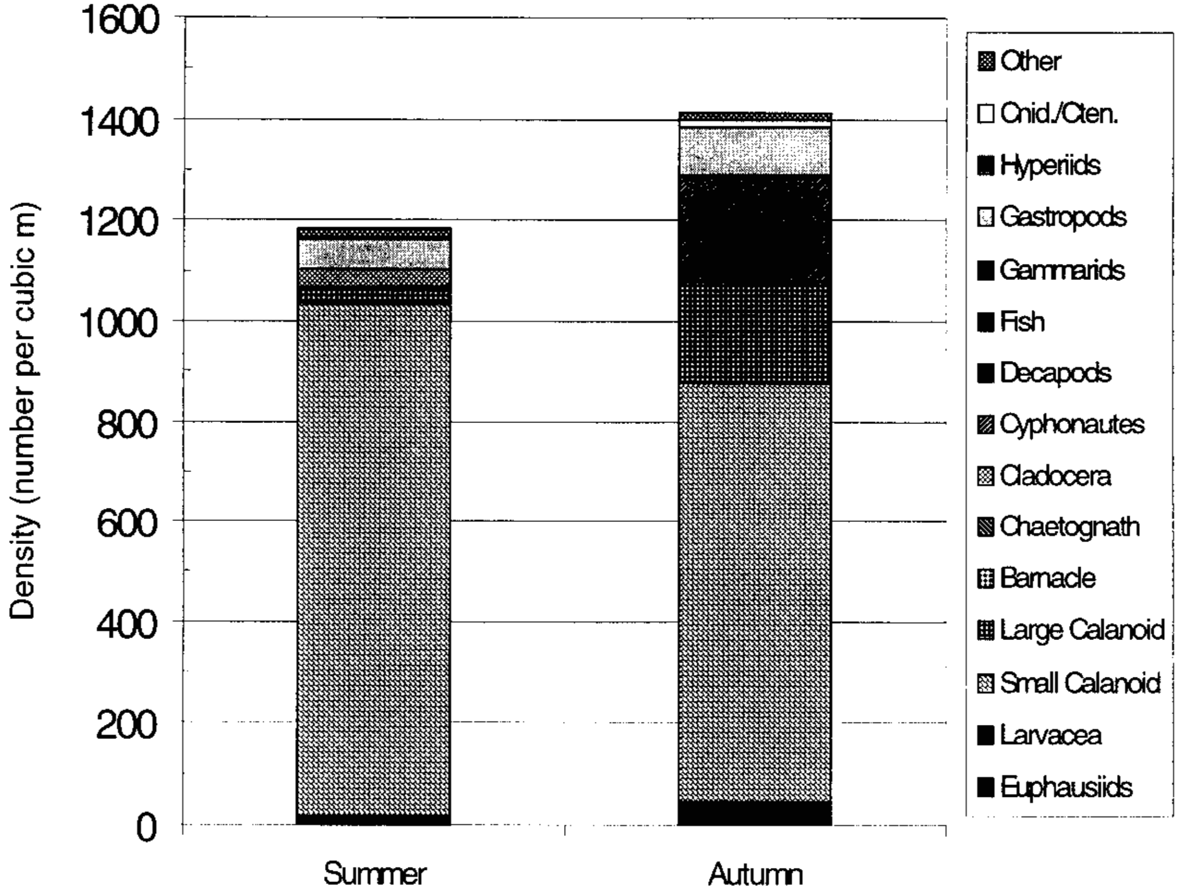

Figure 6. Seasonal zooplankton density and composition by principal taxa in Prince Willam Sound, Alaska, 1995.

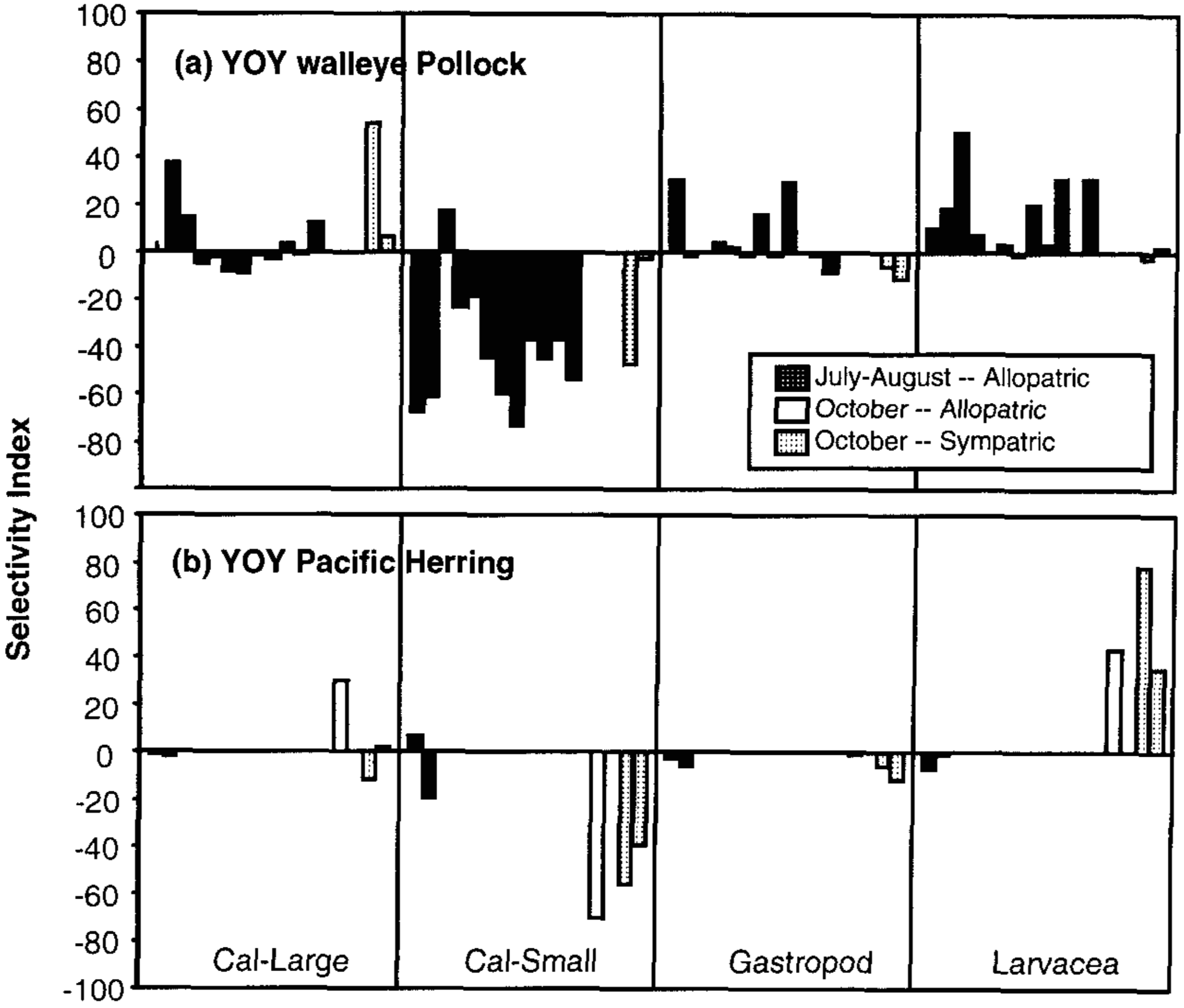

Figure 7. Strauss' Selectivity Index for principal prey groups of (a) YOY walleye pollock and (b) YOY Pacific herring from PWS in July-August and October, 1995. Selection was not computed from November, 1994 because zooplankton were not collected. Positive values indicate selection, negative values avoidance. Each bar represents 10 fish from a single station (stations in the same order as in Table 1).

Chapter 3. Diet Overlap, Prey Selection, and Potential Food Competition among Allopatric and Sympatric Forage Fish Species in Prince William Sound, 1996

Authors: Molly V. Sturdevant and Leland B. Hulbert

Abstract - Chapter 3

We examined forage fish trophic interactions as part of a program studying the abundance, distribution and composition of forage fish populations in Prince William Sound (PWS). Understanding variations in the feeding ecology of these prey of seabirds may help to explain the health of avian predator populations which were impacted during the *Exxon Valdez* Oil Spill.

Juvenile Pacific herring (*Clupea pallasi*), Pacific sandlance (*Ammodytes hexapterus*), and pink salmon (*Oncorhynchus gorbuscha*) occurred sympatrically in 21-41% of the hauls where at least one of the species was present. We examined 467 stomachs of these species collected near shore by beach and purse seine during July, 1996. We also analyzed 50 plankton samples collected concurrently in 20 m vertical hauls with a 0.5 m diameter ring net (243 μm mesh). We compared fish feeding, prey selection from zooplankton, and fish diet overlap in areas with allopatric (single species) and sympatric (multi-species) aggregations.

Zooplankton numerical composition by species was similar at all aggregations (~80% small calanoids). Mean densities ranged from 1800-4200 organisms*m^{-3}. Juvenile herring and sandlance diets were similar (overlap > 60%) only when both were allopatric. Both species consumed small calanoids and larvaceans in proportion to their abundance in the zooplankton, but small calanoids predominated in the diets. Pink salmon diets were not similar to those of either herring or sandlance. Pink salmon selected larvaceans and avoided calanoids. Sandlance were the most adaptable of these planktivores, but pink salmon and herring adhered to similar diets whether allopatric or sympatric.

Changes in diet similarity and declines in prey utilization indicated potential competition among forage species. Diet composition of both herring sympatric with sandlance and sandlance sympatric with herring (n = 4 sets each) shifted significantly ($P < 0.05$), but not dramatically, from that of herring or sandlance in allopatric aggregations (n = 10 and 14 sets, respectively), providing evidence for partitioning of prey. Sandlance also shifted diets when sympatric with pink salmon. Diet composition of juvenile herring and pink salmon also shifted significantly ($P < 0.05$) between fish in allopatric (n = 10 and 3 sets, respectively) and sympatric (n = 6, 4 sets, respectively) aggregations, but fish size may have influenced prey composition.

Feeding declines were the most dramatic indication of competition. Measures of food consumption and fullness declined significantly ($P < 0.05$) for all species in sympatric aggregations compared to those in allopatric aggregations. Only sandlance sympatric with pink salmon did not feed less. Feeding declines did not appear to be related to fish size or density, but may have been related to decreased zooplankton densities in areas of sympatric aggregations. Our results suggest that competitive interactions limit the feeding of these sympatric forage species,

which partially accommodate with shifts in overall diet. The health of forage populations could be affected by such competition if sympatry occurs regularly under conditions of limited food availability.

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Table 1. Sampling region, location, sampling day and time, times at low and high tide, and numbers of fish caught at stations with allopatric and sympatric aggregations of juvenile Pacific herring, Pacific sandlance, and pink salmon in PWS during July, 1996. Samples from stations C and F were collected outside survey sites. Gear abbreviations: BS = beach seine, PS = purse seine, Cast = cast net, Hand = hand dug, P = plankton net. Regions refer to map Figure 1.

Table 2. Mean size and age (A.C.) of fish, preserved fork length (FL) and wet weight, numbers and weights of prey consumed, stomach fullness index, number of empty stomachs (Emp), and prey percent body weight for sets of allopatric and sympatric juvenile Pacific herring, Pacific sandlance and pink salmon at stations in PWS during July, 1996. Ten fish from each station were examined (*indicates exceptions of n = 9). Abbreviations: sem = standard error of the mean.

Table 3. Probability results from 2-way ANOVA on ranks of fish size and measures of total feeding in areas with different species aggregations. The two factors used were "fish species" (Pacific herring, pink salmon and Pacific sandlance) and "aggregation type" (allopatric\sympatric). Specific paired comparisons were performed when $P < 0.05$ for the interaction terms.

Table 4. Fork lengths and measures of total feeding for three forage species in allopatric and sympatric aggregations in PWS during July, 1996. Probability (P) values are results of Rank Sum Tests comparing species values between aggregations. Abbreviations: md = median, sem = standard error of the mean, T = trace contents.

Table 5. Probability results from 2-way ANOVA on ranks of density (numbers*m^{-3}) and percent density of zooplankton by taxonomic category using the factors "fish species" (Pacific herring, pink salmon and Pacific sandlance) and "aggregation type" (allopatric or sympatric). Specific paired comparisons were performed when the $P < 0.05$ for the interaction terms.

Table 6. Zooplankton mean density (numbers*m^{-3}) and biomass (mg*m^{-3} wet weight) available to juvenile Pacific herring, Pacific sandlance and pink salmon at stations corresponding to allopatric and sympatric aggregations sampled in PWS during July, 1996. Replicate zooplankton samples were collected in vertical hauls at each station using a 0.5 m diameter ring net with 243 mm mesh. Abbreviations: sem = standard error of the mean.

Table 7a. Zooplankton density (number* m^{-3}) and percent density by taxonomic group and total organisms at areas of allopatric and sympatric aggregations of Pacific herring (H). SL = Pacific Sandlance, PS = Pink Salmon, md = median, sem = standard error of the mean.

Table 7b. Zooplankton density (number* m^{3}) and percent density by taxonomic group and total at aggregations of allopatric and sympatric pink salmon (PS). H = Herring, SL = Sandlance, md = median, sem = standard error of the mean.

Table 7c. Zooplankton density (number * m^{3}) and percent density by taxonomic group and total at aggregations of allopatric and sympatric sandlance (SL). H = Herring, PS = Pink Salmon, md =

median, sem = standard error of the mean.

Table 8. Diet similarity (PSI) by percent number and percent biomass of prey species within and between forage species in allopatric and sympatric aggregations in PWS during July, 1996. Diet similarity > 60% is significant.

Table 9. Probability results from 2-way ANOVA on ranks of prey number and percent number, prey biomass and percent biomass, and prey selection by taxonomic category in areas with different fish species aggregations. The two factors used were "fish species" (Pacific herring, pink salmon and Pacific sandlance) and "aggregation type" (allopatric\sympatric). Specific paired comparisons were performed when the $P < 0.05$ for the interaction terms. Abbreviations: Allo. = Allopatric, Symp. = Sympatric, DNT = Do Not Test.

Table 10a. Prey utilization and selection for Pacific herring (H). Probability (P) values refer to paired comparisons between allopatric and sympatric aggregations. Abbreviations: PS = Pink Salmon, SL = Sandlance, md = median, sem = standard error of the mean, DNT = Do Not Test.

Table 10b. Prey utilization and selection for Pink salmon (PS). Probability (P) values refer to comparisons paired between allopatric and sympatric aggregations. Abbreviations: H = Herring, SL = Sandlance, md = median, sem = standard error of the mean, DNT = Do Not Test.

Table 10c. Prey utilization and selection for Sandlance (SL). Probability (P) values refer to paired comparisons between allopatric and sympatric aggregations. Abbreviations: H = Herring, PS = Pink Salmon, md = median, sem = standard error of the mean, DNT = Do Not Test.

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Figure 1. Locations of APEX forage fish sampling stations during July, 1996 in PrinceWilliam Sound, Alaska. See also Table 1.

Figure 2. Median fork lengths (FL) of forage fish from sympatric and allopatric aggregations, collected in Prince William Sound during July, 1996. The number of sets (10 fish in each set) is shown below the bars. Results of Mann-Whitney Rank Sum paired comparisons between allopatric and sympatric sizes are indicated: NS = not significant, * $p < 0.05$, *** $p < 0.001$.

Figure 3. Total density (median thousands*m^{-3}) and relative contribution of principal zooplankton taxa available to juvenile Pacific herring, pink salmon, and Pacific sandlance in (a) allopatric and (b) sympatric aggregations in PrinceWilliam Sound during July, 1996.

Figure 4. Diet composition as mean (left side) and median (right side) percent number of prey among allopatric and sympatric aggregations of juvenile forage fish: (a) Pacific herring, (b) pink salmon and © Pacific sandlance collected in Prince William Sound during July, 1996. Legend as in Figure 3. Percentages do not always total 100% due to empty stomachs (see Table 3).

Figure 5. Diet composition as mean (left side) and median (right side) percent biomass of prey among allopatric and sympatric aggregations of juvenile: (a) Pacific herring, (b) pink salmon and © Pacific sandlance collected in Prince William Sound during July, 1996. Legend as in Figure 3. Percentages do not always total 100% due to empty stomachs (see Table 3).

Figure 6. Diet similarity (PSI) by percent number of prey species for forage fish in allopatric and sympatric aggregations collected in Prince William Sound during July, 1996. Line at 60% indicates threshold for significant overlap.

Figure 7. Prey consumption (median prey percent body weight) by forage species in allopatric and sympatric aggregations in Prince William Sound during July, 1996. Results of Mann-Whitney Rank Sum comparisons between groups are indicated: NS = not significant, * $p < 0.05$. See also Table 4.

Figure 8. Feeding selectivity (median Strauss' Linear Selection Index) from principal prey categories among juvenile forage fish: (a) Pacific herring, (b) pink salmon, and © Pacific sandlance. Positive values indicate preference, negative values indicate avoidance. The species composition of allopatric and sympatric aggregations (shown in left-most panels) is repeated across the remaining panels.

Introduction - Chapter 3

The role of forage fish communities is being examined in ecosystems around coastal Alaska and other areas of the world. "Forage fishes are abundant, schooling fishes preyed upon by many species of seabirds, marine mammals, and other fish species. They provide important ecosystem functions by transferring energy from primary or secondary producers to higher trophic levels," (Springer and Speckman, 1997). For example, juvenile Pacific herring (*Clupea pallasi*) and Pacific sandlance (*Ammodytes pacifica*) are forage species with high energy densities that were important to black-legged kittiwakes (*Rissa tridactyla*), while juvenile pink salmon (*Oncorhynchus gorbuscha*)was a low energy density forage species important to tufted puffins (*Fratercula cirhata*; Anthony and Roby, 1997). These and other species have been intensively studied in Prince William Sound (PWS) during damage assessment and ecosystem investigations that ensued with the March, 1989 *Exxon Valdez* (EVOS) oil spill (Brown et. al, 1996). High sea bird mortalities were associated with EVOS and occurred during a period of decline for several sea bird populations in the Gulf of Alaska (Anderson et. al, 1997; Piatt and Anderson 1996). These events were preceded by a two-decade period of shift in the relative abundance of prominent forage fish species (Anderson et al. 1994; Bechtol 1997) and by increased releases of juvenile salmonids into PWS from enhancement facilities. Juveniles of many forage species are abundant and conspicuous during the spring and summer when the breeding and chick- or pup-rearing activities of their avian and mammalian predators are also highly visible. The interplay of environmental conditions, species-specific behaviors, trophic interactions and other factors that influence growth and survival of forage fish and affect the productivity of sea birds are not well understood. However, EVOS studies associated continuing sea bird declines with decreased availability of high quality forage fish prey. Reproductive failures were documented among black-legged kittiwakes from oiled areas (Irons 1996) and may be associated with feeding conditions. Greater declines of pigeon guillemots in oiled areas compared to non-oiled areas were associated with reduced deliveries of Pacific sandlance, a high energy prey, to their chicks (Oakley and Kuletz 1996). Changes in forage fish population could affect their trophic interactions if food availability limits the carrying capacity of PWS (Cooney 1993; Heard 1998).

This diet study is a sub-project of the Alaska Predator Ecosystem Experiment (APEX; Duffy 1997), a multi-disciplinary study designed to understand the PWS food web and its effects on species injured in the *Exxon Valdez* oil spill. Understanding the interactions between forage fish species may help to explain changes in the food habits and reproductive biology of injured marine birds dependent on them, lending support to the APEX hypothesis that "planktivory is the factor determining abundance of the preferred forage species of seabirds." Knowledge about diets, prey availability and selection, shifts in food habits when fish distributions overlap (allopatry vs. sympatry), diel feeding chronology, daily rations and other aspects of feeding ecology, as well as geographic, seasonal, and interannual comparisons of trophic attributes, provides insight into how the population dynamics of forage fish affect the apex predators which use them. Most of what is known about the associations of juvenile Pacific herring, Pacific sandlance and pink salmon relates to them as prey for piscivorous fish, sea birds or marine mammals (Cross et al. 1978; Rogers et al. 1979; Field 1988; Heard 1991; Gilman 1994; Schweigert 1997). Numerous diet reports have been published, yet the interactions among these species are poorly understood. Especially little is known about Pacific sandlance, principally due to lack of a commercial fishery in the eastern Pacific.

Feeding overlap is one indication of competition. Pacific herring, pink salmon and Pacific sandlance have high potential for feeding overlap due to their shared early life history requirement of nearshore residency (e.g., Simenstad et al. 1979). Competition among species can be inferred from an observed shift in resource use when two species co-occur, such as decreased presence in preferred habitat or decreased use of a preferred prey resource (Sogard 1994). The shift is then reflected in some measure of health, such as poorer condition, less energy reserves, or decreased growth. Ultimately, survival may be affected and populations reduced. For this study, the samples collected for diet studies were adapted to an *a posteriori* experimental design with nine types of species aggregations. We addressed the potential for competition between juvenile Pacific herring, Pacific sandlance and pink salmon by comparing feeding attributes of fish in allopatric aggregations to those in sympatric aggregations with each of the other species. We examined for a) feeding declines, by comparing quantities of food consumed, and for b) diet shifts, by comparing prey composition, prey selection and total diet similarity.

Methods - Chapter 3

The field and laboratory methods used to conduct this study are briefly described herein. Additional details and summaries are described in Duffy (1997).

Field Methods

We sampled schools of forage fish in PWS during July, 1996, using several small-mesh nets deployed from small charter vessels and a 16' skiff, in three regions of the sound (northeast, central, southwest; Figure 1). Samples were collected during offshore and nearshore hydroacoustic surveys conducted concurrently, principally to assess the distribution and abundance of forage species. Offshore hydroacoustic surveys were conducted along parallel transects two miles apart. Offshore fish aggregations detected hydroacoustically were sampled with a midwater research trawl; aggregations detected at the surface were sampled with cast nets and dipnets. The trawl effective mouth opening was 50 m^2, with mesh size diminishing to 9.5 mm in the cod end. A cod end liner with 3.2 mm mesh was added, ending in a plankton cup with 0.5 mm nytex mesh. Nearshore surveys were conducted in each region along zig-zag transects near the beach; a purse seine was used to sample hydroacoustic targets along the 1-km shoreline segment that formed the base of the zig-zag (see Haldorson et al. 1997). The purse seine was 200 m long by 20 m deep, with 25 mm stretched mesh. We also beach seined three randomly selected sections out of the ten comprising each shoreline segment. The beach seine was 37 m long with bridles and lines attached. It tapered from 5 m depth at the center to 1.5 m depth at the ends of each wing. The mesh size was 20 mm stretched, with a center panel of 10 mm mesh.

When fish were caught, duplicate zooplankton samples (20 m vertical hauls, 0.5 m diameter ring net, 243μm mesh) were collected to assess the prey available to fish from pelagic production systems. Zooplankton was collected within 100 m of the beach unless the site was too shallow. Samples were preserved in 5% buffered formaldehyde solution in individual 500 ml bottles. Few plankton samples were collected offshore; therefore, samples collected to complement beach seined fish were paired with fish collected by other nets in the same area (see Table 1).

The object of this study was to address competition of forage fish by comparing their diets when in allopatric and sympatric aggregations. We examined the survey catch data to determine species associations of the catch, defining sympatric as the co-occurrence of two species in a single haul at a station. We classified all sets as allopatric or sympatric according to the following criteria:

Allopatric	Sympatric
• mixed species per area in different hauls	• mixed species in same haul
• 2 species with n < 9 for one of them	• 2 species with n ≥ 9 each
• 2 size classes of one species (e.g., sandlance, station 11-2B)	• 2 size classes of one species with a co-occurring second species
• additional species present in low numbers, but not of interest (e.g., tomcod)	

Sufficient samples of three species were available (Pacific herring, Pacific sandlance and pink salmon). We analyzed all sympatric sets available, and most of the allopatric sets, including a few non-survey sets. We adapted these samples to an *a posteriori*, experimental design which considered three factors: a) species, b) allopatric vs. sympatric, and c) sympatric species pairing. The design was thus comprised of nine categories of aggregations. Because we pooled sets across regions, the experimental design was not spatially balanced-- all types of aggregations were not captured throughout the sound, even though all three species were present in each region.

Laboratory methods

We examined fish stomach contents to determine: a) if different forage species consumed the same prey types, and b) if feeding shifts occurred between allopatric and sympatric aggregations of any species. Forage fish stomach samples and prey samples (zooplankton) were analyzed at the NMFS Auke Bay Laboratory . Preserved fish were measured and weighed, stomachs were removed and weighed, and indices of stomach fullness and prey digestion were recorded from visual assessment. Relative fullness was recorded as: 1 = empty, 2 = trace, 3 = 25%, 4 = 50%, 5 = 75%, 6 = 100% full, and 7 = distended. The state of digestion was recorded as: 0 = fresh, 1 = partially digested, 2 = mostly digested, 3 = stomach empty. Stomach contents were teased apart and split according to standard subsampling techniques when stomachs were too full to count every prey item (Kask and Sibert 1976). We identified zooplankton to determine selection from pelagic prey fields by fish at each station. Zooplankton samples were split with a Folsom splitter. Organisms in stomachs and zooplankton samples were identified, enumerated under the microscope, and numbers were expanded. As much as possible, taxa were identified to allow examination of prey selection by species, sex and life history stage, and within size groups. Large copepods were identified as those > 2.5 mm total length (TL). Small copepods were identified as those ≤ 2.5. mm TL, and include the cyclopoid, *Oithona*. Taxa such as euphausiid or amphipod species were similarly defined by length ranges. Prey weight values were taken from data on file at the Auke Bay Laboratory and University of Alaska, Fairbanks, Institute of Marine Science. Prey biomass was calculated by multiplying prey counts by the mean weight per taxon-size class.

Data Summary and Statistical Methods

The abundance and numerical percentage composition of taxa in plankton samples were summarized (means, medians) from pooled stations to characterize the general resources available to planktivores at each station and in the areas of each of the nine types of fish aggregations. The density of planktonic prey was standardized to 1 m^3 water volume using the number of animals per sample divided by the volume (V) of water filtered:

$$X = \frac{x_i(1/f)}{V}\ , \quad V = \pi r^2 D$$

where x_i = number observed per taxon, f = the fraction of the sample analyzed, r = radius of the net (0.25 m) and D = depth of the tow. Depth of plankton samples were generally 20 m, filtering approximately 4 m^3 of water.

Ten fish from each species-size group per station were analyzed from diet sample collections. Mean and median preserved fork lengths (FL) of all specimens in each group were calculated to distinguish between intraspecific size/age groups. In general, Pacific herring and sandlance less than 100 mm were considered 0-age and those greater than 100 mm were considered 1-age. All pink salmon were 0-age, but were assigned to two size classes based on similar lengths. Mean and median fullness index and stomach fullness as prey percent body weight (%BW) were also computed:

$$\%BW = \frac{\sum (x_i w_i)}{BW(\sum x_i w_i)} 100$$

where I = 1 to n prey taxa, x_i = total number of prey per taxon, w_i = the mean weight of each prey taxon in mg, and BW = the fish body weight in mg. Summary fullness indices were then converted back to percentages.

Overall food habits of forage fish species were calculated as means and medians of major prey categories across all specimens in each fish species aggregation. We present prey biomass, percent total biomass, prey numbers and percent total numbers. Diet similarity was measured at the prey species level on pooled fish using the Schoener Index of Overlap (= Percent Similarity Index, PSI; Wieser, 1960; Schoener 1974; Boesch, 1977; Hurlbert 1978; Krebs 1989):

$$PSI_{jk} = \sum \min(p_{ij}, p_{ik}) = 1 - 0.5 * (\sum |p_{ij} - p_{ik}|)$$

where p is the mean numerical or biomass proportion of the i^{th} prey taxon in n taxonomic categories consumed by fish species j and k. The values compared were the means of all fish specimens in the each aggregation type. We calculated three types of diet overlap: interspecific-allopatric fish (two species allopatric), interspecific-sympatric fish (two co-occurring species), and intraspecific allopatric-sympatric fish (an allopatric species compared to itself when sympatric). Values above 60% were considered significant.

Prey selection from zooplankton at the same station was measured for each fish specimen. We used Strauss Linear Selection Index (Ivlev 1961; Krebs 1989; Strauss 1979):

$$L_i = (p_i - e_i)*100$$

where $I = 1$ to n prey taxa, p_i is the numerical proportion consumed and e_i is the numerical proportion in the prey resource sample. We present mean and median selectivity for all major prey taxa observed in either the stomachs or the plankton for each species aggregation. Negative values indicate avoidance, positive values indicate selection, and values near zero indicate predation at a rate proportional to the abundance of the taxon.

Statistical analyses were based on ten fish observations per station, using stations as replicate observations of the allopatric and sympatric categories. We tested the hypotheses that fish size, fish density (using catch as an index of abundance), total feeding, zooplankton prey availability, and prey utilization and selection did not vary between allopatric and sympatric aggregations depending on the fish species. Two-way analysis of variance (ANOVA) was performed using the factors species (three levels: Pacific herring, pink salmon, and Pacific sandlance) and aggregation type (two levels: allopatric and sympatric). Size included fish FL and wet weight. Total feeding measures included total numbers and biomass of prey consumed, stomach fullness index and prey percent body weight. Measurements of prey availability included density of total zooplankton and density and percent density of major prey categories. We considered prey categories present in the diets or plankton by at least 5% number or weight to be biologically important. All data were tested for normality of distribution and homogeneity of variance. Transformations were usually unsuccessful; therefore, a nonparametric analysis was used. We converted observations to ranks, then applied a two-way ANOVA on the ranked data (Conover 1980). Fish density data were ln-transformed. When the interaction term was significant ($P < 0.05$), specific paired comparisons were performed; for each of the three fish species, the allopatric values were compared to the two sets of sympatric values (Mann-Whitney Rank Sum Test) to discern differences between aggregation categories. No statistical tests were conducted on measures of diet similarity, which are computed from pooled data. Changes in diet similarity were used to infer prey partitioning and avoidance of competition. We investigated two hypotheses: if competition does not occur, a) two species' diet similarities will be lower when they occur sympatrically compared to when they occur allopatrically, because of prey partitioning; and b) a single species' diet when allopatric will be similar to its diet when sympatric, ie., will not shift.

Results - Chapter 3

Fish diet samples were analyzed from locations in three geographic regions of PWS (Figure 1). The characteristics of diet sample stations are shown in Table 1 by aggregation type (species x allopatric vs. sympatric with one of the other two species). All samples except one were collected in the second half of July during daylight hours (between 06:35 and 20:15). The frequency of occurrence, abundance and distribution of forage species were summarized elsewhere (Haldorson et al. 1997). In general, forage fish were caught most frequently with beach seines onshore, where fishing effort was focused. They were seldom encountered offshore. Fish were encountered in the northwest more often than in the other regions, with Pacific herring and Pacific sandlance the most frequently-occurring and abundant species. In the central and southwest regions, pink salmon and Pacific tomcod (*Microgadus proximus*) were the most frequently-occurring species. Catches were generally low in the central region, while in the southwest, Pacific herring (mostly adults) were the most abundant species.

Sympatric forage fish aggregations were common on survey transects in July, 1996 (Haldorson et al. 1997). Of the 330 survey hauls that caught fish, juvenile Pacific herring, Pacific sandlance and pink salmon were caught in 39, 22 and 34 sets, respectively. Sympatric species pairs occurred in 21-41% of the hauls catching at least one of these species. All sympatric hauls with sufficient specimens were analyzed (four stations with Pacific herring-Pacific sandlance, four stations with Pacific herring-pink salmon, and one station with Pacific sandlance-pink salmon; Table 1).

The ln-transformed catch by species did not differ between allopatric and sympatric aggregations (2-way ANOVA; interaction term $P > 0.05$). Most hauls caught < 100 individuals of a species, a few caught several hundred, and 3 sets were in the 10's of thousands (Table 1). Large catches were not restricted to certain aggregation categories. In different hauls, we caught large numbers of Pacific herring sympatric with Pacific sandlance, allopatric sandlance, and sandlance sympatric with herring. For herring and sandlance, the magnitude of the catch differed between the species in three of the four hauls and in both directions. For herring and pink salmon, the magnitude of the catch differed between the species in only one of four hauls.

The mean sizes of both allopatric and sympatric forage fish used for the diet study indicated that most were 0-age or 1-age (Table 2). Three age classes were indicated for herring. The FLs of specimens used in diet analyses did not vary greatly at any station. Pacific herring mean FL ranged from approximately 30-191 mm. The FLs of herring clustered at ≤ 55 mm, between 100-130 mm, and at 191 mm (one station). Pacific sandlance mean FLs ranged from 61-134 mm per station. The FLs of sandlance clustered in groups of ≤ 89 mm and > 112 mm FL. The FL of pink salmon ranged from 62-130 mm.

We found size differences between allopatric and sympatric fish for all species. The interaction term in a two-way ANOVA testing lengths of forage species in allopatric vs. sympatric aggregations was marginally significant ($P = 0.0538$; Table 3). Mann Whitney Rank Sum Tests revealed significant differences between median sizes of paired allopatric and sympatric forage fish for each species (Table 4; Figure 2). Herring sympatric with pink salmon were significantly larger (107 mm; $P < 0.0001$) than allopatric herring (47 mm). However, herring sympatric with sandlance were similar in size (47 mm; $P = 0.8280$) to allopatric herring. Pink salmon in either type of sympatric aggregation were significantly larger (98 mm; $P < 0.0033$) than allopatric pink salmon (85 mm). Pacific sandlance sympatric with pink salmon were significantly smaller (64 mm; $P < 0.0001$) than allopatric sandlance (79 mm), but sandlance sympatric with herring were similar in size (77 mm; $P = 0.9287$) to allopatric sandlance.

We did not find that certain sizes of a fish species were limited to a single aggregation category. Small and large herring and sandlance specimens were caught at both allopatric stations and at sympatric stations with the other two species (Table 2). Pink salmon were caught less frequently than the others; their full size range was not exhibited across all aggregation types. We did note that some species-size associations were more common than others. Among Pacific herring, the smallest fish were most commonly either allopatric or sympatric with Pacific sandlance. Conversely, the largest herring were most commonly either allopatric or sympatric with pink salmon. Of all sympatric herring, those that co-occurred with sandlance were approximately 50% smaller in FL than the herring that co-occurred with pink salmon (Rank Sum Test, $P = 0.0015$). Pink salmon sizes varied in sympatric associations with herring. The largest and smallest pink salmon co-occurred with herring, and at two stations, two size classes of pink salmon were present together with herring. Sympatric pink salmon were larger than allopatric individuals, but the two categories of sympatric pink salmon did not differ in FL ($P = 0.8866$). Among sandlance, the smallest fish were either allopatric or were sympatric with pink salmon, while the largest were either allopatric or were sympatric with herring. The sandlance sympatric with pink salmon were significantly smaller than those sympatric with herring ($P < 0.0001$).

We found few differences in feeding environment between areas of different fish aggregations. Zooplankton total densities at areas with allopatric and sympatric fish aggregations did not vary with the fish species present (two-way ANOVA on ranks, interaction term $P = 0.9611$; Table 5). However, densities were marginally significantly higher (2-way ANOVA, species term $P = 0.0615$; *Student-Newman-Keuls all pairwise multiple comparison*, $P < 0.05$) in areas with pink salmon than in areas with sandlance or herring. Mean densities across the nine categories of aggregations ranged from approximately 1800 to $4200 \cdot m^{-3}$ (Table 6).

Zooplankton composition was also similar between allopatric and sympatric aggregations for each species (Figure 3; Table 7a-c). Small copepods comprised at least 72% of the number of zooplankters in the upper 20 m water column. These were principally the calanoids, *Pseudocalanus*, *Acartia*, and *Centropages* and the cyclopoid, *Oithona*. Four taxa comprised the remaining organisms, each < 10%: larvaceans (*Oikopleura dioica*), pteropod gastropods (*Limacina helicina*), cladocerans (*Evadne* sp. and *Podon* sp.), and "other" usually consisting of bivalve larvae. Barnacle larvae and large calanoids (*Calanus pacificus)* were occasionally present (< 3%). The interaction terms from two-way ANOVA's on density and percent density of zooplankton taxa were rarely significant ($P > 0.05$). Among principal taxa, only the interaction term for percent density of larvaceans was significant ($P = 0.0206$). Among minor taxa, significant interactions were found only for density and percent density of cladocera ($P < 0.0306$). Euphausiid larvae density and percent density were marginally significant ($P < 0.0545$). However, paired comparisons for larvaceans revealed no significant differences ($P > 0.05$) in composition between areas of allopatric and sympatric aggregations of a species (Table 7).

Diet compositions of forage species in allopatric and sympatric aggregations are presented as percent numbers (Figure 4) and percent biomass (Figure 5) of major prey groups to indicate principal prey and to examine for differences between aggregations. Principal prey differed among forage species, and were: for herring, small calanoids and larvaceans; for pink salmon, larvaceans and fish; and for sandlance, small calanoids. Minor prey included large calanoids, decapod zoeae, barnacle larvae and molts, hyperiid amphipods, cladocera, gammarid amphipods and harpacticoid copepods.

The PSI was used to compare diets between species within aggregation categories and within species between aggregation categories (Figure 6). Among allopatric aggregations, only the diets of sandlance and herring were similar (PSI = 73.1% number; Table 8a). No sympatric species pairs had similar diets (PSI > 60% number or biomass; Table 8b). However, for both pink salmon and herring, diet similarity was high between fish in allopatric and fish in sympatric aggregations (Table 8c). Allopatric sandlance diet was marginally similar (percent biomass) to diet of sandlance sympatric with herring.

Two-way ANOVA'S on the four measures of total feeding produced significant interaction terms ($P < 0.0092$; Table 3), without exception. This result indicates that, for at least one of the three forage species, measures of total feeding varied according to whether a species occurred allopatrically or sympatrically. Two-way ANOVA's on measures of prey utilization and selection by taxon also yielded significant ($P < 0.05$) interaction terms, indicating that prey utilization also varied with species composition of the fish aggregation (Table 9). A principal prey, small calanoids, was a notable exception. Although the interaction terms for number and biomass of small calanoids were significant ($P < 0.0113$), they were only marginally significant ($P < 0.0673$) for percent number and percent biomass, and were not significant ($P = 0.2609$) for selection of this taxon. Two-way ANOVA's were followed by paired comparisons within each species.

Herring

Total feeding measures for sympatric herring were significantly lower (Rank Sum Test, $P < 0.05$) than measures for allopatric herring (Table 4). All four differences were significant for herring sympatric with pink salmon and three out of four were significant for herring sympatric with sandlance. Among all herring, allopatric stomachs were fullest (75%), prey comprised the greatest percent body weight (1.5%), and the median number (383.5 organisms) and biomass (19.97 mg) of prey consumed were greatest. For herring sympatric with pink salmon compared to allopatric herring, significantly lower values included fullness (trace%, $P < 0.0001$), prey %BW (0.4%, $P < 0.0001$), total number of prey (24.0, $P = 0.0001$) and total prey biomass (1.68 mg, $P = 0.0035$). For herring sympatric with sandlance, values significantly lower than those of allopatric herring included fullness (50%, $P = 0.0143$), total prey number (269.5, $P = 0.0445$) and total prey biomass (11.94 mg, $P = 0.0158$). Only prey %BW was not lower for herring sympatric with sandlance than for allopatric herring (1.1%, $P = 0.2546$; Figure 7).

The overall diet of allopatric herring was similar to the diet of herring sympatric with pink salmon (Table 8). The PSI was greater than 60% by both number and biomass of prey species. The diet of allopatric herring was also similar to the diet of herring sympatric with sandlance, but only when compared as percent number of prey species. The majority of the prey in common was larvaceans in the first species pairing and small calanoids in the second species pairing (Figures 4 and 5).

Compared to allopatric herring, the utilization of principal prey by herring sympatric with pink salmon was lower, but it was not lower for herring sympatric with sandlance. For herring sympatric with pink salmon, small calanoid number, biomass, percent number, and percent biomass were all lower (P < 0.0321; Table 10a) than values for allopatric herring. The median percent biomass of small calanoids, for example, was 5.2% compared to 65.5% (P = 0.0091). Paired comparisons were not performed on small calanoid selection values because the interaction between species and aggregation type was not significant for this measure (Table 9). However, the median selection of small calanoids among herring sympatric with pink salmon was -38.1 compared to +5.7 for allopatric herring. For the second most important prey, larvaceans, all five measures of utilization were significantly (P < 0.0344) lower for herring sympatric with pink salmon than for allopatric herring (Figures 4, 5 and 8). For example, the median percent number of larvaceans was 0.4% compared to 7.3% (P = 0.0344). Herring sympatric with pink salmon avoided larvaceans compared to allopatric herring (L = -6.4 versus +1.3; Rank Sum Test, P = 0.0030; Figure 8). Herring sympatric with pink salmon also consumed significantly more chaetognaths, large calanoids and hyperiid amphipods (P > 0.0010) than allopatric herring.

For herring sympatric with sandlance, none of the measures of prey utilization were significantly lower than for allopatric herring. Small calanoids comprised similar (P = 0.7549) prey percent biomass, for example, 66.6% for herring sympatric with sandlance and 65.6% for allopatric herring. Median selection value for small calanoids was +0.3 for herring sympatric with sandlance compared to 5.7 for allopatric herring. For larvacean prey, the median percent biomass consumed in these aggregations was also similar (P = 0.2835), 4.6% and 2.4%, respectively. Larvaceans were selected by allopatric herring and by herring sympatric with sandlance in proportion to their abundance in zooplankton (L = 0.2 vs. +1.3; Rank Sum Test, P = 0.5885).

Pink Salmon

For pink salmon in both types of sympatric aggregations, two of the four total feeding measures were significantly lower (P < 0.05; Table 4; Figure 7) than for allopatric pink salmon. Allopatric pink salmon had the highest fullness index (75%) and prey %BW (1.6%) among these aggregations. Pink salmon sympatric with herring had significantly lower stomach fullness (50%; P = 0.0138) and prey %BW (0.8%; P < 0.0001). However, total prey numbers were not different (P = 0.2550) and prey biomass was slightly greater (P = 0.0371) than comparable measures for allopatric pink salmon. Stomachs of pink salmon sympatric with sandlance were the least full, only 25% (P = 0.0099) and prey %BW was the lowest, only 0.5% (P < 0.0001), of all pink salmon. However, total prey numbers for pink salmon sympatric with sandlance were significantly higher (P = 0.0378) and prey biomass was not different (P = 0.3568) than for allopatric pink salmon.

The overall diet of allopatric pink salmon was similar to the diet of pink salmon sympatric with herring (Table 8). The PSI was greater than 60% by both number and biomass of prey species. The diet of allopatric pink salmon was also similar to the diet of pink salmon sympatric with sandlance, but only when compared as percent number of prey species. The majority of the prey in common was larvaceans and fish (Figures 4 and 5).

Neither category of sympatric pink salmon utilized less of the principal prey, larvaceans, than allopatric pink salmon (P > 0.0587; Table 10b). Larvaceans constituted high median percent numbers (88-97%) and were strongly selected for by pink salmon in all aggregation categories (L

> +80; Figure 8). Small calanoids were strongly avoided by all categories of pink salmon (L < -80). No biologically important differences in the consumption of small calanoids were found for pink salmon sympatric with herring (Rank Sum Test, P > 0.0411). Fish were consumed by pink salmon in 7 out of 10 total hauls, but predation was uneven, as shown by the contrast between mean and median utilization values. Pink salmon sympatric with herring had two measures of fish prey utilization that were significantly lower than for allopatric pink salmon (percent number and selection, P < 0.0443), and three measures that were marginally lower (0.05 < P < 0.10). Pink salmon sympatric with sandlance had no measures of any prey category that were significantly different from allopatric pink salmon. For minor prey categories that contributed < 5% to the diets of pink salmon (decapods and hyperiid amphipods), small, but significant (P < 0.05) differences in utilization were observed between allopatric and sympatric aggregations.

Sandlance

Measures of total feeding for sympatric sandlance were significantly less than those of allopatric sandlance only when sandlance co-occurred with herring. Allopatric sandlance stomachs were 50% full, containing a median of 450 prey items weighing 25.74 mg; prey constituted 0.7% BW (Table 4). For sandlance sympatric with herring, we observed significantly lower medians for stomach fullness (trace%; P < 0.0001), prey number (14.5 items; P = 0.0120) and prey biomass (0.67 mg; P = 0.0172); however, prey %BW was not significantly lower (0.4%; P = 0.3285; Figure 7). For sandlance sympatric with pink salmon (a single set), no measures of total feeding were significantly (P > 0.3560) different from those of allopatric sandlance.

The overall diet of allopatric sandlance was similar to the diet of sandlance sympatric with herring only when compared as percent biomass of prey species (PSI = 60.5; Table 8). The diet of allopatric sandlance was not similar (PSI < 60%) to the diet of sandlance sympatric with pink salmon either in prey number or biomass. Although sandlance in both aggregation categories did eat small calanoids principally, the taxa differed for the allopatric and sympatric fish (Figures 4 and 5).

Compared to allopatric sandlance, the utilization and selection of principal prey (small calanoids and larvaceans) by sandlance sympatric with herring were lower (P < 0.0381; Table 10c). Small calanoids comprised less than 49% of the prey (numbers or biomass) of sandlance sympatric with herring, significantly (P < 0.0057; Rank Sum Test) less than the >70% observed for allopatric sandlance. Paired comparisons of small calanoids selection were not performed. Nonetheless, in contrast to allopatric sandlance, sandlance sympatric with herring tended to avoid small calanoids (L = +0.7 vs. -31.4; Figure 8). Larvaceans represented small proportions of sandlance diets (less than 3.2% by number), but significantly lower measures of utilization were observed for sandlance sympatric with herring (P < 0.0010) compared to allopatric herring. Larvacean selection values were negative and did not differ significantly (P = 0.2723) from those of allopatric sandlance.

For sandlance sympatric with pink salmon, most measures of the utilization and selection of principal prey were not lower than those for allopatric sandlance (P > 0.0752). The percent number of small calanoids was greater (P = 0.0278) for sandlance sympatric with pink salmon, 94.8% vs. 76.0% for allopatric sandlance. Compared to allopatric sandlance, sandlance sympatric with pink salmon tended to select small calanoids (L = +10.3 vs. +0.7; Figure 8). Larvacean selection values were not different (P = 0.1340), both being negative and of similar magnitude. No significant differences were observed in the utilization of minor prey taxa (P > 0.05); selection values differed (P < 0.0332) but all were near 0.

Discussion - Chapter 3

Few reports exist that examine the co-occurrence and compare the diets of juvenile Pacific herring, Pacific Sandlance, and pink salmon. These species are common residents of nearshore habitats on the Pacific and Arctic coasts in spring and summer (Craig 1984; Cross et al. 1978; Orsi and Landingham 1985; Robards and Piatt 1997; Rogers et al. 1986; Simenstad et al. 1979; Willette et al. in prep.). Their early life history strategies ensure that their spatial and temporal distributions overlap during parts of the juvenile period. Species interactions may be complex, but sharing of habitat and prey resources among them is to be expected at least some of the time. Generally, in the spring, herring larvae hatch in the intertidal zone and spend the first two years of life nearshore (Norcross et al. 1998). Sandlance larvae also hatch intertidally, disperse, then move onshore later in summer (McGurk and Warburton 1992; Blackburn and Anderson 1997). Pink salmon fry migrate from fresh water to nearshore estuaries in the spring before moving to the Gulf of Alaska in the summer of their first year of life (Heard 1991). Population pulses are especially pronounced in areas where hundreds of millions of salmon are released by hatcheries (Heard 1997). These species' spatial overlaps must decline by fall-winter, when pink salmon have left nearshore waters (Heard 1991), sandlance become dormant in soft substrates (Ciannelli 1997), and older juvenile herring have migrated to deeper water (Norcross et al. 1998).

Ours is not the first study to report mixed schools (sympatry) of these or similar species. Richards (1976) observed sympatric schools of Atlantic herring (*Clupea harengus*) and sandlance (*Ammodytes hexapterus*) juveniles. Sekiguchi et al (1974) reported on the feeding habits of YOY *A. personatus* and anchovy (*Engraulis japonica*) collected in trawls in Japanese waters. Likewise, herring-sandlance and herring-salmon co-occurred near Kodiak, Alaska (Harris and Hartt 1977; Haegele 1996). In July of 1996, up to 11% of our survey net hauls in PWS caught juvenile Pacific herring, Pacific sandlance or pink salmon, with close to half of these catching two of the species. Rates of sympatry are likely to be higher if sympatry is loosely defined, for example as two species caught in consecutive hauls at a sampling station. In our report, feeding of sympatric species refers to mixed species aggregations.

Although we have data only for mid-summer, fish diets can vary with ontogeny, season, habitat and even time of day (e.g.. Simenstad 1979; Sturdevant et. al 1996; Willette et. al in prep; Craig 1987; Gordon 1984). Seasonal changes in abundance and distribution could affect both the potential for food and habitat competition among these species and their availability to marine predators. Willette et al. (in prep) observed monthly changes in the frequency of species associations in the southwestern region of PWS from April to October, 1994. The species associations, as well as frequencies of occurrence and abundance of juvenile herring, pink salmon and sandlance, varied widely over time. In general, herring and pink salmon both co-occurred with sandlance earlier than with each other. Pink salmon and sandlance co-occurred together more often than either did with herring. This information suggests that diet overlap and competition for food are likely to occur for portions of the populations in summer.

A comparison of the size of fish species in different categories of aggregations is important because diet can change with size, because of size-selective predation, and because energy requirements can change with growth. Two species with similar feeding habits may avoid competition by feeding in different areas or by feeding in sympatric aggregations with individuals of a different size that have different prey requirements. Our data suggests that some species associations may be size-related. We observed a wide size range of co-occurring herring and sandlance, but those at a given station were similar in size. The pattern of pink salmon size associations with herring was more variable. Size associations may also reflect seasonal patterns of growth and movement. In our study, most of the larger fish of each species were collected in different habitat than the smaller fish, in water as deep as 36 m with purse seines vs. onshore with beach seines. By late summer, juvenile pink salmon are much less abundant in nearshore waters than in spring, most having migrated offshore toward the Gulf of Alaska.

The declines in total feeding observed for sympatric fish were apparently not related to fish size. Some of these declines suggest that competitive interactions limit feeding. Sympatric herring fed less than allopatric herring regardless of their size or which species they co-occurred with. It is possible that the degree of decline is related to species-size composition of the aggregation, however. Herring fed the least when they co-occurred with pink salmon. For pink salmon, allopatric fish fed better than either category of sympatric pink salmon even though they were smaller. These small, allopatric pink salmon ate more fish prey than the sympatric pink salmon, contributing to the higher feeding measures. Among sandlance, only the smaller specimens with pink salmon fed as well as the allopatric specimens; the sandlance sympatric with herring were the same size as allopatric sandlance, but feeding declined.

In a study of neritic fish assemblages, juvenile Pacific herring, Pacific Sandlance, and pink salmon were grouped into one functional feeding group, pelagic planktivores (Simenstad et al. 1979). Sandlance and herring were defined as obligate, while pink salmon were considered facultative planktivores. The diets of all were dominated by calanoid copepods, although overlap was not reported (Simenstad et. al 1979). Calanoids are commonly reported as the majority of prey found in the stomachs of Pacific herring (Willette et. al 1997), Pacific sandlance (e.g., Meyer et al 1979; Craig 1987; Field 1988), and pink salmon (e.g., Bailey et. al 1975; Sturdevant et. al 1996). This similarity of principal prey has been noted (Hobson 1986; Field 1988; McGurk and Warburton 1992; Chapter 1, this report), but ours is one of few studies to compare the three species.

We also found that small calanoids were the principal prey of Pacific herring and Pacific sandlance, but not of pink salmon. The principal prey of pink salmon was larvaceans, which was second-most important for herring and one of several less prominent prey categories for sandlance. Oikopleurans have been reported in juvenile salmon diets (e.g., Healey 1991) and as the nearly-exclusive prey of larval sand-eel, *Ammodytes* spp. (Paffenhofer 1976; Wyatt 1971; Ryland 1964) and occur in the diets of adult fish (C. T. Macer in Ryland 1964) in the North Sea. A changing suite of small calanoids and later, oikopleurans, were prominent in juvenile herring diets throughout the spring (Coyle and Paul 1992). In our study, herring selected small calanoids in close proportion to their abundance, while pink salmon avoided them and were highly selective of larvaceans. For pink salmon, prey biomass was dominated by fish and virtually no copepods were consumed. Differences in feeding between fish caught together in purse seines could reflect feeding in different portions of the water column, as was hypothesized for herring and capelin which partitioned prey between surface and water column in Southeast Alaska (Coyle and Paul 1992).

We considered the possibility that differences in diet between aggregation types were due to fish size differences. Different size classes of a species may select different prey species, sizes or stages within major taxon. Such changes in diet with growth have been reported for numerous fish (e.g., LeBrasseur et. al 1969; Hargreaves and LeBrasseur 1986; Healey 1980, 1991). In fact, our finding of significant diet overlap among herring aggregations containing specimens of different sizes indicates little change in diet with growth for herring up to three years of age. Small calanoids and larvaceans formed the majority of the prey of large herring sympatric with pink salmon and of small herring that were allopatric or sympatric with sandlance, even though the large fish ate marginally more large prey, large calanoids and hyperiids. We could not clearly associate any of the differences in prey consumed by fish species in different aggregations with fish size. However, the calanoids in poor condition in stomachs could have been different species or stages. Sandlance diets were not similar between aggregation types, but all of the calanoid taxa observed were present across all types of aggregations. Similarly, for pink salmon, we did not find greater predation on fish prey by larger individuals. We observed the opposite, in fact: the smallest pink salmon consumed the most fish and exhibited the highest total feeding measures. These observations reinforce the concept of opportunism and facultative planktivory for juvenile pink salmon (Healey 1991).

In our study, overall diet similarities (PSI) were used to indicate potential competitive interactions. We did not observe many instances of diet similarity (PSI > 60%) between allopatric species or between sympatric species (Table 8). Allopatric herring and allopatric sandlance had similar diets that diverged when they became sympatric. This finding suggests that these species have similar prey requirements and that prey partitioning occurs when they share feeding habitats. Another finding supports this interpretation: within-species, allopatric sandlance diets were not similar to sympatric sandlance diets, indicating that a prey shift occurred when sandlance co-occurred with another species. These results suggest a mechanism sandlance use to avoid competition.

No diet shift was indicated by changes in diet similarity between pink salmon and herring or between pink salmon and sandlance. The diets of these species were just as dissimilar when allopatric as when sympatric. Furthermore, a comparison of diets of allopatric fish to diets of the same species when sympatric revealed patterns of diet fidelity for herring and pink salmon. Allopatric herring diets were similar to sympatric herring diets and allopatric pink salmon diets were similar to sympatric pink salmon diets. Because allopatric sandlance diets were not similar (or marginal, at most) to sympatric sandlance diets, the dissimilarity of herring-sandlance diets when sympatric was due to sandlance diet shift, not herring diet shift. The similarity values we report are lower than they would be if calculated based on major taxon instead of species-size.

Because the composition of herring and sandlance diets was similar based on small calanoids (Figures 4 and 5), and yet diet overlap was low in sympatric aggregations, we examined the prey size spectrum of these predators. Although the predominant prey of both herring and sandlance was small calanoids, the suite of available calanoid species and stages may actually be partitioned . Unfortunately, calanoids were often too mangled or digested to identify consistently. These limitations make it difficult to detect selection at the finest levels, prey species and size. We could not make statistical comparisons, but our data suggests that calanoid copepod prey are partitioned by size and species between sympatric herring and sandlance, decreasing the specific overlap. We have found no other report comparing the diets of these two species, but similar observations have been made for pink salmon and sandlance (LeBrasseur et. al 1969). Scott (1973) also observed that *A. dubius* (15-31 cm) filter fed non-selectively on small prey and selected large prey, although large calanoids were their principal prey.

Avoidance of predation may be another factor that influences the relative size of co-occurring fish species, and therefore the potential for diet overlap, in late summer. Pink salmon, in particular, become piscivorous with growth (Landingham et al. 1997), and both herring and sandlance have been observed in their stomachs. Most of the fish found in the pink salmon stomachs in our study could not be identified. No herring were identified. However, unidentified fish larvae were found in stomachs of both size classes of pink salmon from the only station where 0-age herring (38 mm FL) co-occurred with them (station 10-1B; Table 2). These herring were probably not large enough to avoid predation by the pink salmon. If so, it would obviously be advantageous for such small herring to avoid sympatry with pink salmon and explains the low frequency of co-occurrence that we observed for these sizes of herring and pink salmon. We did identify sandlance from stomachs of pink salmon that were not caught with sandlance (stations 58-2U and 3-2U) and unidentified fish larvae in a pink salmon at the only station where the two co-occurred (48-1B). These sandlance co-occurring with pink salmon may have been large enough to avoid predation (FL = 64 mm). If so, sympatry would not be detrimental with respect to predation.

The declines in feeding that we observed for sympatric forage fish compared to allopatric forage fish may have explanations other than competitive interactions. Principal among them are the that less food was available in the sympatric areas or that fish densities were greater. Fish could have been attracted to areas of initially high food density which they then cropped down. We have no data to support this idea. However, because we could not show significantly lower total zooplankton densities or lower densities of the predominant taxon (Table 5) in areas with sympatric aggregations compared to areas with allopatric aggregations, we concluded that the feeding declines we observed for sympatric fish (Table 4; Figure 8) were not related to prey availability. The lower density trends we observed (Table 7) could be biologically important, however.

Changes in prey density can greatly affect the success of fish feeding. For example, the food supply available to larval herring during autumn and winter was strongly related to their survival (Campbell and Graham 1991). For fish similar in size to the smaller herring we studied, a doubling of the density of zooplankton maximized larval survival, while halving the density decreased survival by 10-16%. Herring larvae feeding on copepod nauplii did well at densities of about 4*liter^{-1} in one study (Purcell and Grover 1990), but another study found that 5-12*liter^{-1} was needed for good feeding, survival and growth (Kiorboe et al. 1985 in Purcell and Grover 1990). We observed differences in zooplankton mean density as great as 3x between stations. Small calanoids occurred in densities of approximately 2-3*liter^{-1}, with up to 4*liter^{-1} at allopatric aggregations. These density differences could affect the feeding success of small fish. Densities were low compared to reported spring densities. In early May, densities of zooplankton estimated by the same methodology were 6-7*liter^{-1} in PWS (Celewycz et. al 1997) and up to 16*liter^{-1} in Southeast Alaska (Sturdevant and Landingham 1993).

The direction of the trend in zooplankton density for areas with sympatric herring aggregations varied depending on the co-occurring species. Mean zooplankton density at allopatric herring aggregations was 40% higher than at herring-sandlance aggregations, but was not higher than at herring-pink salmon aggregations. Yet, herring total feeding declined in both types of sympatric aggregations. However, herring feeding on small calanoids and larvaceans declined only when they were sympatric with pink salmon and not when they were sympatric with sandlance. This is surprising because pink salmon did not feed on the predominant resource, while sandlance did. However, the large herring sympatric with pink salmon also tended to consume more large calanoids and hyperiids, even though these prey were no more abundant at the sympatric aggregations than at the allopatric aggregations. This suggests that, for herring (like pink salmon), the patchy availability of larger prey is important in the bioenergetics of the growing fish, even though the greatest proportion of the diet continues to come from small prey.

Plankton density was also higher for areas with allopatric pink salmon than for areas with pink salmon sympatric with herring. The decline in total feeding measures for pink salmon sympatric with herring could not have been driven by reduced density of the predominant taxon, which they did not feed on. The larvaceans they did feed on also declined, from approximately 300 to 200*m^{-3}. But for sympatric pink salmon, utilization and selection of larvaceans did not decline when availability declined. Larvaceans made up more than 88% of prey numbers for pink salmon in all aggregation categories, but fish dominated prey biomass. For pink salmon sympatric with herring, measures of fish prey utilization were lower and measures for hyperiid amphipod utilization were higher than for pink salmon in allopatric aggregations. These pink salmon were not larger than the pink salmon with sandlance, which did not shift prey, but they were larger than the allopatric pink salmon. The herring they co-occurred with were also large and also partially shifted prey. These findings suggest that for pink salmon, feeding declines were due to opportunistic feeding on large prey, such as fish and hyperiids, and were perhaps exacerbated by the competition from large herring which had also begun to require larger prey. Because larval fish were not quantitatively sampled by our zooplankton net, we have no estimate of their relative abundance. The occasional availability of larval fish prey with higher nutritional value may be an important factor in the bioenergetics of juvenile pink salmon during late summer. For herring, however, lack of prey switching when principal prey utilization declined suggests that competitive inhibitions did occur. If a size association between sympatric species exists, larger co-occurring fish that require larger prey may both shift the prey resource for which they compete.

Zooplankton densities were lower in areas with sympatric herring and sandlance than in areas where either species occurred in allopatric aggregations. Because their principal prey is the predominant plankter, these trends suggest that the combined feeding of herring and sandlance may have reduced the resource. This idea is supported by the decline in total feeding for both herring and sandlance in sympatric aggregations compared to those in allopatric aggregations. However, herring sympatric with sandlance did not consume less small calanoids or less larvaceans than allopatric herring. Sandlance sympatric with herring did consume less of these prey and tended to consume more alternative prey.

For the single station of sympatric sandlance and pink salmon, zooplankton density was not lower than in areas of allopatric sandlance but was slightly lower than in areas of allopatric pink salmon. This finding may be related to the fact that pink salmon did not contribute to the cropping of small calanoids and is supported by our finding that plankton density was also higher where pink salmon occurred than where either herring or sandlance occurred. When pink salmon and sandlance were sympatric, sandlance feeding did not decline, but pink salmon feeding did. Sandlance tended to eat more small calanoids when with pink salmon, while pink salmon tended to eat more larvaceans. Because these two species did not have similar diets, competition for available prey was not a limiting factor.

The juvenile fish in our study may also have prey density requirements, but size of prey is also likely to be important (Parsons and LeBrasseur 1969). Large plankters were rare in our 20 m zooplankton samples. Large copepods were not abundant, in contrast to spring samples from PWS (Celewycz et. al 1997; Cooney 1998). Large calanoids are common prey of juvenile herring, pink salmon and sandlance at some times in some areas (LeBrasseur and Parsons 1969; Bailey et al. 1975; Sturdevant et al. 1996; Willette et al 1997). However, we did not commonly observe large calanoids in fish stomachs. This is notable because in July, at least the pink salmon have grown too large to obtain their daily ration from small calanoids, although they will feed on them (LeBrasseur and Parsons 1969). Bailey et al. (1975) concluded that a maximum of 544 copepod prey daily was sufficient for pink salmon up to 58 mm FL. Our result that sympatric pink salmon fed less well than allopatric pink salmon may not have been due to sympatry but to the appropriateness of the available prey size for the smaller allopatric fish. Parsons and LeBrasseur (1970) noted that both prey density and prey size affected the ability of 90 mm pink salmon to obtain their daily ration. If the energy budget of forage species requires a minimum density of appropriately-sized prey in order for calories consumed to balance calories expended, then synergistic effect of larger size, sympatry and lower prey densities could produce food limitations.

Our pink salmon diets consisted of larvaceans and larval fish at all aggregations. Larvaceans were the numerically dominant prey of pink salmon even though their abundance was far exceeded by small calanoids. We observed up to 570 larvaceans (median) in 98 mm pink salmon (Table 4; Table 10b). Other investigators have suggested that larvaceans are targeted by juvenile salmon because they are highly visible (Bailey et. al 1975). When their mucous houses are intact, they are relatively large, and unlike other gelatinous taxa, their caloric density is similar to copepods (Davis et al. 1997). Combined with a low escape response and high visibility, larvaceans may be a rich alternative prey for fish (Knoechel and Steel-Flynn 1989). This may explain why our pink salmon were highly selective of larvaceans even though they contributed < 10% to zooplankton composition, on the order of $0.5*\text{liter}^{-1}$. Larvaceans were not more abundant in areas with allopatric aggregations. The decreased energy expenditure to capture prey with a low escape response could also decrease the rate of encounters with a competitor.

We did not observe shifts in the principal prey targeted by any of the fish species from allopatry to sympatry. However, we did observe shifts in the proportions that the principal prey contributed to the diets. Prey shifts occurred for herring only when they were sympatric with pink salmon, not when they were sympatric with sandlance. Herring consumed proportionately less small calanoids and larvaceans when sympatric with pink salmon. Pink salmon did not shift prey when sympatric with either species. Shifts occurred for sandlance sympatric with both herring and pink salmon. Sandlance shifted away from their principal prey, small calanoids, when with the herring that also ate small calanoids, and increased consumption of small calanoids when with pink salmon, which did not eat small calanoids. Sandlance shifted away from larvaceans and tended to increase prey diversity when sympatric with either herring or pink salmon.

Sandlance were the most adaptable of these species when in sympatric aggregations. Sandlance prey utilization shifted when they were sympatric with either pink salmon or herring, but their total food consumption declined only when they were with herring. Sandlance with pink salmon was the only sympatric species combination in which feeding did not decline significantly from the amount consumed in allopatric aggregations. This was possible because of complete prey partitioning, yet the sandlance were large enough to avoid predation by the pink salmon. However, sandlance mean stomach fullness was already the lowest observed for these species, suggesting a factor other than competition contributed to the low incidence of feeding. Pacific sandlance are known to have a longer digestion time and food retention in the gut (Ciannelli 1997), so perhaps they feed less frequently than other species. The lesser sandeel, *A. marinus*, remained buried longer when food abundances were low (Winslade 1974).

Density dependent interactions could also explain the declines in feeding we observed for sympatric fish. However, because we did not find differences in the ln-transformed catch at allopatric and sympatric stations for any species, we concluded that the declines in total feeding and the prey shifts we observed among species between fish in allopatric and sympatric aggregations were not density-dependent differences. However, these indices of abundance may be very low (see Haldorson et. al 1997). Paul and Willette (1997) concluded that growth of pink salmon may have been limited by intraspecific, density-dependent competition for food in western PWS, and noted a lack of data on the abundance of other competitors. For all of these species, the degree of food-limiting, negative interactions and competition experienced in spring and summer could have a profound effect on nutritional status and survival.

In summary, juvenile Pacific herring, Pacific sandlance and pink salmon co-occur commonly during spring (Willette et al. in prep) and summer in PWS. Forage fish catches were variable but we could not attribute feeding declines to density dependent interactions. Diets of herring and sandlance were sometimes similar, but pink salmon consumed different prey. All, however, exhibited reduced feeding when sympatric. The declines may have been related to reduced prey densities in some cases. Contrary to others' findings of a specialized diet for sandlance (Simenstad et al. 1979) we found that sandlance were the more adaptive of these species because of their feeding flexibility. Our findings suggest that pink salmon and herring had distinctive diets which they adhered to even when sympatric with another species. Sandlance adhered less strongly to the preferred diet when sympatric.

Our findings from tests of diet similarity indicate several important ideas about the trophic relationships of these species: 1) that herring and sandlance consume similar prey when in allopatric aggregations, but when co-occurring in the same prey environment, they tend to partition prey; 2) sandlance shifted prey most; and 3) pink salmon and herring adhere to similar diets whether allopatric or sympatric. Diet shifts were generally not disadvantageous in terms of nutritional value. The predominantly crustacean prey, as well as larvaceans, are all relatively energy dense (Davis et. al 1996). However, total food consumption decreased for all three species when they were sympatric compared to when they were allopatric. This downward shift in feeding, which occurred even though lower plankton densities in areas of some sympatric aggregations were not significant and composition did not differ between allopatric and sympatric stations, suggests that competitive interactions do occur among nearshore forage species. The behavioral interactions which reduce feeding or cause prey shifts in these forage species have not been examined. The lack of differences in zooplankton and the overabundance of available small calanoids suggested by negative selection values for them indicate that reduced availability of prey was not the principal cause of feeding declines. Rather, fish interactions that inhibit feeding, such as aggressive behavior, could result in the observed feeding declines. This would also explain our observations of reduced feeding even when two species do not prey on the same taxa. Pink salmon and sandlance, for instance, did not compete for the same foods, yet both fed less in the presence of the other. The intensity/frequency of these interactions and their negative effects could vary with shifts in the component species densities/abundances between years and areas. Competition resulting in a less ideal diet, either in composition or quantity, could lead to lower survival or slower growth. Such effects of competitive interactions among forage fish remain to be tested, but if forage species occur sympatrically frequently enough to suggest that competition is a regulating factor, their interactions could lead to a decrease in the availability of high quality forage species to marine birds and mammals.

Acknowledgments - Chapter 3

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Table 1. Sampling region, location, sampling day and time, times at low and high tide, and numbers of fish caught at stations with allopatric and sympatric aggregations of juvenile Pacific herring, Pacific sandlance, and pink salmon in PWS during July, 1996. Samples from stations C and F were collected outside survey sites. Gear abbreviations: BS = beach seine, PS = purse seine, Cast = cast net, Hand = hand dug, P = plankton net. Regions refer to map Figure 1.

										Catch per Species		
Fish Station	**Zoop. Station**	**Gear Type**	**Region**	**Location**	**Transect Leg**	**Day-Month**	**Sampl Time**	**High Tide**	**Low Tide**	**Herring**	**Sand-lance**	**Pink Salmon**
Allopatric Aggregations												
14-1B	14-P	BS	SW	W of Pt. Countess	S1002	17-July	10:10	15:48	9:16	13	--	--
47-2S	60-P	Cast	NE	NE Bligh Island	N1703A	23-July	17:30	7:26	12:45	414	--	--
47-5U	60-P	PS	NE	NE Bligh Island	N1703A	23-July	16:15	7:26	12:45	176	--	--
54-1B	54-P	BS	NE	Galena Bay W. of Narrows	N1904	23-July	11:10	7:26	12:45	17	--	--
61-1B	61-P	BS	NE	W Landlocked Bay Bidarka Pt.	N1302	24-July	11:45	8:15	13:39	95	--	--
68-1B	68-P	BS	NE	E Porcupine Pt.	N0704	25-July	10:40	9:40	14:48	10	--	--
68-5U	68-P	PS	NE	Goose Island, off Porcupine Pt.	N0701B	26-July	19:00	11:00	16:09	234	--	--
79-1B	79-P	BS	NE	Knowles Bay	N0505	27-July	9:55	11:56	5:31	303	--	--
87-1B	87-P	BS	NE	Knowles Bay	N0505	28-July	4:40	12:52	6:24	88	--	--
C-?-15	48-P	BS	C	NW Naked Is., E Bob Day Bay	C070	22-July	----	12:12	18:47	90	--	--
49-1B	49-P	BS	C	S Storey Island	C0608	22-July	12:10	18:47	11:59	--	--	137
53-1B	53-P	BS	NE	N Galena Bay	N1908	23-July	9:00	7:26	12:45	--	--	67
58-2U	68-P	PS	NE	Outer Port Fidalgo, Porcupine Pt.	N0901A	25-July	13:30	9:40	14:48	--	--	61
11-2B	11-P	BS	SW	Bainbridge Pt.	S0806	16-July	17:40	15:18	8:43	--	33	--
11-2B	11-P	BS	SW	Bainbridge Pt.	S0806	16-July	17:40	15:18	8:43	--	33	--
47-1B	47-P	BS	C	S Cabin Bay	C0705	22-July	9:55	18:47	11:59	--	50	--
63-1B	63-P	BS	NE	Boulder Bay (inside Bidarka Pt.)	N1306	24-July	13:35	8:15	13:39	--	52	--
64-2B	64-P	BS	NE	Irish Cove, Port Fidalgo	N0905	24-July	15:20	8:15	13:39	--	579	--
66-1B	66-P	BS	NE	Port Fidalgo	N0909	24-July	18:05	8:15	13:39	--	127	--
80-1B	80-P	BS	NE	Knowles Bay/Red Head	N0506	27-July	11:10	11:56	5:31	--	11000	--
82-1B	82-P	BS	NE	West Bligh Island	N1507	27-July	15:00	11:56	17:21	--	11	--
88-1X	88-P	Hand	NE	Knowles Bay/Red Head	N0506	28-July	6:35	12:52	6:24	--	16	--

F-1-D8	47-P	BS	C	Cabin Bay, Fuel Cache, Naked Is.	C0704	21-July	19:55	18:02	11:33	--	12	--
F-1-D12	47-P	BS	C	Cabin Bay, Fuel Cache, Naked Is.	C0704	22-July	8:00	5:59	12:12	--	15	--
F-2-D13	47-P	BS	C	Cabin Bay, Fuel Cache, Naked Is.	C0704	22-July	12:10	5:59	12:12	--	17	--
F-1-D15	47-P	BS	C	Cabin Bay, Fuel Cache, Naked Is.	C0704	22-July	16:05	18:47	12:12	--	32	--
F-2-D16	47-P	BS	C	Cabin Bay, Fuel Cache, Naked Is.	C0704	22-July	20:15	18:47	0:07	--	15	--
Sympatric Aggregations												
03-2U	10-P	PS	SW	Prince of Wales Passage	S0604	16-July	15:48	15:18	8:43	650	--	78
10-1B	10-P	BS	SW	Bainbridge Pt.	S0805	16-July	15:30	15:18	8:43	430	--	199
20-1B	20-P	BS	SW	Paddy Bay	S1609	17-July	18:42	15:48	9:16	56	--	46
24-1B	24-P	BS	SW	Italian Bay, SW Knight Is.	S2008	18-July	13:00	16:19	9:50	48	--	25
18-2U	29-P	PS	C	Bay of Isles, E Knight Is.	C0105B	19-July	12:30	16:50	10:20	1300	28	--
60-1B	60-P	BS	NE	West Bligh Island	N1507	24-July	9:50	8:15	13:39	32000	600	--
72-1B*	71-P	BS	NE	Knowles Bay/Red Head	N0505	25-July	15:20	9:40	14:48	595	13500	--
84-1B	84-P	BS	NE	Knowles Bay/Red Head	N0506	27-July	18:00	23:29	17:21	9	17	--
48-1B	48-P	BS	C	N Cabin Bay	C0701	22-July	10:50	18:47	11:59	--	151	64

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*Stations 71-1B and 72-1B were virtually identical in time and space.

Table 2. Mean size and age (A.C.) of fish, preserved fork length (FL) and wet weight, numbers and weights of prey consumed, stomach fullness index, number of empty stomachs (Emp), and prey percent body weight for sets of allopatric and sympatric juvenile Pacific herring, Pacific sandlance and pink salmon at stations in PWS during July, 1996. Ten fish from each station were examined (*indicates exceptions of n = 9). Abbreviations: sem = standard error of the mean.

Fish station	A. C.	FL (mm)		Body Weight (g)		Number of Prey		Prey Weight (mg)		Fullness Index		Emp	Prey % BW	
		mean	sem	mean	sem	mean	sem	mean	sem	mean	sem		mean	sem
Pacific Herring														
Allopatric														
14-1B	1	99.7	3.4	6.6	0.7	59.6	19.9	3.89	1.48	18	8	1	0.8	0.2
47-2S	0	55.1	0.7	0.9	0.0	2507.9	221.8	193.68	27.20	26	3	0	6.4	0.6
47-5U	1	115.3	1.7	13.3	0.6	5211.1	932.3	233.11	33.47	95	20	0	2.2	0.2
54-1B	0	30.4	0.6	0.1	0.0	28.1	44.5	0.70	0.34	23	15	2	0.0	0.0
61-1B	0	40.5	0.9	0.4	0.0	372.8	48.8	11.84	2.46	73	13	0	1.4	0.2
68-1B	0	49.3	1.0	0.5	0.1	532.4	278.9	39.22	6.45	68	8	0	2.1	0.3
68-5U	1	130.1	2.6	19.5	1.2	677.5	218.0	326.91	173.15	38	5	0	0.8	0.1
79-1B	0	44.8	0.9	0.5	0.0	606.9	114.4	95.23	37.79	98	8	0	2.3	0.4
87-1B	0	42.1	0.7	0.4	0.0	179.8	19.6	10.57	2.10	75	8	0	1.3	0.1
C-?-15	0	37.8	0.7	0.2	0.0	490.0	70.4	13.00	1.79	85	8	0	1.3	0.2
Sympatric with Pink Salmon														
03-2U	2	191.3	3.2	68.6	4.8	598.8	364.1	666.59	164.47	70	8	0	0.9	0.1
10-1B	0	38.2	1.4	0.2	0.0	22.0	27.3	0.97	0.61	20	13	1	0.1	0.1
20-1B	1	113.5	3.7	12.3	1.4	117.3	255.9	4.51	2.81	18	15	4	1.4	0.7
24-1B	0	105.9	2.3	9.0	0.7	31.9	63.9	6.53	2.95	18	5	3	0.2	0.1
Sympatric with Pacific Sandlance														
18-2U*	1	125.6	4.2	17.0	2.1	402.2	328.2	42.05	9.15	20	5	1	0.2	0.1
60-1B	0	47.6	1.4	0.5	0.1	343.3	194.6	11.82	2.12	80	8	0	2.9	0.4
72-1B	0	46.3	1.2	0.5	0.0	679.7	580.4	22.58	4.07	70	8	0	1.8	0.2
84-1B*	0	33.2	0.4	0.1	0.0	44.2	42.7	1.63	0.44	28	10	1	0.5	0.2
Pink Salmon														
Allopatric														
49-1B	0	83.3	1.6	4.7	0.3	443.4	53.3	19.71	2.51	55	5	0	1.3	0.1
53-1B	0	74.2	3.1	3.7	0.5	356.8	83.6	40.32	1.20	58	8	0	1.3	0.2
58-2U	0	98.1	2.0	7.1	0.5	46.9	7.0	847.50	123.27	20	8	0	2.8	0.4
Sympatric with Pacific Herring														
03-2U	0	102.8	1.8	8.7	0.5	178.0	78.2	78.21	20.86	38	8	0	0.6	0.1
03-2U	0	130.0	1.6	17.7	0.5	56.7	26.1	289.21	168.38	53	13	0	1.0	0.3
10-1B	0	64.1	1.7	2.3	0.2	379.9	64.7	59.34	15.17	5	8	0	1.7	0.4
10-1B	0	102.4	3.1	9.6	1.0	180.0	85.1	13.91	5.74	40	13	0	1.1	0.2

20-1B	0	90.3	3.0	6.6	0.6	821.9	298.7	24.80	10.01	55	13	0	1.4	0.3
24-1B	0	96.8	1.9	8.1	0.6	91.9	21.3	11.24	5.58	25	8	0	0.8	0.1

Sympatric with Pacific Sandlance

48-1B	0	97.9	1.1	7.4	0.4	588.7	143.5	29.50	20.6	40	20	0	0.6	0.3

Pacific Sandlance

Allopatric

11-2B	0	72.3	2.6	1.3	0.1	971.4	69.7	51.24	4.42	70	3	0	2.2	0.2
11-2B	1	134.6	2.3	11.4	1.3	3244.8	473.2	355.77	80.60	78	3	0	2.2	0.4
47-1B	0	86.5	1.8	1.8	0.2	76.0	52.5	5.33	3.89	3	10	4	0.3	0.2
63-1B*	0	88.9	3.4	2.2	0.3	422.8	179.2	31.51	13.86	35	18	1	0.5	0.2
64-2B	0	65.8	1.1	0.7	0.0	1109.4	247.4	68.54	17.64	63	8	0	1.5	0.2
66-1B	0	95.9	2.0	2.8	0.2	2182.7	506.1	179.02	56.29	90	13	0	1.6	0.3
80-1B	0	75.5	2.7	1.2	0.1	31.1	13.6	0.85	0.37	13	5	0	0.3	0.1
82-1B	0	78.4	2.5	1.3	0.1	689.8	171.6	35.44	8.81	73	10	0	1.1	0.2
88-1X-	1	109.6	3.2	4.0	0.5	0.8	0.4	0.41	0.23	10	5	6	0.2	0.1
F-1-D8	0	68.9	2.2	0.9	0.0	313.4	195.1	15.56	10.91	15	15	4	0.6	0.4
F-1-D12	1	114.1	4.8	5.4	0.6	975.3	213.0	63.31	13.78	88	13	0	1.1	0.2
F-2-D13	0	61.1	2.1	0.7	0.1	616.2	547.9	30.04	5.06	83	10	0	1.2	0.3
F-1-D15	0	73.5	1.9	1.1	0.1	849.9	203.7	37.73	10.89	65	10	0	0.5	0.1
F-2-D16	0	72.4	2.3	1.1	0.2	78.1	58.9	3.34	2.49	8	10	1	0.2	0.0

Sympatric with Pacific Herring

18-2U	1	111.8	2.0	5.5	0.3	2082.0	169.0	138.71	12.67	68	5	0	2.1	0.2
60-1B	0	71.6	1.8	0.9	0.1	71.2	32.9	5.45	2.91	20	13	1	0.7	0.2
71-1B	0	76.1	1.3	1.2	0.1	111.5	70.7	4.81	3.15	5	10	4	0.4	0.2
84-1B-	0	75.5	2.7	1.1	0.1	0.1	0.1	0.00	0.00	3	3	9	0.1	0.0

Sympatric with Pink Salmon

48-1B	0	64.3	0.8	0.8	0.0	221.3	64.1	12.00	2.14	48	8	0.00	0.9	0.2

Table 3. Probability results from 2-way ANOVA on ranks of fish size and measures of total feeding in areas with different species aggregations. The two factors used were "fish species" (Pacific herring, pink salmon and Pacific sandlance) and "aggregation type" (allopatric\sympatric). Specific paired comparisons were performed when $P < 0.05$ for the interaction terms.

	Fish Species	Allopatric\ Sympatric	Interaction Term
Measures of Fish Size			
Length (mm FL)	<0.0001	0.0002	0.0538
Weight (mg)	<0.0001	0.0002	0.1050
Measures of Total Feeding			
Fullness Index	0.0068	<0.0001	0.0092
Prey Percent Body Weight	0.0004	0.0019	<0.0001
Total Weight of Prey	0.0002	0.0081	0.0020
Total Number of Prey	0.6525	0.0564	0.0003

Table 4. Fork lengths and measures of total feeding for three forage species in allopatric and sympatric aggregations in PWS during July, 1996. Probability (P) values are results of Rank Sum Tests comparing species values between aggregations. Abbreviations: md = median, sem = standard error of the mean, T = trace contents.

Species/		Fork Length				% Fullness				Total Prey Number				Total Prey Biomass				Prey % Body			
Aggregation type	n	P	md	mean	sem	P	md	mea	sem	P	md	mean	sem	P	md	mean	sem	P	md	mea	sem
Pacific Herring																					
Allopatric	10	---	47.0	64.5	3.5	---	75	70	5	---	383.5	1066.6	181.3	---	19.97	92.80	13.50	---	1.4	1.9	0.2
Sympatric with Pink Salmon	40	<0.0001	107.0	112.2	8.8	<0.0001	13	25	8	<0.0001	24.0	192.4	51.1	0.0035	1.68	169.70	60.60	<0.0001	0.4	0.7	0.2
Sympatric with Sandlance	38	0.8280	46.5	62.3	6.0	0.0143	50	50	5	0.0445	269.5	374.2	66.2	0.0158	11.95	19.40	3.38	0.2546	1.1	1.4	0.2
Pink Salmon																					
Allopatric	30	---	85.0	85.2	2.2	---	75	68	5	---	288.5	282.4	45.0	---	24.81	302.50	82.1	---	1.6	1.8	0.2
Sympatric with Herring	60	0.0031	98.0	97.7	2.7	0.0138	50	48	5	0.2550	123.0	284.7	62.4	0.0371	25.10	79.50	30.02	<0.0001	0.8	1.1	0.1
Sympatric with Sandlance	30	0.0033	98.0	97.9	1.2	0.0099	25	40	8	0.0378	412.5	588.7	143.5	0.3568	22.81	29.50	6.51	<0.0001	0.5	0.6	0.1
Pacific Sandlance																					
Allopatric	13	---	79.0	85.8	1.9	---	50	48	5	---	450.0	828.7	95.7	---	25.74	62.60	10.54	---	0.7	1.0	0.1
Sympatric with Herring	40	0.9287	76.5	83.8	2.8	<0.0001	T	20	8	0.0120	14.5	566.2	147.2	0.0172	0.67	37.20	9.92	0.3285	0.4	0.8	0.2
Sympatric with Pink Salmon	10	<0.0001	63.5	64.3	0.8	0.8565	50	48	8	0.4333	175.5	221.3	64.1	0.3560	11.72	12.00	2.14	0.6431	0.8	0.9	0.2

Table 5. Probability results from 2-way ANOVA on ranks of density (numbers*m^{-3}) and percent density of zooplankton by taxonomic category using the factors "fish species" (Pacific herring, pink salmon and Pacific sandlance) and "aggregation type" (allopatric or sympatric). Specific paired comparisons were performed when the $P < 0.05$ for the interaction terms.

	Density			**Percent Density**		
Zooplankton Category	Fish Species	Allopatric \ Sympatric	Interaction term	Fish Species	Allopatric\ Sympatric	Interaction term
Barnacle Larvae	0.6705	0.6096	0.4426	0.8421	0.7064	0.2858
Large Calanoids	0.2709	0.0177	0.3425	0.0573	0.0374	0.3856
Small Calanoids	0.0150	0.0826	0.8585	0.2750	0.1408	0.4668
Chaetognaths	0.3096	0.0083	0.1593	0.4983	0.0036	0.2250
Cladocerans	0.7411	0.1004	0.0264	0.9273	0.0315	0.0306
Cyphonautes	0.0227	0.9943	0.6602	0.0333	0.9709	0.6346
Decapods	0.4710	0.0027	0.4969	0.8982	0.0100	0.7344
Euphausiids	0.4994	0.2415	0.0545	0.5449	0.3383	0.0544
Fish	0.7206	0.1523	0.2485	0.7241	0.1810	0.2548
Gastropods	0.6415	0.0001	0.8880	0.7575	0.0002	0.9938
Hyperiid Amphipods	0.9511	0.4460	0.6932	0.9353	0.8400	0.7619
Cnidarians\Ctenophores	0.0277	0.2998	0.4271	0.0058	0.1444	0.6064
Larvaceans	0.1626	0.2380	0.4300	0.0060	0.5237	0.0206
Other	0.6989	0.0712	0.6261	0.7641	0.4043	0.3934
Total Zooplankters	0.0615	0.1120	0.9611			

Table 6. Zooplankton mean density (numbers*m^{-3}) and biomass (mg*m^{-3} wet weight) available to juvenile Pacific herring, Pacific sandlance and pink salmon at stations corresponding to allopatric and sympatric aggregations sampled in PWS during July, 1996. Replicate zooplankton samples were collected in vertical hauls at each station using a 0.5 m diameter ring net with 243 μm mesh. Abbreviations: sem = standard error of the mean.

Zooplankton Station	**Total Density**		**Total Biomass**		**Gear Depth**	**Day**	**Time**
	mean	sem	mean	sem			
			Pacific Herring				
Allopatric							
14-P	3723.3	408.6	300.7	44.3	20	July 17	10:40
48-P	3642.0	265.9	223.1	54.1	20	July 22	11:00
54-P	1680.2	45.1	389.4	227.8	20	July 23	11:30
60-P	1989.2	128.7	168.9	2.1	20	July 24	10:10
61-P	2406.4	227.4	345.7	34.4	20	July 24	12:00
68-P	6641.5	191.3	526.0	7.1	8	July 25	10:55
79-P	3432.7	162.5	358.2	24.7	10	July 27	10:20
87-P	645.0	19.6	93.0	1.4	20	July 28	05:30
Grand mean	3020.0		300.6				
Sympatric with Pink Salmon							
10-P	2501.0	140.4	239.5	38.9	20	July 16	16:20
20-P	3242.9	1017.3	166.1	32.3	20	July 17	18:55
24-P	3099.1	577.8	221.7	48.0	20	July 18	13:30
Grand mean	2947.7		209.1				
Sympatric with Pacific Sandlance							
29-P	2907.2	330.4	238.6	0.8	20	July 19	16:55
60-P	1989.2	128.7	168.9	2.1	20	July 24	10:10
71-P	950.9	113.6	94.9	6.2	20	July 25	15:35
84-P	1359.9	93.3	87.6	1.5	20	July 27	18:38
Grand mean	1801.8		147.5				
			Pink Salmon				
Allopatric							
49-P	4029.0	602.8	372.0	167.3	20	July 22	12:20
53-P	1918.0	285.7	189.0	43.1	20	July 23	10:30
68-P	6641.5	191.3	526.0	7.1	8	July 25	10:55
Grand mean	4196.2		362.3				
Sympatric with Pacific Herring							
10-P	2501.0	140.4	239.5	38.9	20	July 16	16:20
20-P	3242.9	1017.0	166.1	32.3	20	July 17	18:55
24-P	3099.1	577.8	221.7	48.0	20	July 18	13:30
Grand mean	2947.7		209.1				

Sympatric with Pacific Sandlance							
48-P	3642.0	265.9	223.1	54.1	20	July 20	11:05
			Pacific Sandlance				
Allopatric							
11-P	2481.2	200.3	198.7	37.5	20	July 16	18:15
47-P	2798.2	326.6	229.0	70.1	20	July 22	10:10
63-P	3042.5	334.1	264.9	2.3	20	July 24	13:50
64-P	3046.9	170.9	412.5	81.5	20	July 24	15:30
66-P	2742.1	180.0	311.2	33.1	20	July 24	18:20
80-P	3163.1	433.3	226.3	9.8	20	July 27	11:55
82-P	1084.0	216.5	138.9	50.3	20	July 27	15:15
88-P	774.6	79.4	101.5	31.9	20	July 28	06:58
Grand mean	2391.6		235.4				
Sympatric with Pacific Herring							
29-P	2907.2	330.4	238.6	0.8	20	July 19	16:55
60-P	1989.2	128.7	168.9	2.1	20	July 24	10:10
71-P	950.9	113.6	94.9	6.2	20	July 25	15:35
84-P	1359.9	93.3	87.6	1.5	20	July 27	18:38
Grand mean	1801.8		147.5				
Sympatric with Pink Salmon							
48-P	3642.0	265.9	223.1	54.1	20	July 22	11:05

Table 7a. Zooplankton density (number* m^{-3}) and percent density by taxonomic group and total organisms at areas of allopatric and sympatric aggregations of Pacific herring (H). SL = Pacific Sandlance, PS = Pink Salmon, md= median, sem = standard error of the mean.

Prey Category	Aggregation Type	Density			Percent Density		
		md	mean	sem	md	mean	sem
Barnacle Larvae	H	8.2	9.8	2.7	0.3	0.2	0.1
	H+PS	16.3	13.2	3.4	0.6	0.4	0.1
	H+SL	6.1	4.8	25.8	0.4	1.5	0.8
Large Calanoids	H	4.2	21.6	11.1	0.2	0.8	0.3
	H+PS	12.5	11.2	3.0	0.4	0.4	0.1
	H+SL	24.6	34.7	8.2	1.5	2.4	0.7
Small Calanoids	H	2236.8	2518.8	353.6	78.7	74.4	3.3
	H+PS	2149.2	2264.3	192.3	81.6	80.1	1.9
	H+SL	1295.8	1291.0	155.0	77.2	75.1	4.6
Chaetognaths	H	0.0	1.5	0.7	0.0	0.0	0.0
	H+PS	2.3	1.8	0.5	0.1	0.1	0.0
	H+SL	0.0	1.3	1.1	0.0	0.1	0.1
Cladocerans	H	28.5	35.3	5.8	0.9	1.7	0.4
	H+PS	65.2	81.0	13.1	2.8	2.9	0.3
	H+SL	17.3	75.6	43.0	1.2	2.9	1.4
Cyphonautes	H	1.0	14.0	6.9	0.1	0.3	0.1
	H+PS	4.1	10.0	4.2	0.1	0.4	0.2
	H+SL	0.0	1.4	1.0	0.0	0.1	0.1
Decapods	H	9.9	11.9	2.6	0.5	0.5	0.1
	H+PS	1.2	4.8	2.6	0.0	0.2	0.1
	H+SL	0.9	4.1	2.3	0.1	0.2	0.1
Euphausiids	H	4.1	22.8	8.2	0.2	0.5	0.1
	H+PS	0.1	2.1	1.3	0.0	0.1	0.0
	H+SL	1.2	6.6	4.5	0.1	0.7	0.5
Fish	H	0.0	0.2	0.2	0.0	0.0	0.0
	H+PS	0.0	0.1	0.1	0.0	0.0	0.0
	H+SL	0.0	0.0	0.0	0.0	0.0	0.0
Gastropods	H	158.9	330.7	71.6	7.0	11.7	2.5
	H+PS	85.6	96.3	21.0	3.2	3.3	0.4
	H+SL	36.7	103.9	43.7	3.1	4.6	1.3
Hyperiid Amphipods	H	0.6	1.0	0.2	0.0	0.1	0.0
	H+PS	0.0	2.4	1.4	0.0	0.1	0.1
	H+SL	1.0	0.9	0.3	0.1	0.1	0.0

Larvaceans	H	130.4	190.9	36.5	5.7	5.5	0.6
	H+PS	209.8	207.3	23.1	8.2	7.4	0.7
	H+SL	105.9	153.0	44.7	7.0	7.8	1.4
Other	H	59.1	103.5	24.2	2.5	3.3	0.7
	H+PS	61.1	127.4	53.9	2.3	4.3	1.6
	H+SL	48.9	69.0	23.4	3.3	3.2	0.6
Total	H	2952.0	3279.1	441.1			
	H+PS	2581.4	2836.0	258.3			
	H+SL	1656.9	1801.8	288.1			

Table 7b. Zooplankton density (number* m^3) and percent density by taxonomic group and total at aggregations of allopatric and sympatric pink salmon (PS). H = Herring, SL = Sandlance, md = median, sem = standard error of the mean.

Prey Category	**Aggregation Type**	**Density**			**Percent Density**		
		md	mean	sem	md	mean	sem
Barnacle Larvae	PS	18.3	17.7	6.0	0.4	0.5	0.2
	PS+H	16.3	11.6	2.7	0.6	0.4	0.1
	PS+SL	4.1	4.1	4.1	0.1	0.1	0.1
Large Calanoids	PS	1.5	13.0	8.2	0.1	0.3	0.2
	PS+H	12.5	9.7	2.3	0.4	0.3	0.1
	PS+SL	2.0	2.0	2.0	0.1	0.1	0.1
Small Calanoids	PS	3292.1	3271.7	642.6	78.5	79.3	2.1
	PS+H	2149.2	2207.6	130.7	81.8	81.3	1.4
	PS+SL	3074.1	3074.1	181.3	84.5	84.5	1.2
Chaetognaths	PS	0.0	0.3	0.2	0.0	0.0	0.0
	PS+H	2.3	2.0	0.4	0.1	0.1	0.0
	PS+SL	0.5	0.5	0.3	0.0	0.0	0.0
Cladocerans	PS	26.5	36.7	13.0	0.7	1.0	0.3
	PS+H	65.2	75.7	8.8	2.8	2.8	0.2
	PS+SL	44.8	44.8	12.2	1.3	1.3	0.4
Cyphonautes	PS	4.1	21.7	16.4	0.2	0.4	0.3
	PS+H	4.1	10.8	3.5	0.1	0.5	0.2
	PS+SL	2.0	2.0	2.0	0.1	0.1	0.1
Decapods	PS	18.7	18.9	8.3	0.5	0.6	0.2
	PS+H	1.2	3.6	1.8	0.0	0.1	0.1
	PS+SL	8.3	8.3	8.3	0.2	0.2	0.2
Euphausiids	PS	24.6	38.9	18.7	0.5	0.6	0.3
	PS+H	0.3	1.4	0.9	0.0	0.0	0.0
	PS+SL	4.1	4.1	4.1	0.1	0.1	0.1
Fish	PS	0.0	0.0	0.0	0.0	0.0	0.0
	PS+H	0.0	0.1	0.0	0.0	0.0	0.0
	PS+SL	0.0	0.0	0.0	0.0	0.0	0.0
Gastropods	PS	146.7	328.8	134.1	5.4	6.6	1.6
	PS+H	85.6	87.3	14.7	3.2	3.1	0.3
	PS+SL	142.6	142.6	12.2	3.9	3.9	0.1
Hyperiid Amphipods	PS	0.5	1.4	0.7	0.0	0.1	0.0
	PS+H	0.0	3.1	1.3	0.0	0.1	0.1
	PS+SL	0.0	0.0	0.0	0.0	0.0	0.0

Larvaceans	PS	362.6	300.1	85.6	7.0	6.3	1.4
	PS+H	209.8	193.9	17.7	8.3	7.2	0.6
	PS+SL	297.4	297.4	53.0	8.1	8.1	0.9
Other	PS	105.9	144.6	47.5	3.3	4.3	1.7
	PS+H	61.1	103.9	36.6	2.3	3.6	1.1
	PS+SL	50.9	50.9	26.5	1.4	1.4	0.6
Total	PS	4029.0	4196.2	882.4			
	PS+H	2581.4	2836.0	258.8			
	PS+SL	3642.0	3642.0	265.9			

Table 7c. Zooplankton density (number * m^3) and percent density by taxonomic group and total at aggregations of allopatric and sympatric sandlance (SL). H = Herring, PS = Pink Salmon, md = median, sem = standard error of the mean.

Prey Category	Aggregation Type	Density			Percent Density		
		md	mean	sem	md	mean	sem
Barnacle Larvae	SL	12.2	12.4	2.6	0.5	0.6	0.2
	SL+H	41.8	25.8	6.1	0.4	1.5	0.8
	SL+PS	4.1	4.1	4.1	0.1	0.1	0.1
Large Calanoids	SL	8.4	17.8	5.5	0.5	0.7	0.2
	SL+H	24.6	34.7	8.2	1.5	2.4	0.7
	SL+PS	2.0	2.0	2.0	0.1	0.1	0.1
Small Calanoids	SL	2086.8	1891.3	115.7	72.5	73.4	1.5
	SL+H	1295.8	1291.0	155.0	77.2	75.1	4.6
	SL+PS	3074.1	3074.1	181.3	84.5	84.5	1.2
Chaetognaths	SL	0.0	0.2	0.0	0.0	0.0	0.0
	SL+H	0.0	1.3	1.1	0.0	0.1	0.1
	SL+PS	0.5	0.5	0.3	0.0	0.0	0.0
Cladocerans	SL	44.8	79.4	13.5	1.8	2.9	0.5
	SL+H	17.3	75.6	43.0	1.2	2.9	1.4
	SL+PS	44.8	44.8	12.2	1.3	1.3	0.4
Cyphonautes	SL	0.0	0.9	0.5	0.0	0.0	0.0
	SL+H	0.0	1.4	1.0	0.0	0.1	0.1
	SL+PS	2.0	2.0	2.0	0.1	0.0	0.0
Decapods	SL	6.9	12.7	2.6	0.5	0.6	0.1
	SL+H	0.9	4.1	2.3	0.1	0.2	0.1
	SL+PS	8.3	8.3	8.3	0.2	0.2	0.2
Euphausiids	SL	0.0	8.9	4.9	0.0	0.4	0.2
	SL+H	1.2	6.6	4.5	0.1	0.7	0.5
	SL+PS	4.1	4.1	4.1	0.1	0.1	0.1
Fish	SL	0.0	0.6	0.6	0.0	0.0	0.0
	SL+H	0.0	0.0	0.0	0.0	0.0	0.0
	SL+PS	0.0	0.0	0.0	0.0	0.0	0.0
Gastropods	SL	130.4	181.0	21.8	5.3	7.5	0.9
	SL+H	36.7	103.9	43.7	3.1	4.6	1.3
	SL+PS	142.6	142.6	12.2	3.9	3.9	0.1
Hyperiid Amphipods	SL	0.3	0.6	0.1	0.0	0.0	0.0
	SL+H	1.0	0.9	0.3	0.1	0.1	0.0
	SL+PS	0.0	0.0	0.0	0.0	0.0	0.0

Larvaceans	SL	248.5	229.8	12.8	9.4	10.0	0.7
	SL+H	105.9	153.0	44.7	7.0	7.8	1.4
	SL+PS	297.4	297.4	53.0	8.1	8.1	0.9
Other	SL	97.8	91.6	9.7	4.0	3.6	0.4
	SL+H	48.9	69.0	23.4	3.3	3.2	0.6
	SL+PS	50.9	50.9	26.5	1.4	1.4	0.6
Total	SL	2681.4	2473.7	175.9			
	SL+H	1656.9	1801.8	288.1			
	SL+PS	3642.0	3642.0	265.9			

Table 8. Diet similarity (PSI) by percent number and percent biomass of prey species within and between forage species in allopatric and sympatric aggregations in PWS during July, 1996. Diet similarity > 60% is significant.

(a) Diet similarity between species in allopatric aggregations

allopatric aggregation	allopatric aggregation	Percent Number	Percent Biomass
pink salmon	Pacific sandlance	15.3	11.0
pink salmon	Pacific herring	25.6	17.1
Pacific sandlance	Pacific herring	**73.1**	51.3

(b) Diet similarity between species in sympatric aggregations

sympatric aggregation	sympatric aggregation	Percent Number	Percent Biomass
pink salmon with Pacific sandlance	Pacific sandlance with pink salmon	0.5	3.2
pink salmon with Pacific herring	Pacific herring with pink salmon	36.2	37.8
Pacific herring with Pacific sandlance	Pacific sandlance with Pacific herring	46.1	53.5

(c) *Diet similarity within species between allopatric and sympatric aggregations*

allopatric aggregation	sympatric aggregation	Percent Number	Percent Biomass
pink salmon	pink salmon with Pacific sandlance	**66.5**	56.1
pink salmon	pink salmon with Pacific herring	**69.1**	**61.0**
Pacific sandlance	Pacific sandlance with pink salmon	42.8	54.9
Pacific sandlance	Pacific sandlance with Pacific herring	55.6	**60.5**
Pacific herring	Pacific herring with pink salmon	**62.9**	38.2
Pacific herring	Pacific herring with Pacific sandlance	**72.7**	**70.2**

Table 9. Probability results from 2-way ANOVA on ranks of prey number and percent number, prey biomass and percent biomass, and prey selection by taxonomic category in areas with different fish species aggregations. The two factors used were "fish species" (Pacific herring, pink salmon and Pacific sandlance) and "aggregation type" (allopatric\sympatric). Specific paired comparisons were performed when the $P < 0.05$ for the interaction terms. Abbreviations: Allo. = Allopatric, Symp. = Sympatric, DNT = Do Not Test.

	Number of Prey			**Percent Number of Prey**			**Biomass of Prey**			**Percent Biomass of Prey**			**Selection of Prey**		
Prey Category	Species	Allo.\ Symp.	Interaction Term	Species	Allo.\ Symp.	Interaction Term	Species	Allo.\ Symp.	Interaction Term	Species	Allo.\ Symp.	Interaction Term	Species	Allo.\ Symp.	Interaction Term
Barnacle Larvae	<0.0001	0.1724	0.4698	<0.0001	0.0513	0.5265	<0.0001	0.1199	0.3662	<0.0001	0.0434	0.4832	<0.0001	0.2957	<0.0001
Small calanoids	<0.0001	0.0163	0.0113	<0.0001	0.1766	0.0821	<0.0001	0.0381	0.0100	<0.0001	0.2572	0.0673	<0.0001	0.0097	0.2609
Large Calanoids	0.0030	0.4403	0.0302	0.0002	0.5948	0.0459	0.0019	0.4892	0.0317	0.0041	0.9088	0.0144	<0.0001	0.0062	0.0004
Chaetognath	<0.0001	<0.0001	0.0056	<0.0001	<0.0001	0.0050	<0.0001	< 0.0001	0.0056	<0.0001	<0.0001	0.0072	0.0104	0.0007	0.0010
Cladoceran	< 0.0001	0.1969	0.5251	<0.0001	0.8531	0.6917	<0.0001	0.1969	0.5251	<0.0001	0.4750	0.8991	0.0072	<0.0001	<0.0001
Cyphonautes	0.8475	0.4019	0.8475	0.8469	0.4017	0.8469	0.8475	0.4019	0.8475	0.8480	0.4020	0.8480	<0.0001	0.0007	0.4770
Decapod	<0.0001	<0.0001	0.0036	<0.0001	<0.0001	0.0013	<0.0001	<0.0001	0.0061	<0.0001	<0.0001	0.0125	<0.0001	<0.0001	0.5431
Euphausiid	0.7794	0.0886	0.9509	0.8408	0.0736	0.9353	0.7886	0.0672	0.9231	0.7998	0.0686	0.9076	0.2539	0.0040	<0.0001
Fish	<0.0001	0.0005	0.0002	<0.0001	0.0004	0.0002	<0.0001	0.0005	0.0002	<0.0001	0.0005	0.0002	<0.0001	<0.0001	<0.0001
Gammarid Amphipod	0.9310	0.5149	0.2584	0.9317	0.5123	0.2560	0.9338	0.5172	0.2561	0.9267	0.5064	0.2589	DNT*	DNT*	DNT*
Gastropod	0.7501	0.2957	0.3700	0.7803	0.6247	0.2145	0.5452	0.2780	0.3274	0.7833	0.4778	0.2229	DNT*	DNT*	DNT*
Hyperiid Amphipods	<0.0001	<0.0001	0.0002	<0.0001	<0.0001	0.0001	<0.0001	<0.0001	0.0002	<0.0001	<0.0001	0.0002	0.4366	0.0313	0.0032
Insect	0.2372	<0.0001	0.1454	<0.0001	0.2471	0.1566	<0.0001	0.2475	0.1548	<0.0001	0.2520	0.1583	DNT*	DNT*	DNT*
Cnidarian\Ctenophore	0.0098	0.0043	0.0098	0.0096	0.0043	0.0096	0.0369	0.0438	0.0369	0.0369	0.0438	0.0369	DNT*	DNT*	DNT*
Larvacean	<0.0001	0.0030	<0.0001	<0.0001	0.5352	<0.0001	<0.0001	0.0030	<0.0001	<0.0001	0.1412	0.0006	<0.0001	0.4006	0.0022
Malocostraca	0.0007	0.0520	0.2945	0.0007	0.0494	0.2812	0.0007	0.0418	0.2784	0.0008	0.0399	0.2766	DNT*	DNT*	DNT*
Other	<0.0001	0.3725	0.0490	<0.0001	0.2567	0.1542	<0.0001	0.1111	0.1430	<0.0001	0.4864	0.4255	0.0036	<0.0001	0.0198

Table 10a. Prey utilization and selection for Pacific herring (H). Probability (P) values refer to paired comparisons between allopatric and sympatric aggregations. Abbreviations: PS = Pink Salmon, SL = Sandlance, md = median, sem = standard error of the mean, DNT = Do Not Test.

Prey Category	Aggregation	Number of Prey				Percent Number of Prey				Biomass of Prey				Percent Biomass of Prey				Strauss Linear Selection			
		md	mean	sem	P	md	mean	sem	P	md	mean	sem	P	md	mean	sem	P	md	mean	sem	P
Barnacle Larvae	H	0.0	0.9	0.3	- - -	0.0	0.3	0.2	- - -	0.00	0.22	0.07	- - -	0.0	1.4	0.7	- - -	-0.1	+0.1	0.2	- - -
	H+PS	0.0	0.0	0.0	DNT	0.0	0.0	0.0	DNT	0.00	0.00	0.00	DNT	0.0	0.0	0.0	DNT	-0.4	-0.4	0.0	0.00
	w/SL	0.0	1.9	0.5	DNT	0.0	0.4	0.1	DNT	0.00	0.46	0.12	DNT	0.0	2.4	0.7	DNT	-0.2	-0.9	0.3	0.89
Large Calanoids	H	0.0	1.2	0.4	- - -	0.0	0.3	0.2	- - -	0.00	1.91	0.76	- - -	0.0	0.8	0.3	- - -	-0.2	-0.5	0.2	- - -
	H+PS	0.0	75.0	27.8	0.08	0.0	12.3	3.6	0.06	0.00	136.60	51.60	0.08	0.0	24.0	5.8	0.05	-0.3	+12.0	3.7	0.02
	H+SL	0.0	1.2	0.1	0.28	0.0	0.0	0.0	0.22	0.00	0.13	0.09	0.29	0.0	0.7	0.5	0.32	-2.2	-2.4	0.3	0.00
Small Calanoids	H	214.5	484.4	68.7	- - -	77.4	61.8	3.8	- - -	7.65	34.97	6.39	- - -	65.6	53.7	3.9	- - -	+5.7	-12.6	4.3	- - -
	H+PS	6.5	67.6	19.2	0.00	44.3	44.2	6.3	0.03	0.24	4.82	1.45	0.00	5.2	30.4	6.5	0.01	-38.1	-35.9	5.9	DNT
	H+SL	142.5	280.1	59.4	0.33	80.3	68.2	4.8	0.88	6.80	10.41	1.82	0.29	66.6	60.6	4.9	0.75	+0.3	-7.4	4.2	DNT
Chaeto-gnaths	H	0.0	0.0	0.0	- - -	0.0	0.0	0.0	- - -	0.00	0.00	0.00	- - -	0.0	0.0	0.0	- - -	-0.0	-0.0	0.0	- - -
	H+PS	0.0	0.6	0.2	0.01	0.0	0.1	0.0	0.01	0.00	0.26	0.09	0.01	0.0	1.0	0.1	0.00	-0.1	+0.1	0.0	0.87
	H+SL	0.0	0.0	0.0	1.00	0.0	0.0	0.0	1.00	0.00	0.00	0.00	1.00	0.0	0.0	0.0	1.00	-0.0	-0.1	0.0	0.57
Cladocerans	H	2.0	6.4	1.4	- - -	0.2	2.1	0.8	- - -	0.08	0.25	0.05	- - -	0.1	2.7	1.0	- - -	-0.5	+0.4	0.7	- - -
	H+PS	0.0	0.8	0.4	DNT	0.0	0.6	0.3	DNT	0.00	0.03	0.01	DNT	0.0	0.7	0.4	DNT	-2.6	-2.3	0.3	0.00
	H+SL	3.0	5.0	1.2	DNT	1.1	1.5	0.3	DNT	0.12	0.20	0.05	DNT	1.0	1.2	0.2	DNT	-0.6	-1.3	0.6	0.46
Decapods	H	0.0	7.9	2.2	- - -	0.0	2.2	0.9	- - -	0.00	32.27	9.58	- - -	0.0	10.7	2.5	- - -	-0.2	+1.8	1.0	- - -
	H+PS	0.0	0.5	0.3	0.12	0.0	0.1	0.0	0.20	0.00	1.93	1.03	0.11	0.0	0.4	0.2	0.11	-0.1	-0.1	0.1	DNT
	H+SL	0.0	0.9	0.4	0.21	0.0	0.4	0.3	0.36	0.00	3.79	1.67	0.20	0.0	6.4	2.6	0.37	-0.2	+0.2	0.3	DNT
Euphausiids	H	0.0	0.1	0.0	- - -	0.0	0.0	0.0	- - -	0.00	0.02	0.01	- - -	0.0	0.1	0.0	- - -	-0.2	-0.5	0.1	- - -
	H+PS	0.0	0.3	0.1	DNT	0.0	0.0	0.1	DNT	0.00	2.16	1.01	DNT	0.0	0.4	0.2	DNT	-0.1	-0.0	0.0	0.00
	H+SL	0.0	0.1	0.1	DNT	0.0	0.2	0.2	DNT	0.00	0.02	0.02	DNT	0.0	0.2	0.2	DNT	-0.2	-0.7	0.2	0.89
Fish	H	0.0	0.0	0.0	- - -	0.0	0.0	0.0	- - -	0.00	0.00	0.00	- - -	0.0	0.0	0.0	- - -	+0.0	-0.0	0.0	- - -
	H+PS	0.0	0.0	0.0	1.00	0.0	0.0	0.0	1.00	0.00	0.00	0.00	1.00	0.0	0.0	0.0	1.00	-0.0	-0.0	0.0	0.00
	H+SL	0.0	0.1	0.1	0.81	0.0	0.0	0.0	0.81	0.00	0.35	0.35	0.81	0.0	0.5	0.5	0.81	+0.0	+0.1	0.1	0.05
Hyperiid Amphipods	H	0.0	0.1	0.1	- - -	0.0	0.0	0.0	- - -	0.00	1.23	0.67	- - -	0.0	1.2	0.7	- - -	-0.0	-0.0	0.0	- - -
	H+PS	0.0	1.9	1.0	0.05	0.0	0.4	0.2	0.05	0.00	20.24	13.31	0.05	0.0	3.3	1.4	0.06	+0.0	+0.3	0.2	0.01
	H+SL	0.0	0.2	0.1	0.73	0.0	0.5	0.4	0.71	0.00	0.86	0.83	0.78	0.0	3.0	2.1	0.75	+0.1	+0.4	0.4	0.28
Larvaceans	H	17.0	544.9	172.2	- - -	7.3	23.2	3.3	- - -	0.57	18.14	5.73	- - -	2.4	16.0	2.7	- - -	+1.3	+17.6	3.4	- - -
	H+PS	0.5	42.8	20.1	0.00	0.4	16.8	4.8	0.03	0.02	1.42	0.67	0.00	0.0	11.8	4.3	0.00	-6.4	+9.4	4.8	0.00
	H+SL	16.0	66.0	23.9	0.49	7.3	18.2	3.7	0.77	0.53	2.20	0.79	0.49	4.6	12.4	2.5	0.28	+0.2	+10.4	3.5	0.59
Other	H	4.0	15.8	2.3	- - -	0.6	6.2	1.2	- - -	0.09	0.56	0.12	- - -	0.2	5.5	1.3	- - -	-2.9	+3.0	1.3	- - -
	H+PS	0.0	1.2	0.3	0.00	0.0	3.8	1.4	DNT	0.00	0.06	0.03	DNT	0.0	1.3	0.7	DNT	-1.8	-0.5	1.5	0.78
	H+SL	6.0	14.8	3.2	0.84	2.6	4.2	0.9	DNT	0.06	0.18	0.04	DNT	0.3	2.3	0.9	DNT	1.5	+1.2	1.0	0.08

Table 10b. Prey utilization and selection for Pink salmon (PS). Probability (P) values refer to comparisons paired between allopatric and sympatric aggregations. Abbreviations: H = Herring, SL = Sandlance, md = median, sem = standard error of the mean, DNT = Do Not Test.

		Number of Prey				Percent Number of Prey				Biomass of Prey				Percent Biomass of Prey				Strauss Linear Selection			
Prey Category	**Aggregation**	md	mea	sem	P	md	mean	sem	P	md	mean	sem	P	md	mean	sem	P	md	mean	sem	P
Barnacle Larvae	PS	0.0	0.0	0.0	- - -	0.0	0.0	0.0	- - -	0.00	0.00	0.00	- - -	0.0	0.0	0.0	- - -	-0.5	+0.5	0.0	- - -
	PS+H	0.0	1.2	0.0	DNT	0.0	0.4	0.2	DNT	0.00	1.20	0.69	DNT	0.0	3.4	1.5	DNT	-0.3	-0.0	0.2	0.06
	PS+SL	0.0	0.9	0.8	DNT	0.0	0.1	0.1	DNT	0.00	0.59	0.40	DNT	0.0	1.8	1.4	DNT	-0.1	-0.1	0.0	0.00
Large Calanoids	PS	0.0	1.2	0.4	- - -	0.0	2.3	0.8	- - -	0.00	2.21	0.74	- - -	0.0	1.1	0.8	- - -	-0.1	+1.9	0.8	- - -
	PS+H	0.0	3.5	1.4	0.47	0.0	3.9	1.6	0.58	0.00	5.33	1.77	0.45	0.0	10.0	2.8	0.14	-0.3	+3.6	1.6	0.75
	PS+SL	0.0	0.0	0.0	0.16	0.0	0.0	0.0	0.16	0.00	0.00	0.00	0.16	0.0	0.0	0.0	0.16	-0.1	-0.1	0.0	0.12
Small Calanoids	PS	0.0	1.1	0.5	- - -	0.0	1.1	0.6	- - -	0.00	0.08	0.04	- - -	0.0	0.2	0.1	- - -	-81.3	-78.2	0.9	- - -
	PS+H	1.0	7.5	3.6	0.04	0.5	4.2	1.4	0.04	0.07	0.42	0.17	0.02	0.2	2.4	1.1	0.01	-80.6	-77.0	1.4	DNT
	PS+SL	0.5	2.3	1.6	0.42	0.2	0.3	0.1	0.81	0.04	0.07	0.02	0.45	0.1	0.3	0.1	0.32	-84.3	-84.2	0.1	DNT
Chaetognaths	PS	0.0	0.1	0.1	- - -	0.0	0.0	0.0	- - -	0.00	0.04	0.02	- - -	0.0	0.2	0.1	- - -	+0.0	+0.0	0.0	- - -
	PS+H	0.0	0.8	0.3	0.13	0.0	2.6	1.0	0.10	0.00	0.35	0.13	0.13	0.0	2.4	1.6	0.17	-0.1	+2.5	0.0	0.04
	PS+SL	0.0	0.3	0.2	0.61	0.0	0.0	0.0	0.65	0.00	0.13	0.09	0.61	0.0	0.3	0.2	0.67	-0.0	+0.0	0.0	0.10
Cladocerans	PS	0.0	0.3	0.1	- - -	0.0	0.1	0.0	- - -	0.00	0.01	0.00	- - -	0.0	0.1	0.0	- - -	-1.0	-0.9	0.1	- - -
	PS+H	0.0	1.1	0.5	DNT	0.0	0.7	0.3	DNT	0.00	0.04	0.02	DNT	0.0	0.1	0.0	DNT	-2.6	-2.1	0.3	0.00
	PS+SL	0.0	0.0	0.0	DNT	0.0	0.0	0.0	DNT	0.00	0.00	0.00	DNT	0.0	0.0	0.0	DNT	-1.3	-1.3	0.0	0.06
Decapods	PS	0.0	5.8	1.7	- - -	0.0	12.6	3.6	- - -	0.00	18.14	6.38	- - -	0.0	7.3	2.8	- - -	-0.5	+12.1	3.7	- - -
	PS+H	0.0	0.1	0.1	0.00	0.0	0.8	0.6	0.00	0.00	0.66	0.30	0.00	0.0	2.3	1.7	0.00	-0.1	+0.6	0.5	DNT
	PS+SL	0.0	0.1	0.1	0.06	0.0	0.1	0.1	0.07	0.00	0.47	0.47	0.07	0.0	2.3	2.3	0.11	-0.2	-0.1	0.1	DNT
Euphausiids	PS	0.0	0.1	0.1	- - -	0.0	0.2	0.2	- - -	0.00	0.36	0.36	- - -	0.0	0.0	0.0	- - -	-0.5	-0.4	0.2	- - -
	PS+H	0.0	0.1	0.1	DNT	0.0	0.4	0.3	DNT	0.00	0.38	0.14	DNT	0.0	0.7	0.3	DNT	+0.0	+0.4	0.3	0.00
	PS+SL	0.0	0.0	0.0	DNT	0.0	0.0	0.0	DNT	0.00	0.00	0.00	DNT	0.0	0.0	0.0	DNT	-0.1	-0.1	0.0	0.22
Fish	PS	0.0	6.1	1.8	- - -	0.0	20.4	5.7	- - -	0.00	271.63	77.70	- - -	0.0	37.4	8.5	- - -	+0.0	+20.3	5.7	- - -
	PS+H	0.0	1.0	0.5	0.05	0.0	2.4	1.2	0.04	0.00	50.07	29.83	0.05	0.0	14.2	4.0	0.06	+0.0	+2.4	1.2	0.00
	PS+SL	0.0	0.1	0.1	0.12	0.0	0.0	0.0	0.11	0.00	5.00	5.00	0.12	0.0	7.0	7.0	0.11	+0.0	+0.0	0.0	0.11
Hyperiid Amphipods	PS	0.0	0.0	0.0	- - -	0.0	0.0	0.0	- - -	0.00	0.00	0.00	- - -	0.0	0.0	0.0	- - -	-0.0	-0.1	0.0	- - -
	PS+H	0.0	1.8	0.5	0.00	0.0	3.5	1.1	0.00	0.00	8.55	3.03	0.00	0.0	13.1	3.2	0.00	+0.0	+3.3	1.1	0.07
	PS+SL	0.0	0.1	0.1	0.65	0.0	0.1	0.1	0.65	0.00	0.79	0.79	0.65	0.0	3.8	3.8	0.65	+0.0	+0.1	0.1	0.00
Larvaceans	PS	276	261.	47.1	- - -	96.9	58.8	8.9	- - -	9.21	8.71	1.57	- - -	55.5	48.7	8.0	- - -	+87.9	+52.5	8.9	- - -
	PS+H	85.	233.	61.1	0.81	88.3	70.6	4.4	0.89	2.83	7.76	2.03	0.81	18.8	41.2	5.4	0.49	+80.8	+63.3	4.4	0.93
	PS+SL	399	569.	142.3	0.06	96.8	94.8	1.7	0.45	13.30	18.98	4.74	0.06	85.1	70.8	9.5	0.20	+88.7	+86.7	1.7	0.44
Other	PS	0.0	1.0	0.4	- - -	0.0	0.3	0.1	- - -	0.00	0.11	0.06	- - -	0.0	0.5	0.3	- - -	-3.2	-4.0	0.5	- - -
	PS+H	0.0	29.8	18.9	0.44	0.0	6.9	2.2	DNT	0.00	0.50	0.21	DNT	0.0	1.6	1.0	DNT	-1.9	+3.3	2.2	0.00
	PS+SL	1.5	1.8	0.7	0.18	0.4	0.4	0.1	DNT	0.01	0.01	0.00	DNT	0.0	0.0	0.0	DNT	-1.0	-1.0	0.1	<0.00

Table 10c. Prey utilization and selection for Sandlance (SL). Probability (P) values refer to paired comparisons between allopatric and sympatric aggregations. Abbreviations: H = Herring, PS = Pink Salmon, md = median, sem = standard error of the mean, DNT = Do Not Test.

Prey	Aggregation	Number of Prey				Percent Number of Prey				Biomass of Prey				Percent Biomass of Prey				Strauss Linear Selection			
		md	mean	sem	P	md	mean	sem	P	md	mean	sem	P	md	mean	sem	P	md	mea	sem	P
Barnacle Larvae	SL	1.0	8.2	1.5	- - -	0.2	3.5	1.3	- - -	0.29	2.34	0.43	- - -	0.6	7.4	1.6	- - -	+0.0	+3.0	1.2	- - -
	SL+H	0.0	20.4	7.7	DNT	0.0	6.5	3.5	DNT	0.00	4.38	1.57	DNT	0.0	10.6	3.6	DNT	-0.0	+5.5	3.5	0.89
	SL+PS	4.0	4.2	1.0	DNT	2.2	2.5	0.7	DNT	1.10	1.48	0.47	DNT	8.6	14.8	5.7	DNT	+2.1	+2.4	0.6	0.00
Large Calanoids	SL	0.0	5.1	1.8	- - -	0.0	0.2	0.1	- - -	0.00	9.10	3.50	- - -	0.0	3.2	0.8	- - -	-0.4	-0.5	0.1	- - -
	SL+H	0.0	0.1	0.0	0.11	0.0	0.0	0.0	0.12	0.00	0.09	0.07	0.11	0.0	1.1	1.1	0.13	-2.2	-2.4	0.3	0.00
	SL+PS	0.0	0.0	0.0	0.27	0.0	0.0	0.0	0.27	0.00	0.00	0.00	0.27	0.0	0.0	0.0	0.27	-0.1	-0.1	0.0	0
Small Calanoids	SL	147.0	592.8	71.6	- - -	76.0	60.6	3.2	- - -	5.39	41.01	7.00	- - -	70.2	56.9	3.2	- - -	+0.7	-12.8	3.0	- - -
	SL+H	8.0	435.6	115.1	0.03	48.8	41.6	6.0	0.00	0.40	28.99	7.91	0.04	36.0	39.8	6.1	0.01	-31.4	-33.7	6.9	DNT
	SL+PS	164.0	194.1	65.1	0.77	94.8	81.7	9.0	0.03	10.65	10.07	2.12	0.94	86.1	78.8	7.8	0.08	+10.3	-2.8	9.0	DNT
Chaetognaths	SL	0.0	0.1	0.0	- - -	0.0	0.0	0.0	- - -	0.00	0.00	0.00	- - -	0.0	0.0	0.0	- - -	+0.0	+0.0	0.0	- - -
	SL+H	0.0	0.0	0.0	0.97	0.0	0.0	0.0	0.95	0.00	0.00	0.00	0.95	0.0	0.0	0.0	0.95	-0.0	-0.1	0.0	0.03
	SL+PS	0.0	0.0	0.0	0.95	0.0	0.0	0.0	0.97	0.00	0.00	0.00	0.97	0.0	0.0	0.0	0.97	-0.0	-0.0	0.0	0.00
Cladocerans	SL	0.0	4.3	0.7	- - -	0.0	0.8	0.2	- - -	0.00	0.17	0.03	- - -	0.0	0.8	0.3	- - -	-1.4	-2.1	0.3	- - -
	SL+H	0.0	15.6	5.1	DNT	0.0	2.0	0.6	DNT	0.00	0.61	0.20	DNT	0.0	1.2	0.3	DNT	-0.8	-1.0	0.7	0.17
	SL+PS	0.0	0.3	0.3	DNT	0.0	0.0	0.0	DNT	0.00	0.01	0.01	DNT	0.0	0.1	0.1	DNT	-1.3	-1.2	0.0	0.37
Decapods	SL	0.0	0.5	0.2	- - -	0.0	0.1	0.1	- - -	0.00	1.90	0.72	- - -	0.0	2.7	1.0	- - -	-0.7	-0.5	0.1	- - -
	SL+H	0.0	0.0	0.0	0.49	0.0	0.0	0.0	0.49	0.00	0.00	0.00	0.49	0.0	0.0	0.0	0.49	-0.2	-0.2	0.0	DNT
	SL+PS	0.0	0.0	0.0	0.71	0.0	0.0	0.0	0.71	0.00	0.00	0.00	0.71	0.0	0.0	0.0	0.71	-0.2	-0.2	0.0	DNT
Euphausiids	SL	0.0	0.2	0.1	- - -	0.0	0.0	0.0	- - -	0.00	0.01	0.01	- - -	0.0	0.0	0.0	- - -	+0.0	-0.4	0.1	- - -
	SL+H	0.0	6.2	3.8	DNT	0.0	0.3	0.2	DNT	0.00	0.12	0.07	DNT	0.0	0.0	0.0	DNT	-0.2	-0.4	0.2	0.01
	SL+PS	0.0	0.0	0.0	DNT	0.0	0.0	0.0	DNT	0.00	0.00	0.00	DNT	0.0	0.1	0.1	DNT	-0.1	-0.1	0.0	0.03
Fish	SL	0.0	0.0	0.0	- - -	0.0	0.0	0.0	- - -	0.00	0.54	0.37	- - -	0.0	0.7	0.4	- - -	+0.0	-0.0	0.0	- - -
	SL+H	0.0	0.0	0.0	0.78	0.0	0.0	0.0	0.78	0.00	0.00	0.00	0.78	0.0	0.0	0.0	0.78	+0.0	+0.0	0.0	0.27
	SL+PS	0.0	0.0	0.0	0.88	0.0	0.0	0.0	0.88	0.00	0.00	0.00	0.88	0.0	0.0	0.0	0.88	+0.0	+0.0	0.0	0.55
Hyperiid Amphipods	SL	0.0	0.0	0.0	- - -	0.0	0.0	0.0	- - -	0.00	0.06	0.06	- - -	0.0	0.1	0.1	- - -	-0.0	-0.0	0.0	- - -
	SL+H	0.0	0.0	0.0	0.86	0.0	0.0	0.0	0.86	0.00	0.20	0.20	0.86	0.0	0.7	0.7	0.86	-0.0	-0.1	0.0	0.00
	SL+PS	0.0	0.0	0.0	0.97	0.0	0.0	0.0	0.97	0.00	0.00	0.00	0.97	0.0	0.0	0.0	0.97	+0.0	+0.0	0.0	0.00
Larvaceans	SL	6.0	189.1	36.2	- - -	3.2	14.7	2.1	- - -	0.20	6.30	1.20	- - -	1.6	9.2	1.5	- - -	-5.6	+5.0	2.1	- - -
	SL+H	0.0	6.3	2.6	0.00	0.0	5.2	1.6	0.00	0.00	0.21	0.08	0.00	0.0	3.0	1.0	0.00	-7.2	-2.7	1.8	0.27
	SL+PS	0.0	2.3	2.2	0.01	0.0	0.3	0.3	0.00	0.00	0.08	0.08	0.01	0.0	0.3	0.3	0.00	-8.1	-7.8	0.3	0.13
Other	SL	4.0	25.1	4.5	- - -	1.2	5.8	1.3	- - -	0.07	0.90	0.27	- - -	0.4	3.7	1.1	- - -	-1.3	+2.2	1.3	- - -
	SL+H	1.0	75.4	24.3	0.16	1.6	8.0	2.7	DNT	0.00	1.94	0.83	DNT	0.2	4.4	2.5	DNT	-1.5	+4.6	2.7	0.01
	SL+PS	3.0	19.9	13.3	0.72	2.7	15.0	8.6	DNT	0.10	0.29	0.14	DNT	0.8	5.4	2.9	DNT	+1.3	+13.	8.6	0.00

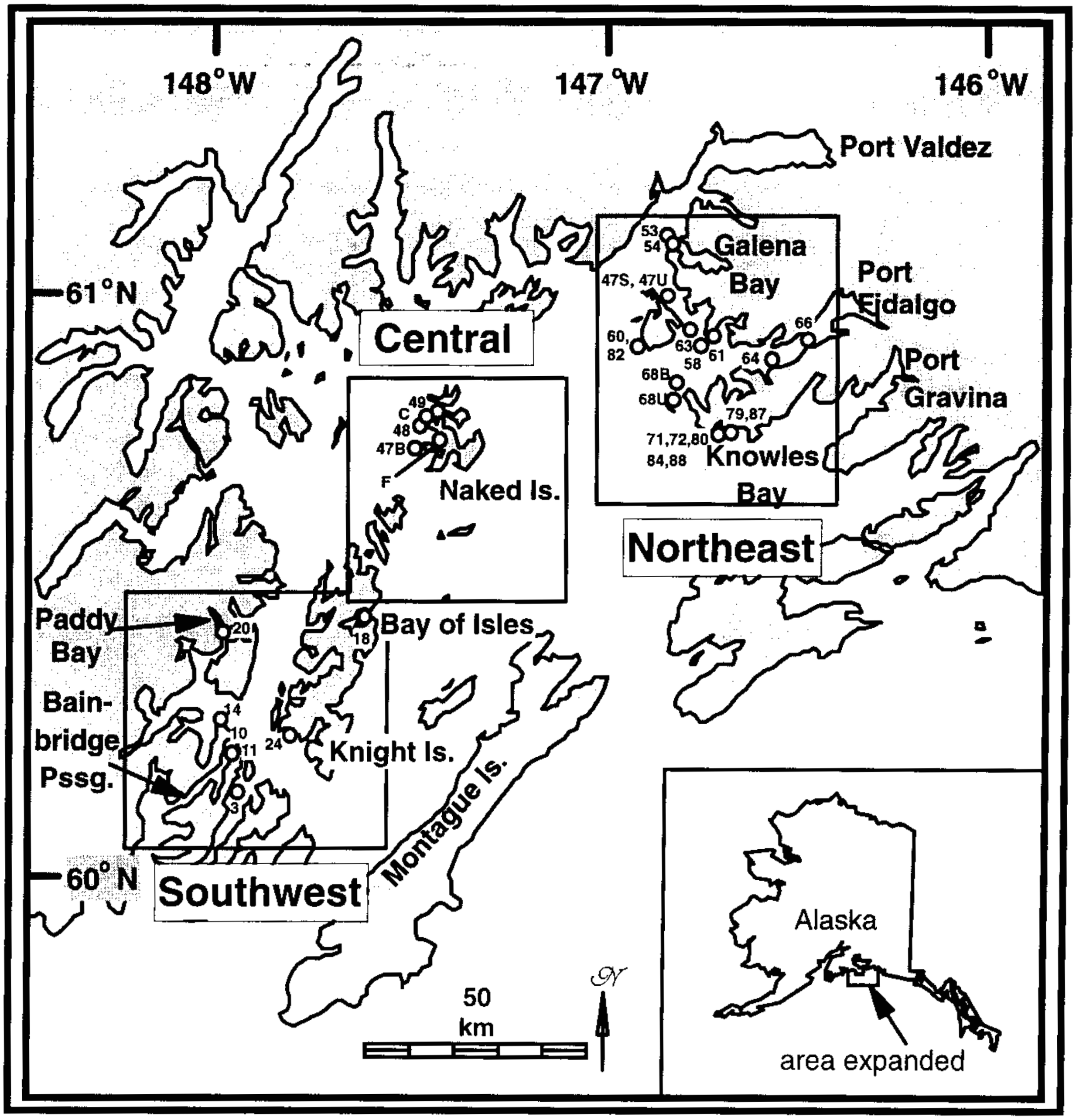

Figure 1. Locations of APEX forage fish sampling stations during July, 1996 in Prince William Sound, Alaska. See also Table 1.

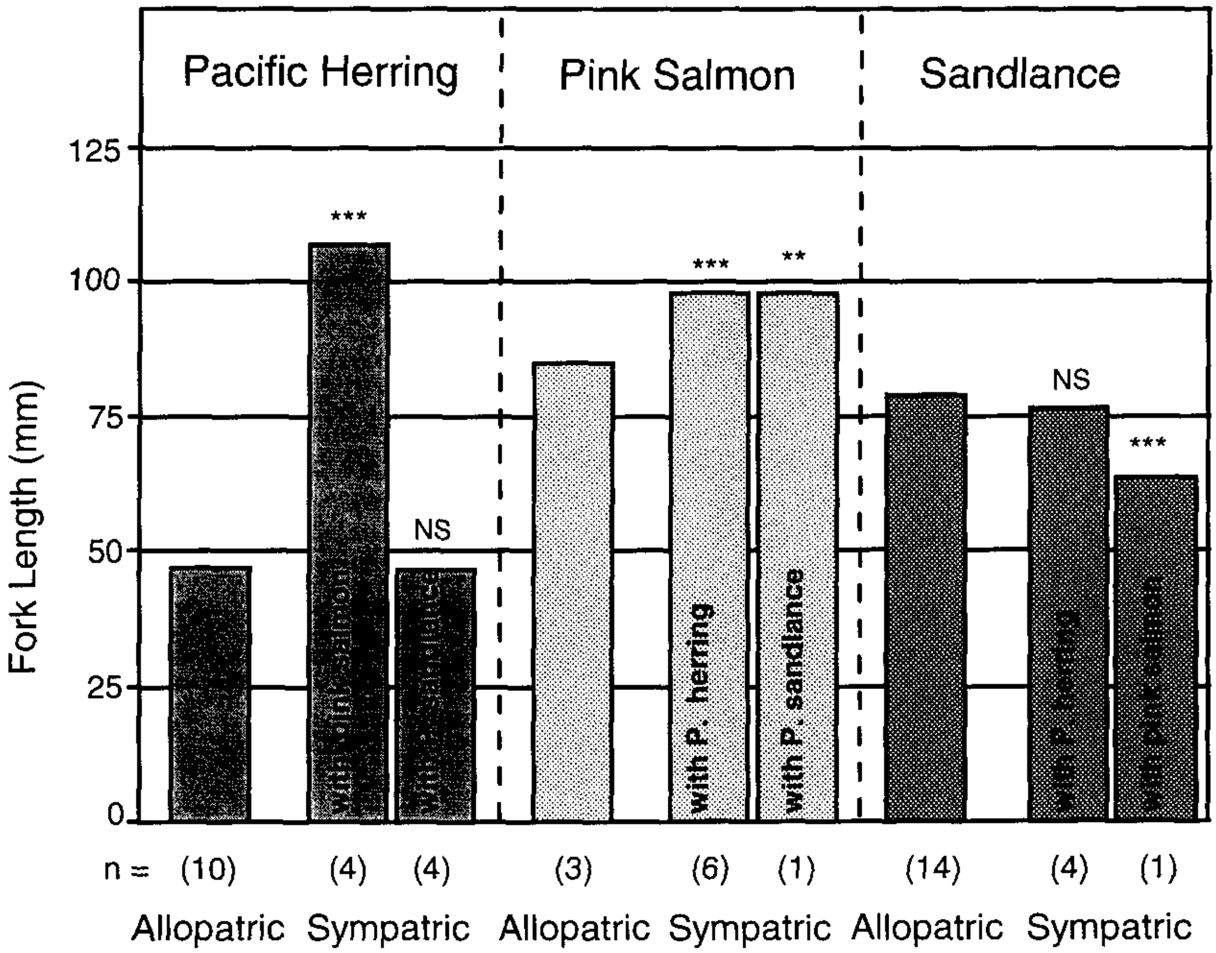

Figure 2. Median fork lengths (FL) of forage fish from sympatric and allopatric aggregations, collected in Prince William Sound during July, 1996. The number of sets (10 fish in each set) is shown below the bars. Results of Mann-Whitney Rank Sum paired comparisons between allopatric and sympatric sizes are indicated: NS = not significant, * $p < 0.05$, *** $p < 0.001$.

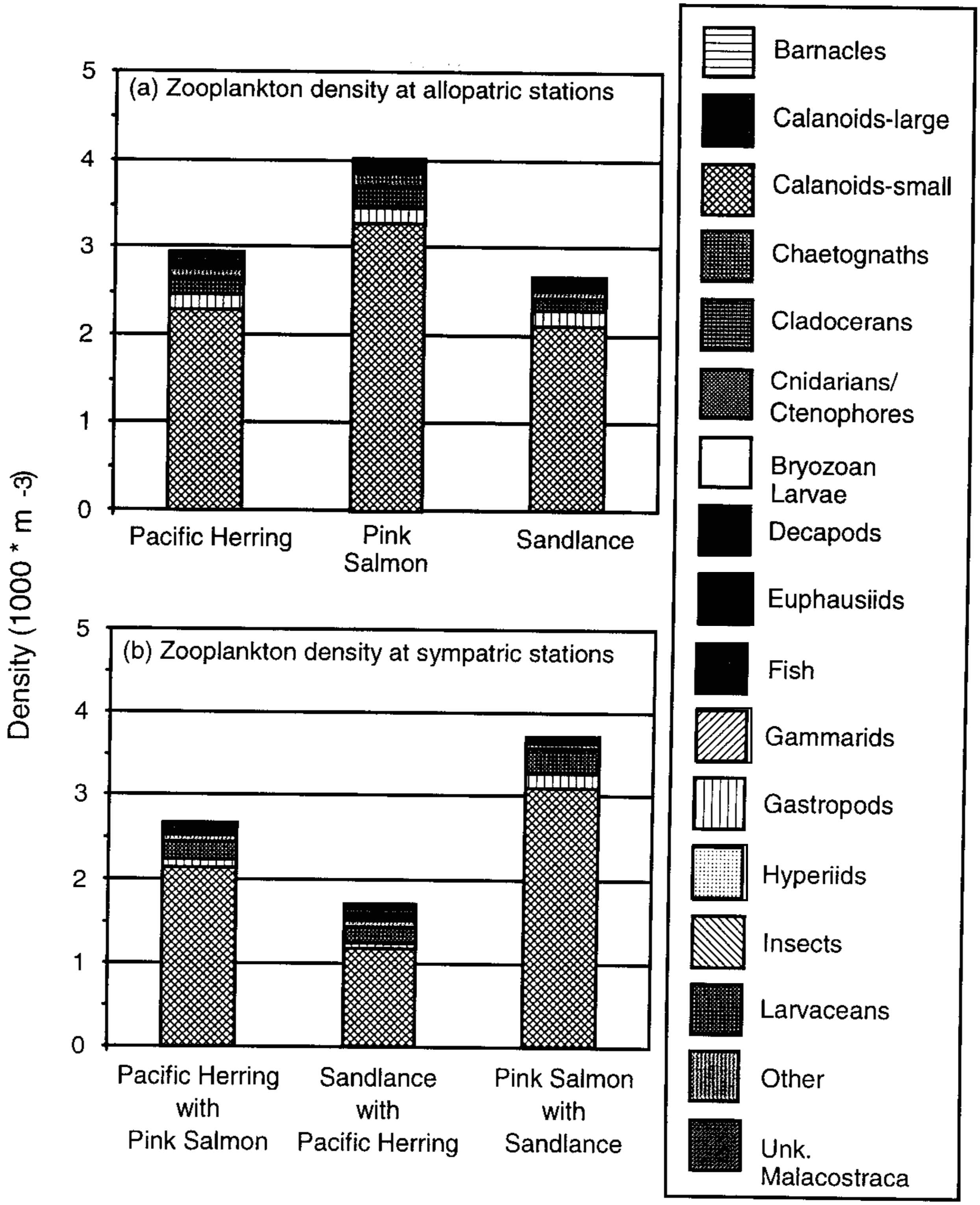

Figure 3. Total density (median thousands*m-3) and relative contribution of principal zooplankton taxa available to juvenile Pacific herring, pink salmon, and Pacific sandlance in (a) allopatric and (b) sympatric aggregations in PrinceWilliam Sound during July, 1996.

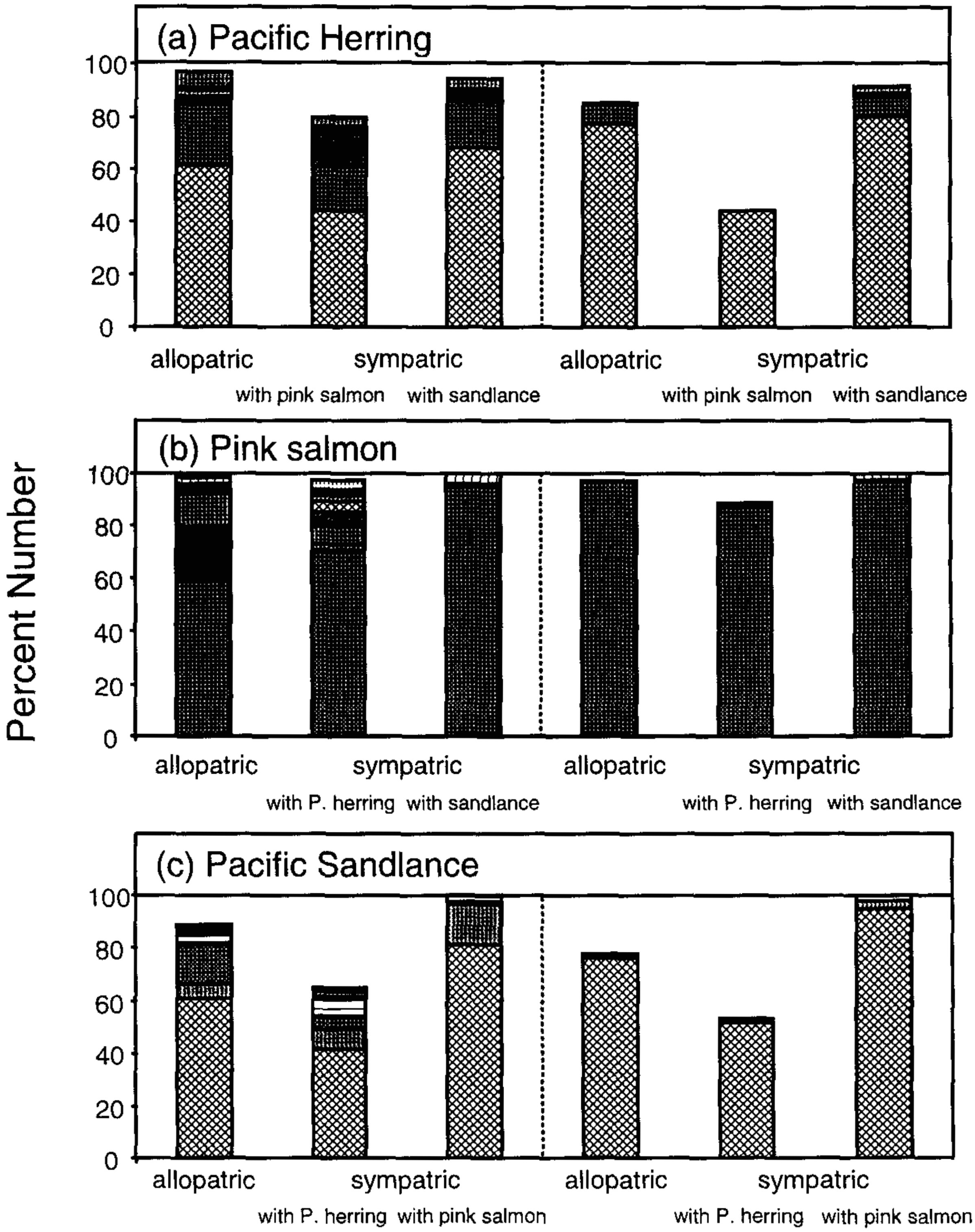

Figure 4. Diet composition as mean (left side) and median (right side) percent number of prey among allopatric and sympatric aggregations of juvenile forage fish: (a) Pacific herring, (b) pink salmon and © Pacific sandlance collected in Prince William Sound during July, 1996. Legend as in Figure 3. Percentages do not always total 100% due to empty stomachs (see Table 3).

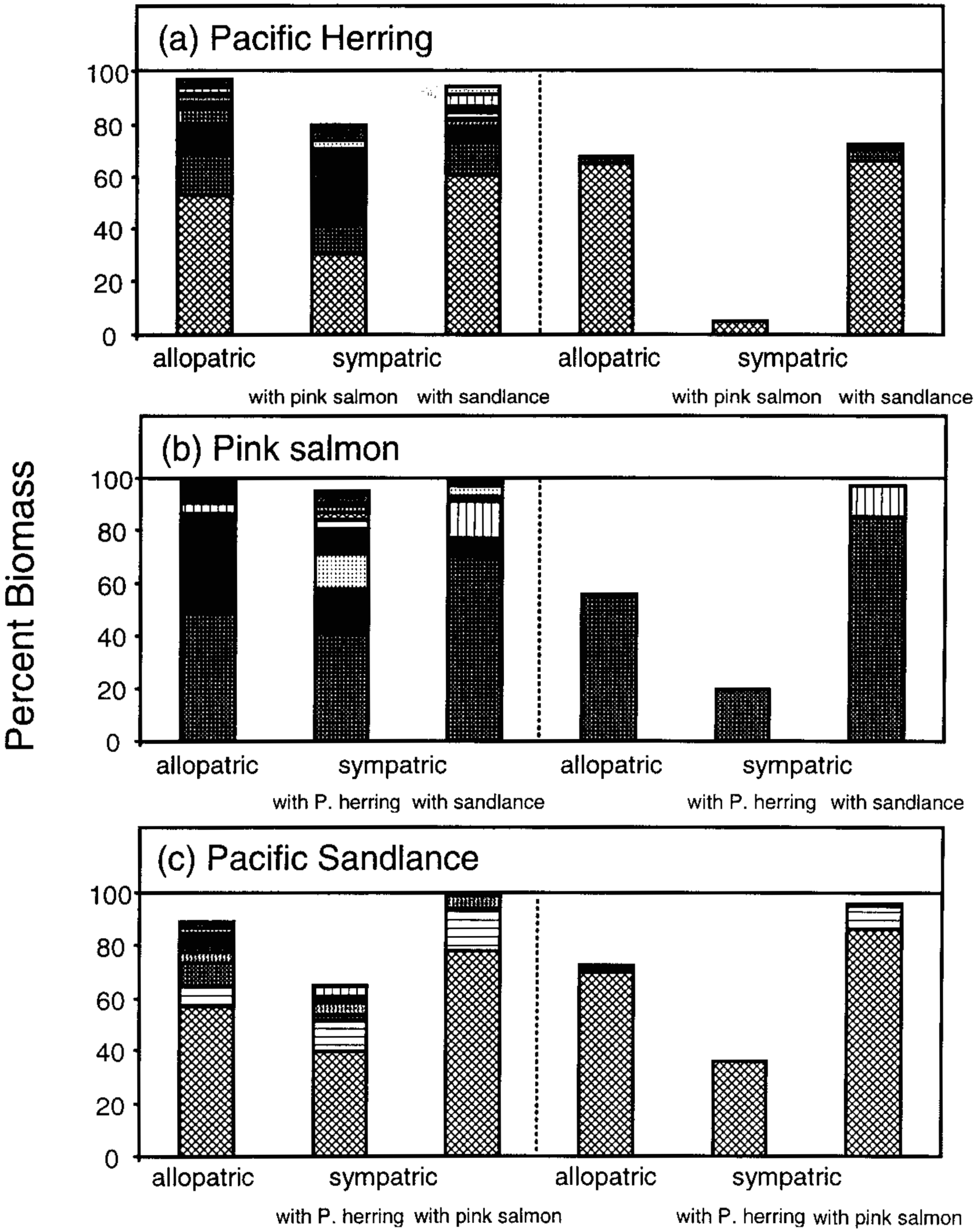

Figure 5. Diet composition as mean (left side) and median (right side) percent biomass of prey among allopatric and sympatric aggregations of juvenile: (a) Pacific herring, (b) pink salmon and © Pacific sandlance collected in Prince William Sound during July, 1996. Legend as in Figure 3. Percentages do not always total 100% due to empty stomachs (see Table 3).

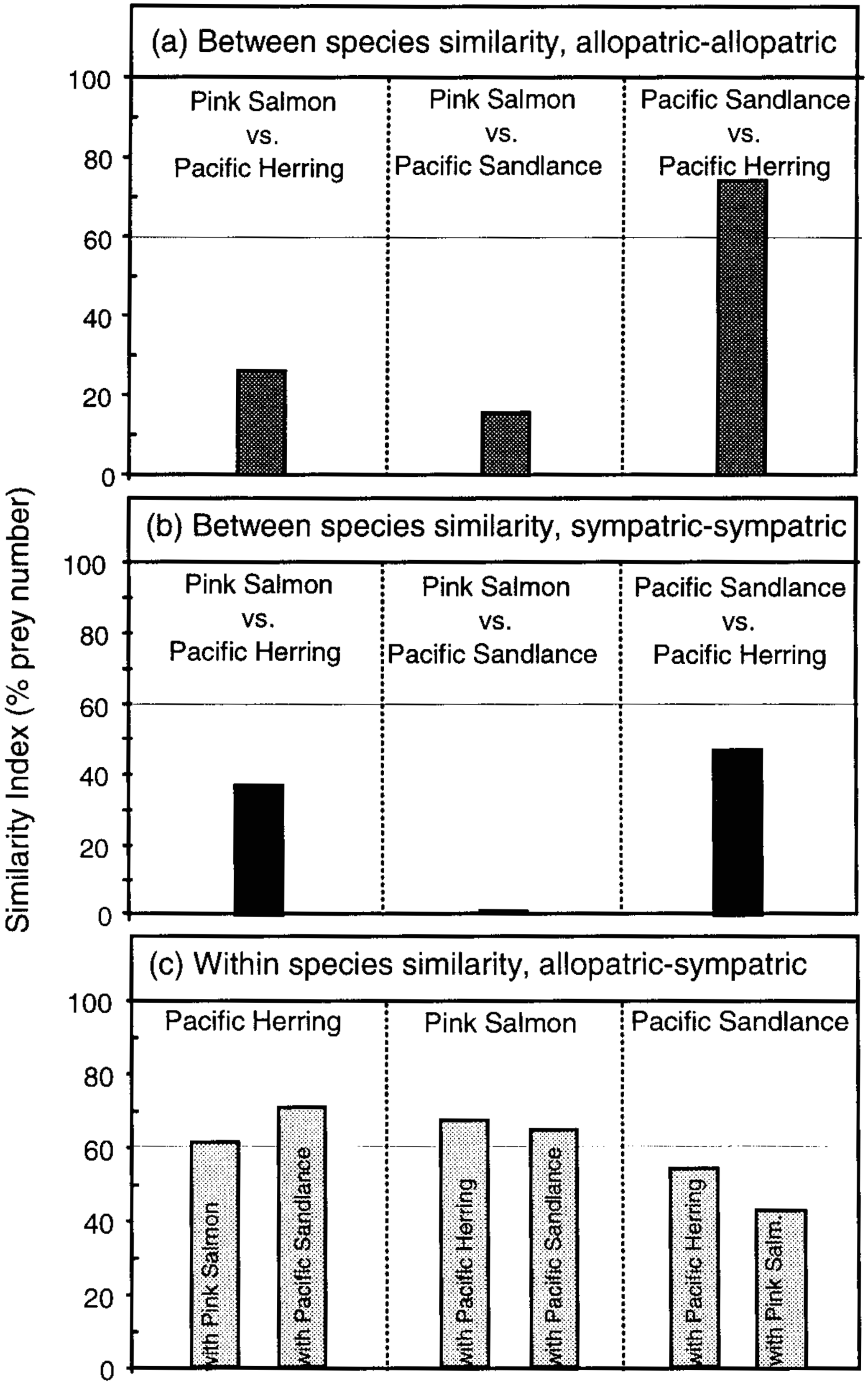

Figure 6. Diet similarity (PSI) by percent number of prey species for forage fish in allopatric and sympatric aggregations collected in Prince William Sound during July, 1996. Line at 60% indicates threshold for significant overlap.

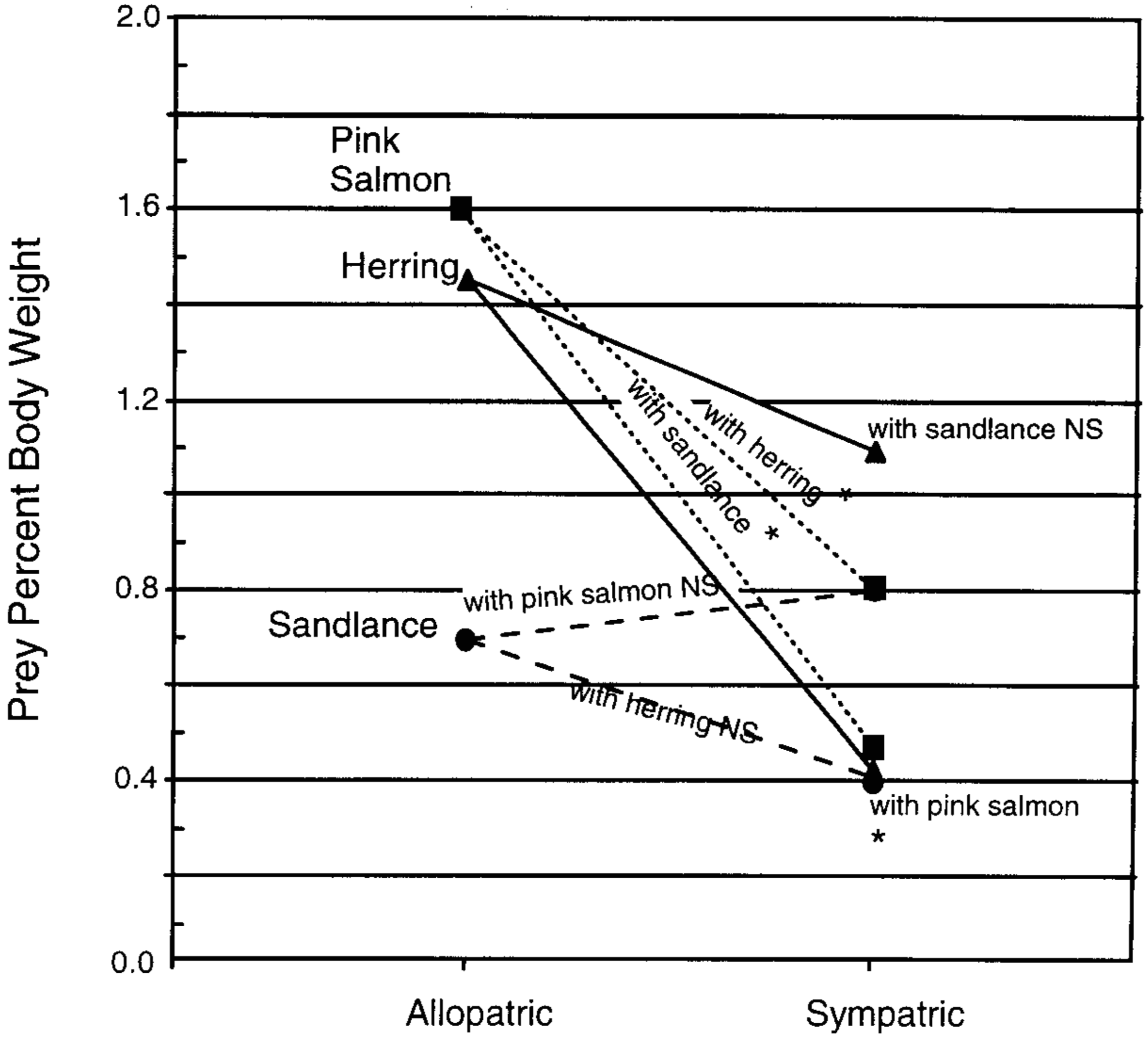

Figure 7. Prey consumption (median prey percent body weight) by forage species in allopatric and sympatric aggregations in Prince William Sound during July, 1996. Results of Mann-Whitney Rank Sum comparisons between groups are indicated: NS = not significant, * $p < 0.05$. See also Table 4.

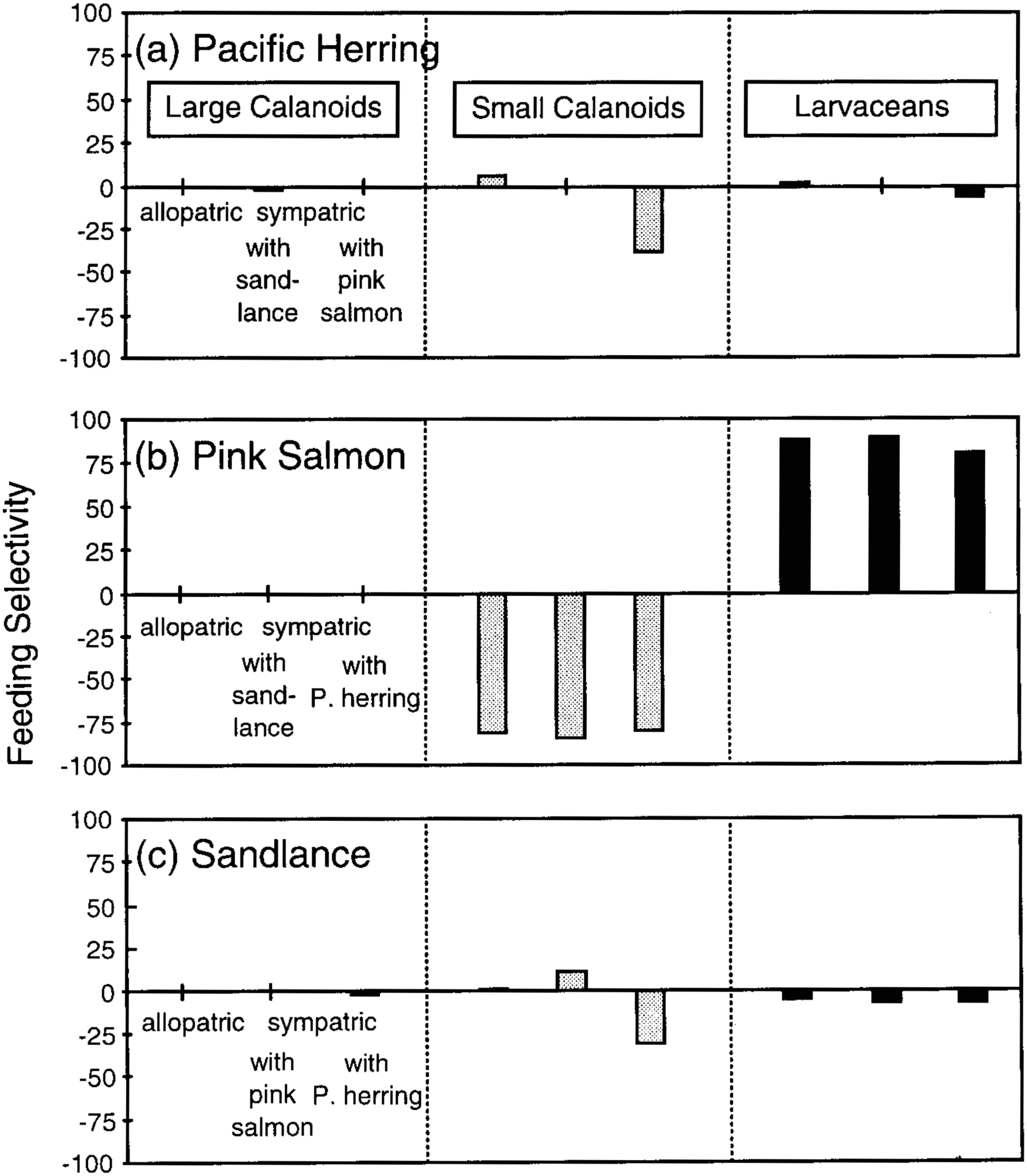

Figure 8. Feeding selectivity (median Strauss' Linear Selection Index) from principal prey categories among juvenile forage fish: (a) Pacific herring, (b) pink salmon, and © Pacific sandlance. Positive values indicate preference, negative values indicate avoidance. The species composition of allopatric and sympatric aggregations (shown in left-most panels) is repeated across the remaining panels.

DISCUSSION AND CONCLUSIONS

The Forage Fish Diet Overlap project has made progress in addressing the hypothesis that "planktivory is the factor determining abundance of the preferred forage species of seabirds." We have attempted to show that forage fish feeding ecology could relate to the abundance of piscivorous seabirds impacted during the *Exxon Valdez* oil spill by examining fish food habits, prey partitioning, preferred prey items, diet overlap and potential competition from 1994-1996. We have described seasonal and interannual prey composition and diet overlap of 14 forage species, including pollock (*Theragra chalcogramma*), Pacific herring (*Clupea pallasi*), Pacific sandlance (*Ammodytes hexapterus*), pink salmon (*Oncorhynchus gorbuscha*), chum salmon (*O. keta*), sockeye salmon (*O. nerka*), Pacific cod (*Gadus macrocephalus*), Pacific tomcod (*Microgadus proximus*), prowfish (*Zaprora silenus*), northern smoothtongue (*Leuroglossus schmidti*), eulachon (*Thaleichthys pacificus*), capelin (*Mallotus villosus*), threespine stickleback (*Gasterosteus aculeatus*), and Pacific sandfish (*Trichodon trichodon*). We have also compared prey fields and prey selection of juvenile pollock and herring in summer and autumn, 1995 and of juvenile herring, sandlance and pink salmon in summer, 1996. We have examined impacts of forage fish trophic interactions by comparing fish feeding in allopatric and sympatric aggregations. All of these aspects of feeding ecology can impact growth, survival and perhaps distribution, thereby affecting their availability as prey resource for seabirds.

This project has, however, been limited by several factors. It requires further information from Project 163A, Biomass and Distribution of Forage Species, which has not been completed. Therefore, we have not fully addressed the aspect of density dependent interactions based on forage fish school density and biomass. The scope of sampling was limited spatially (1994) and temporally (1995, 1996), methodology varied between years, little directed sampling of different types of forage fish aggregations was possible, and expensive and time consuming (but necessary) laboratory analysis was limited after 1994. Forage fish trophic interactions with jellyfish are a new area of investigation. Nonetheless, a number of findings from APEX and SEA have helped to focus fish dietary descriptions. Central pieces of information on fish biology from the APEX project include: different forage species within PWS are pelagic offshore or nearshore; habitats vary ontogenetically and seasonally; forage species abundance varies interannually; school size varies tremendously and both spatial and temporal distribution are uneven; fish aggregations are sometimes mono-specific in composition and sometimes multi-species/age class in composition. Central pieces of information on seabirds include: seabirds mainly feed nearshore; some travel long distances from colonies to familiar feeding areas; their fish prey species vary, and size, type and quality all are selected for; reproductive characteristics vary between colonies and in relation to prey type, quality and abundance.

When considering the relationship of forage fish feeding to their abundance and availability to seabirds, all of these pieces of the ecosystem puzzle are important. Directed sampling is needed to make specific diet/prey field comparisons among forage fish that opportunistic sampling from surveys cannot address. In lieu of such directed sampling, the Forage Fish Diet Overlap project has attempted to "salvage" sample sets from survey samples to examine similarity of species' diets and to examine the influence of species on one another's feeding, ie., evidence of competition. Changes in prey composition, changes in diet similarity, and feeding declines indicated that competitive trophic interactions do occur among forage species. All of the core objectives of the diet study have been met, providing information toward the unravelling of the trophic cascade that contributed to lack of seabird recovery. Principal findings include:

1. Most forage fish species were planktivorous during the six months sampled in 1994, with large and small calanoid copepods a consistent component of prey biomass. *Pseudocalanus*, *Neocalanus/Calanus* spp., and a succession of large calanoids were consumed throughout the season.

2. Small calanoid copepods were the predominant zooplankter available in both summer and autumn, 1995, but seasonal and depth-related differences in prey fields and in prey selection were found. Zooplankton densities (243 μm mesh, 20 m vertical tow) ranged from 1800-4200 organisms*m^{-3} in 1996.

3. Species' diets shifted to a variety of macrozooplankters in summer and autumn, but in different months.

4. Pacific tomcod and salmonids were the least planktivorous forage species, but piscivory was occasionally observed among other species. Cods were also more benthiphagous than other species.

5. Food webs were the most complex in June. Significant diet overlap and prey partitioning were commonly observed. Diet overlap between species pairs shifted monthly.

6. Herring and pollock diets overlapped the most consistently of all species pairs. Information on other species pairs is limited.

7. Interannual differences in diet were correlated with size for some species and not for others. Herring, tomcod, capelin, and pink and chum salmon diets differed each year in July, but sandlance and pollock diets were consistent between years.

8. Evidence for trophic competition was found through several avenues that indicate feeding was inhibited or altered. A) In autumn, 1994 and 1995, YOY herring and pollock consumed greater numbers of prey in allopatric aggregations than in sympatric aggregations. This observation could relate to the seasonal decline in prey abundance. In summer, 1996 food quantity and stomach fullness declined for sympatric herring, pink salmon and sandlance compared to allopatric fish. This observation may have been related to a trend for decreased zooplankton densities in areas of sympatric aggregations. B) In autumn, allopatric herring selected different prey than herring sympatric with pollock. In summer, 1996, juvenile sandlance and herring were non-selective and juvenile pink salmon were highly selective of prey. Prey selection among these species changed subtly from allopatric to sympatric aggregations. C) For herring and pollock, diets of allopatric fish overlapped in summer and diets of sympatric fish overlapped in autumn. In summer, 1996, prey partitioning was indicated by low interspecific diet overlap between sympatric sandlance, herring and pink salmon and high diet overlap between allopatric species pairs. Intraspecific comparisons showed that sandlance shifted diets in the presence of other planktivores, but pink salmon and herring diets remained similar whether they occurred allopatrically or sympatrically.

9. The incidence of sympatry in PWS varied seasonally and among species. In 1994 after May, > 50% of sets that caught herring also caught pollock, and after July, > 50% of sets that caught pollock also caught herring. In July, 1996, juvenile herring, sandlance, and pink salmon (*Oncorhynchus gorbuscha*) occurred sympatrically in 21-41% of the hauls where at least one of the species was present.

Our results show that food webs in PWS are complex. Each of the three chapters of this report discussed particular aspects of forage fish feeding ecology. The prey suite available to fish in an area may change with time or may vary in different habitats; growth to larger body size may be accompanied by increased swimming speed and mouth gape, which facilitate predation on different taxa; increasing energy requirements may be more efficiently met by consuming larger items if the costs of consuming them are not too great; large, calorie-dense but nutrient-poor taxa may not meet fish nutritional requirements; diet overlap between species can shift seasonally based on ontogenetic prey requirements, fish movement patterns, and the timing of the onset of piscivory; forage fish interactions may be density dependent and depend on the incidence of sympatry; and interactions with other species may prompt shifts in prey consumption to avoid potential competition. Although shifts in diet may compensate to some degree, competitive interactions among forage species can result in reduced feeding. Energy may be the most important, but it is not the only currency. The nutritional requirements of forage species and the influences of different diets on their nutritional quality and growth are an area needing more intensive study. Diets of forage species may be adapted to their life history strategies. Lipid content was generally ranked highest for adult eulachon/lanternfish, second for herring, third for sandfish, sandlance and capelin, fourth for prowfish, and fifth for salmonids and gadids, and young fish generally had lower lipid content than larger/older fish (Roby et al, 1998). Since different zooplankters have different nutritional profiles, the nutritional quality of planktivorous forage species could be influenced by any of the diet attributes mentioned above. If sympatry occurs regularly under conditions of limited food availability, interspecific competition could affect the carrying capacity of PWS for these species. Density dependent effects have not been thoroughly examined. However, the migration of the majority of juvenile pink salmon to the Gulf of Alaska early in the summer reduces their interactions with other planktivorous forage fish in PWS. It is important to consider the frequency and duration of species co-occurrence to evaluate the importance of diet similarity and effects of trophic interactions. Our results indicate that planktivory is a factor that can determine the abundance of the preferred forage species of seabirds, but that careful consideration must be given to many factors, including sampling methodology, spatial and temporal distribution, allopatry vs. sympatry, school density, size distribution, prey availability, and oceanographic variations when evaluating results of diet analyses, and that directed sampling and perhaps manipulative studies are necessary to further elucidate the impacts of these variables. To further develop our understanding of the impacts of forage fish interactions and diet on their availability as seabird prey resources will require further studies with control for these factors.