Exxon Valdez Oil Spill
Restoration Project Annual Report

Monitoring, Habitat Use, and Trophic Interactions of Harbor Seals in Prince William Sound, Alaska

Restoration Project 96064
Annual Report

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

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Study History: Restoration Project 96064 continues the study effort conducted under Marine Mammal Study Number 5 (Assessment of Injury to Harbor Seals in Prince William Sound, Alaska, and Adjacent Areas) in 1989 through 1991. The project was reclassified as Restoration Study Number 73 (Harbor Seal Restoration Study) in 1992, and continued as 93046 (Habitat Use, Behavior, and Monitoring of Harbor Seals in Prince William Sound) in 1993. A final report was issued in 1994 for the combined Marine Mammal Study Number 5 and Restoration Study Number 73, entitled Assessment of Injury to Harbor Seals in Prince William Sound, Alaska, and Adjacent Areas Following the *Exxon Valdez* Oil Spill. Subsequently, annual reports were submitted entitled Habitat Use, Behavior, and Monitoring of Harbor Seals in Prince William Sound: 1994 Annual Report, 1995 Annual Report, and 1996 Annual Report. Fatty acid studies funded under Restoration Project 94320-F (Trophic Interactions of Harbor Seals in Prince William Sound) were included in the 1994 annual report for 94064. Fatty acid studies were continued under 95064 and 96064.

Abstract: Restoration studies of harbor seals, *Phoca vitulina richardsi*, that began in Prince William Sound (PWS) in 1991 were continued in 1996. Adjusted mean counts of harbor seals at 25 haulout sites in Prince William Sound (PWS) were 33% lower in 1996 than in 1989 and over 60% lower than counts made in 1984. Molt counts in 1996 were the lowest since 1991. Skin, blubber, whiskers, blood, and morphometric measurements were collected from 39 captured seals in 1996; satellite-linked depth recorders were attached to 14. Seals tagged in fall 1995 and spring 1996 were tracked for up to 264 days. Overall, of 22 seals tracked during April-July 1992-1994, only 3 made substantial movements out of PWS. In contrast, 12 of 15 seals tagged in September of 1995 and 1996 left PWS to feed in the Gulf of Alaska (GOA) or Copper River delta for all or part of winter and spring. This is consistent with fatty acid analysis that indicates the diet of seals was much different in winter 1995/6 than in previous years. The tagging and fatty acid data suggest that some change occurred in the PWS/GOA ecosystem beginning in 1995 which caused seals to change their winter feeding behavior.

Key Words: Behavior, diving, *Exxon Valdez* oil spill, fatty acids, habitat use, harbor seal, movements, *Phoca vitulina richardsi*, Prince William Sound, recovery, satellite telemetry.

Project Data: The following types of data have been collected by this project: aerial survey count data for 1989-1996, morphometric measurements of all seals that have been caught and handled, location and dive data for 51 seals that have been satellite tagged since 1992, results of disease assays conducted on harbor seal blood serum, and results of fatty acid signature analysis. All data exist as computer databases, either as FoxPro, Excel, or text files. All aerial survey, morphometric, location, dive behavior, and disease data are maintained by the principal investigator, Kathryn J.

Frost, at the Alaska Department of Fish and Game, Division of Wildlife Conservation, 1300 College Road, Fairbanks, AK 99701-6009. E-mail: kfrost@fishgame.state.ak.us. Phone (907) 459-7214. Fax (907) 452-6410. Fatty acids data are maintained by Dr. Sara Iverson at Dalhousie University, Department of Biology, Halifax, Nova Scotia B3H 4J1. E-mail: siverson@is.dal.ca. Phone (902) 494 2566. Fax (902) 494-3736. Aerial survey data are available in annual reports of this project. Interested parties should contact the principal investigator about the availability of other data.

Citation:

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EXECUTIVE SUMMARY

Harbor seals (*Phoca vitulina richardsi*) and their habitats in Prince William Sound (PWS) were impacted by the *Exxon Valdez* oil spill. Natural resource damage assessment (NRDA) studies estimated that about 300 harbor seals died in oiled areas of PWS. The impacts of the spill on harbor seals were of particular concern since the counts of harbor seals along a trend count route in PWS had declined by over 40% from 1984 to 1988, and similar declines were occurring in other parts of the northern Gulf of Alaska. Because of concerns for harbor seals, a restoration science study was designed to monitor their trend in numbers, and to gather data on their habitat use and behavior.

Results of harbor seal restoration studies conducted from 1991 through October 1994 were reported previously. This report describes work done under Restoration Science Study No. 96064 from October 1995 through September 1996. Emphasis is on analysis of the trend in seal numbers during 1989-1996, and on presentation of data collected from satellite tagged seals during September 1995-July 1996. Results of fatty acid signature analysis of seals and seal prey are also reported.

In 1996, aerial surveys were flown during the molting period at 25 trend count haulout sites that have been used for NRDA and other studies. Unadjusted counts were lower than for any other year since surveys began except 1994. For trend analysis, counts were adjusted using parameter estimates from a generalized linear model that took into account effects of date, time of day, and time relative to low tide. Adjusted molting period counts for 1996 were 15% lower than 1995 counts and 33% lower than counts in 1989 ($p=0.001$). Overall, molt period counts have declined by over 60% since the first trend count surveys were conducted in the early 1980s. These results show that harbor seal numbers in PWS have not yet recovered from the spill, nor has the long-term decline ended.

Wind speed and sky conditions were incorporated into the full generalized linear model for the first time in 1996. Wind speed was found to have no significant effect on surveys counts, probably because surveys are generally not flown in very windy weather. Sky conditions did significantly affect counts, but the effect was very small. Inclusion of this factor in the analysis changed overall counts by less than 2%. For this reason, and because earlier survey data do not contain records of sky conditions, we did not include sky conditions in the overall trend analysis.

It is essential to continue to monitor the trend in abundance of PWS harbor seals, and to continue to develop better statistical methods for analyzing the trend count data. While the existing approach to adjusting counts has greatly improved our ability to detect trend, some problems still exist with the calculation of sample variance and therefore our ability to statistically evaluate trend results. Thirty-nine seals were captured, sampled, and tagged in 1996 and 14 seals were instrumented with satellite-linked depth recorders (SDRs). Six of the eight SDRs deployed in September functioned properly and transmitted data for 146-264 days. One was a prototype 0.25 watt unit that never functioned properly and failed prematurely. Six SDRs attached to seals in April 1996 transmitted for 42-81 days. For SDRs that were not duty cycled, seals were located on 54%-100% of the days transmitters were operating, in contrast to 31%-49% for SDRs that were duty-cycled to conserve battery power. During fall and winter, 2-4 locations/day/seal were obtained on days the SDRs were turned on. During May-July, 6-9 locations per day were obtained for adult females, and 1-4 for subadults.

Five of seven seals tagged in September 1995 left PWS to feed, going either to Middleton Island (one seal), the Copper River delta (three seals), or both (one seal). Again in 1996, 7 of the 8 seals that were tagged in September left PWS to feed offshore in the Gulf of Alaska or the Copper River delta during winter and spring. This is in marked contrast to 1993-1994, when only 2 of 14 tagged seals left PWS during winter. It appears that there has been a change in the feeding behavior of PWS seals during the past two winters, suggesting that food availability has changed either in PWS, the GOA or both.

All six seals tagged in April 1996 stayed within PWS during the tracking period. These results are consistent with data from seals previously tagged during spring in 1992-1995. Of 22 total seals tracked during April-July, only 3 have shown substantial movements out of PWS. The majority spent most of their time near the location where they were captured. A few have made trips to tidewater glaciers in northern PWS.

Most seals hauled out principally at the capture location and adjacent haulout sites. An analysis of haulout site use by the 13 seals tagged in September 1996 and April 1996 showed that within each month seals on average used only a few sites (1.3-3.7) and that they used a "preferred" site 60%-90% of the time. The number and use of preferred haulouts was similar for these and the 30 other seals previously tagged in PWS.

The seals tagged in fall 1995 and spring 1996 used fewer haulouts and showed a higher proportional use in May-July than during September through March. Adult females used the greatest number of sites and juvenile females the fewest. However sample sizes were small and there was considerable variability in the monthly mean values for all age-sex classes. In the earlier tagged sample (1992-1995), seals showed opposite trends: juveniles used more haulouts than adult females, more haulouts were used in May-July, and proportional use was lower in May-July. Patterns and differences in haulout behaviors should become more clear when data from all SDR tagged seals are analyzed together, as will be done for the final project report.

During October-April, seals hauled out on 45%-63% of the days, compared to 71%-92% in May-July when pupping, breeding and molting occur. Adult females hauled out on a higher proportion of days than did subadults (76% vs. 51%) both overall and in every month except May. Seasonal differences on the proportion of days hauled out were less pronounced for adult females than for subadults.

Preliminary analysis of dive data showed considerable individual and seasonal variability in diving behavior. During fall and winter, 65% of the dives were to depths of 20 m or less, and 74% to 50 m or less. Only 5% of the total dives were deeper than 150 m. Diving in May to July was generally similar, with 58% of all dives shallower than 20 m and 83% shallower than 50 m. Most seals did their deepest diving during December through late March.

To date, 51 harbor seals have been satellite tagged in PWS, including 26 adults (11 males, 15 females), 23 subadults (12 males, 11 females), and 2 female pups. We do not anticipate tagging additional adults and subadults in PWS in the foreseeable future. During 1997, we plan to thoroughly analyze the entire dataset for demographic, regional, and annual differences in movements and diving behavior of adults and subadults. Because only two harbor seal pups have been tagged in PWS to date, our 1997 satellite-tagging studies in PWS will focus on newly weaned pups, the age class considered most likely to be involved in the ongoing decline. Following the 1997 season, data from these pups will be evaluated in order to recommend whether further satellite tagging of pups should be conducted.

Fatty acid composition has been determined for over 500 individual prey from PWS, representing 16 taxa (capelin, flathead sole, rex sole, yellowfin sole, unidentified flatfish, herring, octopus, Pacific cod, pink salmon (adults and smolt), pollock, rainbow smelt, copper rockfish, sandlance, shrimp, squid, and tomcod). Species were clearly distinguishable by their fatty acid signatures. In addition, fatty acid signatures of prey such as pollock and herring differed by size class and location, with season having little effect. In contrast, fat content of prey did vary substantially by season, with fat content lowest in spring (March-May) and highest in fall (September-November). Of particular interest were prey from northwestern PWS. In both herring and pollock, individuals were consistently high in fat content regardless of season or size class. Herring and pollock from northwestern PWS also differed from other areas in the relationship between fatty acid signatures and size. In the northwestern individuals, fatty acid components which normally increase with size deviated significantly from this pattern: both small and large individuals were high in components usually directly related to larger sizes. These differences in fat content and fatty acid signatures in northwestern PWS likely arise form differences in primary production and should be further explored.

Blubber samples from 218 harbor seals have also been analyzed for fatty acid types. Analyses of fatty acid signatures indicated differences in the diets of seals from PWS, southeast Alaska, and the Kodiak area. Within PWS there were differences between seals sampled near Montague Island and those from the northern and eastern Sound. Seals from southern PWS were more similar to seals from Kodiak than they were to seals in northern PWS. This is not surprising considering that some southern PWS seals travel to and feed in the GOA, and some of their prey may spend part of the year in the GOA. Diets of seals also differ by sex and probably age. Although not all age classes are available from all areas, it is clear that diets of adult males differ from diets of adult females and subadults.

Fatty acid signatures in blubber of seals sampled since 1994 indicate that diets have changed over the three years of the study, particularly in 1996. The pronounced difference in diet in 1996 is consistent with results from seals that were satellite tagged in September 1995. All but one of the seals tagged in September 1995 traveled to and fed in the Copper River delta and the GOA during winter and/or spring, in contrast to previous years when most tagged seals remained within PWS.

We highly recommend continuation of fatty acid studies after 1997. This component of the harbor seal research program has provided information on demographic differences in harbor seal diets, as well as about annual and small as well as large scale regional differences in foraging. The combination of satellite tagging and fatty acid data for 1994-1996 allowed us to correlate dietary changes with changes in foraging behavior and feeding areas.

INTRODUCTION

The *Exxon Valdez* oil spill occurred in Prince William Sound (PWS) in March 1989. Because harbor seals (*Phoca vitulina richardsi*) and their haulouts became oiled by the spill, harbor seal studies began almost immediately as part of the Natural Resources Damage Assessment (NRDA) program. The NRDA studies were conducted by the Alaska Department of Fish and Game (ADF&G), and included aerial surveys to quantify mortality, and necropsies to document levels of hydrocarbons and tissue damage in oiled seals (Frost and Lowry 1994*a*). Based on those investigations, it was estimated that more than 300 harbor seals (36% of the seals in oiled areas) died in PWS following the spill (Frost et al. 1994). As NRDA studies progressed, it also became clear that the harbor seal population was declining throughout eastern and central PWS, and had been doing so since at least 1984. Therefore, beginning in 1991 as NRDA studies neared completion, the Trustee Council funded a harbor seal restoration study in which ADF&G continued to monitor the trend of harbor seals in PWS and began to investigate the causes of the ongoing decline. Early restoration studies addressed a broad array of possible causes for the decline including disease, predation, human-caused mortality, reproduction, and food limitation. More recently, restoration studies have concentrated on the question of food limitation, and continued monitoring to determine when and if the population decline ceases.

In PWS, harbor seals are one of the most abundant and widely distributed marine mammals, hauling out and/or breeding at more than 50 sites. Since 1984 harbor seal numbers in PWS have declined by about 60%, with only part of this decline attributable to the 1989 *Exxon Valdez* oil spill (Frost and Lowry 1994a, Frost et al. 1994). A change in the trophic structure of the ecosystem, and hence the availability of prey, is among the hypothesized causes for this observed decline. Because harbor seals are apex predators in ecosystems in which fishes and cephalopods are important prey, a strong relationship is expected between predator populations and the abundance of fish stocks. This relationship is likely to be influenced by factors such as commercial fisheries and ecosystem changes (e.g., Beddington et al. 1985, Springer 1993).

In many parts of the world pinniped populations have increased as predicted after protection from over-exploitation (e.g., Olesiuk et al. 1990, Shelton et al. 1995). However, large declines in populations of harbor seals and Steller sea lions (*Eumetopias jubatus*) have been documented in the Bering Sea and the Gulf of Alaska (GOA), including PWS (Pitcher 1990, Loughlin et al. 1992). These declines occurred despite implementation of the 1972 Marine Mammal Protection Act which ended commercial hunting for pups and bounty payments for adults. Likewise, since the 1970s numerous species of seabirds have also declined in PWS. These unanticipated declines have prompted monitoring and assessment of marine mammal, seabird, and fish population trends, and perhaps most importantly, have furthered the idea of using predators as samplers of forage fish abundance (Duffy 1996, Roseneau and Byrd 1996). The latter aspect may provide the most useful information towards addressing the question of "Is it food?", since the mean abundance of prey at large spatial scales, as determined from fisheries surveys, may not be relevant to the scale at which seals and seabirds forage (e.g., Duffy 1996, NRC 1996). For this reason, understanding the diet of harbor seals and how they may depend on seasonal or area-specific concentrations of prey is not only needed in the management of harbor seals as a resource, but because harbor seals may also act as important indicators of other marine resources.

Recently, the use of fatty acid signature analysis (Iverson 1993) has been proposed to study marine food webs and pinniped diets (Iverson 1995). Certain "indicator" fatty acids (Iverson 1993) exist which are particularly useful in food web studies since they can arise only or mostly from the diet. Although methods of fatty acid signature analysis are still being developed, the technique has been used both to identify general trophic level of diets and to detect major and minor shifts in diet within populations (Iverson et al. 1997, Smith et al. 1997).

Work in PWS conducted as part of this harbor seal restoration study is one of the two most comprehensive ecosystem studies ever conducted using fatty acids signature analysis (Iverson et al. in press, Iverson et al. unpublished data), and has come the farthest in advancing the development of this method. To date, fatty acid signatures have indicated that fine-scale structure in the foraging of harbor seals can be discerned, and that this is due not only to localized feeding patterns in seals, but also to specific differences in prey species with size and location or habitat within PWS (Iverson et al. in press).

Since harbor seals are likely to adjust their foraging patterns to changes in abundance of local prey (Olesiuk 1993, Tollit & Thompson 1996), this suggests that determining diets or changes in diets of harbor seals over time using fatty acid signatures may provide clues not only to changes in foraging patterns, but also to differences in local prey availability, predominant prey size classes, and species abundance at the spatial and temporal scales that are essential to the nutrition of individual animals. It has been proposed that one cause for the decline in some Alaskan pinniped populations may have been a change in community structure over time that resulted in an ecosystem dominated by large predatory pollock, thus making small forage fish less available to pinnipeds (NRC 1996). Fatty acid signature analysis could begin to address such hypotheses by detecting relationships between and within predators and prey on a small spatial scale.

To evaluate the food limitation hypothesis, information is not only needed about the diets of harbor seals but also about habitats used for feeding, seasonal movements, seasonal or annual changes in feeding areas, and feeding behavior. Satellite-linked telemetry can be used to gather these types of information (e.g., Stewart et al. 1989, Boveng et al. 1989). Since 1992, the harbor seal oil spill studies have included attachment of satellite-linked depth recorders (SDRs) to seals to examine their behavior and habitat use (Frost and Lowry 1994*b*, Frost et al. 1995).

Because restoration studies of harbor seals in PWS are ongoing, some of the results presented in this report are preliminary. This report contains a detailed analysis of the recent trend in numbers of harbor seals based on molting surveys, as well as an analysis of the effects of weather on survey counts. The movements and behavior of satellite-tagged seals are described in some detail. However, because some tags attached in September 1996 are still operational, a full statistical analysis of movements and diving will be presented in later reports. When the 1996 tags have all finished transmitting, we will commence analysis of data from all 50 SDRs that have been attached to adult and subadult seals since 1992. In 1997, satellite tagging will focus on pups. Results of fatty acid studies to date are described and included in this report as Appendix A.

OBJECTIVES

The objectives of this restoration study for October 1995-September 1996 were to:

1) monitor and assess the trend in numbers of harbor seals in PWS:
   a) conduct aerial surveys of harbor seals at 25 trend count sites in PWS during molting;
   b) conduct a multivariate analysis of aerial survey data to evaluate the effects of weather, as well as date, time of day, and time and height of low tide on survey counts;

c) compare data from 1996 surveys to data collected during 1989-1995 to determine whether seal numbers are recovering;

2) describe habitat use by harbor seals in PWS:
   a) describe hauling out and diving behavior, and by inference, feeding behavior of satellite tagged seals in PWS;
   b) describe use of haulouts and frequency of movements between haulouts;
   c) determine movement patterns within PWS and between PWS and adjacent areas;

3) investigate the trophic relationships of harbor seals in PWS:
   a) determine fatty acid composition of blubber from PWS harbor seals;
   b) determine fatty acid composition of prey species;
   c) use statistical analyses of fatty acid signatures in blubber and prey to determine harbor seal prey and to compare diets of harbor seals;

4) provide samples to and assist other researchers who are investigating genetics, stable isotopes, blood chemistry, morphometrics, disease, and other factors that may be affecting harbor seals.

METHODS

Aerial Surveys

Aerial surveys were conducted in PWS along a previously established trend count route (Calkins and Pitcher 1984; Pitcher 1986, 1989). The trend count route covered 25 haulout sites, and included 7 sites that were substantially impacted by the spill and 18 unoiled sites that were north, east, and south of the primary area impacted by oil (Table 1, Figure 1).

Survey methods were identical to those used during the NRDA harbor seal study (Frost and Lowry 1994*a*, Frost et al. 1994) and harbor seal restoration studies in 1992-1995 (Frost and Lowry 1994*b*, Frost et al. 1995, Frost et al. 1996). Surveys were conducted from a single engine fixed-wing aircraft (Cessna 185). Visual counts of seals were made at altitudes of 200-300 m, usually with the aid of 7-power binoculars. Each site was circled until the observer was confident that an accurate count had been made. For larger groups of seals (generally those of 40 or more) photographs were taken using a hand-held 35-mm camera with a 70-210 mm zoom lens and high speed film (ASA 400). Color slides were commercially developed, and seals were counted from images projected on a white surface. Replicate counts (usually 7-8) were made at each site. Counts were usually done within two hours before and after low tide.

For each survey the date, time and height of low tide, and time of sunrise and sunset were recorded. As each site was counted the observer recorded time of the count, air temperature, sky conditions, and wind speed according to the categories shown in Table 2. Air temperature, of necessity, was measured at survey altitude.

Analysis of Factors Affecting when Seals are Hauled Out

Complete methods for the analysis of factors affecting the counts of seals were described in Frost et al. (1995, 1996) and will not be repeated here. In brief, a Poisson regression was used to analyze the factors that may affect the number of seals hauled out and available to be counted during surveys. This is a generalized linear model (McCullagh and Nelder 1989) with a log link function and a Poisson distribution. To assign an average count to each site in any given year, a model was first used which considered site, year, and the interaction of site by year. Other factors (Table 2) were subsequently added into the model one at a time. The factor with the most significant χ^2-value was retained in the model, and then other factors were again entered into the model one at a time until any remaining factors were insignificant.

In 1996, we considered wind speed and sky conditions as part of the model for the first time. After the August 1996 survey those data had been collected for five years and therefore were sufficient for the modeling exercise. The full model containing site, year, and site by year interactions, along with time of day, date, and time relative to low tide was always fit. An additional factor (sky conditions or wind speed) was then added to see if it significantly improved the fit. Because temperature records were only available for four years, no attempt was made to see if temperature significantly improved the fit after including wind speed and sky conditions in the model.

Time of day, time relative to low tide, sky conditions, and wind speed were analyzed as categorical data. Initially, time increments before and after midday and before and after low tide were placed in six and eight separate categories (Table 2). Some categories were combined when preliminary analysis indicated that it could be done without changing the fit. Date was centered to 15 August for molt period counts, and scaled so that each day was equal to 0.1. Sky conditions were initially analyzed as five separate categories but later combined as three.

Using significant parameter estimates from the model for time of day, date, time relative to low tide, and sky conditions, the daily count for each site for each year (1992-1996) was adjusted to an expected count. These adjusted counts should be more comparable across years when, for example, survey dates, the distribution of counts relative to time and tide, or weather were not the same.

Trend Analysis of Adjusted Survey Counts

Data were analyzed to determine whether there was an identifiable trend in the counts of harbor seals in PWS since 1989. For each year, adjusted daily counts were averaged for each site and then sites were summed to produce adjusted yearly estimates for the total trend count area. Two sets of counts were produced: one for 1992-1996 in which the adjusted counts considered weather as well as time, date, and tide; and another for 1984-1996 which did not include weather variables. We took this approach because weather information is not available for pre-1992 surveys, yet it is desirable to continue to examine trend for the entire period.

A linear regression model was fitted to the adjusted 1989-1996 mean count data for the 25 trend count sites combined (see Frost et al. 1995). The significance of regression coefficients was tested using analysis of variance (Snedecor and Cochran 1969).

Capture and Tagging of Seals

Field work was conducted at locations throughout PWS during April/May and September 1996. Personnel were transported from Whittier to the study sites aboard the vessel *Pacific Star*.

Detailed descriptions of methods used to capture and tag seals have been given in previous reports (Frost et al. 1995, 1996). The following is an abbreviated description, and readers should consult earlier reports for full details.

Seals were caught by entanglement in nets deployed near their haulouts. Most animals were sedated with a mixture of ketamine and diazepam administered intramuscularly at standard doses (Geraci et al. 1981). Each seal was weighed, measured, and tagged in the hindflippers with individually numbered plastic tags. Approximately 50 cc of blood was drawn from the extradural intervertebral vein and the following samples were collected: whiskers for stable isotope analysis (Project 96170), flipper-punch skin samples for genetic analysis (G. O'Corry-Crowe and R. Westlake, Southwest Fisheries Science Center, La Jolla, CA), blubber biopsies for analyses of fatty acids (S. Iverson, Dalhousie University) and energy content (M. Castellini, University of Alaska Fairbanks, Project 96001), and muscle biopsies for a study of mitochondrial density in locomotor and non-locomotor muscles (S. Kanatous, Texas A & M University). Deuterium oxide and Evans blue were injected into some seals (M. Castellini).

SDRs were glued to the mid-dorsal surface of the seal using Devcon quick-setting epoxy (Fedak et al. 1984, Stewart et al. 1989). The SDRs were manufactured by Wildlife Computers (Redmond, WA), and produced 0.5 watts of power. Four of the units deployed in 1996 measured 14.8 x 10.0 x 3.8 cm, weighed about 750 g, and were powered by four lithium C cells. They were attached to large adult females (70-101 kg). A smaller version which measured 11.9 cm x 5.1 cm x 4.5 cm, weighed 385 g, and was powered by six lithium 2/3 A cells was attached to the nine smaller (42-53 kg) seals. All 0.5-watt SDRs used version 3.10 software. In addition, in fall 1996 we attached one 0.25-watt transmitter (10 cm x 5 cm x 3 cm, 170 g, powered by 2 lithium 2/3 A cells) with timeline software (version 3.14) to a pup weighing 25 kg. The larger units had a projected capacity of about 100,000 transmissions, while the smaller units were rated for approximately 30,000 transmissions. The 0.25-watt test unit was rated for about 15,000 transmissions.

SDRs were programmed as described in Frost et al. (1996). Dive depths, dive durations, and the amount of time spent at depth were stored in six hour blocks (0300-0900 hrs, 0900-1500 hrs, 1500-2100 hrs, and 2100-0300 hrs local time) and transmitted to the satellite once the six hour period was complete. Dive data were accumulated in 10 bins as follows: depths of 4-20 m, 21-50 m, 51-75 m, 76-100 m, 101-150 m, 151-200 m, 201-250 m, 251-300 m, 301-350 m, and over 350 m; and durations of 0-2 minutes, >2-4 minutes, >4-6 minutes, >6-8 minutes, >8-10 minutes, >10-12 minutes, >12-14 minutes, >14-16 minutes, >16-18 minutes, and greater than 18 minutes.

SDRs attached in spring were not duty-cycled and transmitted continuously. To conserve battery power, all tags attached in the fall were programmed to not transmit during hours of poor satellite coverage (2200-0300 hours local time). In addition, small tags attached in the fall were set for a transmission cycle of one day on and two days off. The duty cycle setting in the SDRs is based on Greenwich mean time, and therefore based on local time the units transmitted from 1400-2300 on day 1, 0300-1400 on the day 2, and not at all on the day 3.

Satellite Tag Data Analysis

Detailed descriptions of methods used to compile and analyze satellite tag data have been given in previous reports (Frost et al. 1995, 1996). The following is an abbreviated description, and readers should consult earlier reports for full details.

Data from satellite tagged seals were obtained from Service Argos. Data included a location for the SDR if sufficient signals were received during a satellite pass, or sensor data if only one uplink occurred. For analysis and presentation of data, dates and times reported by Service Argos were converted to true local time from Greenwich mean time by subtracting 10 hours.

A system was developed for identifying and eliminating erroneous location records based on an error index value (Keating 1994) and the time, distance, and speed between sequential pairs of locations. Location records that did not fit set parameters were removed from the database. Numbers of location records referred to in this report include only those records that remained after the complete screening process.

Land-sea sensor data were merged with location records to produce a datafile that included SDR number, date, time, latitude, longitude, location quality, and whether sensors indicated that the seal was on land or at sea. A computer program calculated from this datafile the average location of the seal during each haulout bout and the average daily position for at sea locations.

The all-location and average-position datafiles were used to produce geographic information system coverages in ArcInfo, and datasets were selected and displayed using ArcView. Figures shown in this report are from the average position datafiles. Average position datafiles were used to determine the locations where seals hauled out and where they were when at sea. The average locations of haulout bouts were displayed in ArcView on a map of PWS, and each location record was assigned to the nearest known seal haulout site. If a location plotted more than 5 km from any known haulout, or if it was approximately equidistant between haulouts, the location of that haulout bout was categorized as unknown. In some cases where nearby haulouts are very close together it was not practical to distinguish which location was actually used. In those instances, if one of the haulouts was where the seal was captured and tagged the positions were assigned to that haulout.

Average daily locations were used to identify the specific haulouts used by seals in PWS. Two measures of site fidelity were calculated from the haulout data. The first was the number of separate haulout locations used, which was analyzed separately by month and age-sex class. The second index was based on the proportional use at separate haulouts. For each seal in each month it was observed, the proportion of average daily locations was calculated for each haulout used by that seal. The index was the largest of these proportions. The means of these two indices were compared in a mixed model analysis-of-covariance (ANCOVA) with factors age-sex (adult female, juvenile female, and juvenile male), period (period 1 = October-March, period 2 = April-July), and month as a linear covariate (months were numbered from October = 1 to July = 10). We used procedures appropriate for unbalanced samples (SAS Type III, Milliken and Johnson 1984). Individual seals were also included as a nested random factor which was used as the error term for testing hypotheses about age-sex. Satterthwaite's approximation (Milliken and Johnson 1984) was used to adjust these tests for unbalanced samples. Observations in the analyses were weighted by the number of days each seal was located. The maximum proportional use was analyzed untransformed and with an arcsine-square root transformation; the results were the same for both analyses so only those from the untransformed variable are presented. The analyses started with all factors, covariates, and their interactions included. Unimportant factors ($p>0.05$) were deleted sequentially beginning with the slopes and higher order interactions and continued until all terms left had $p<0.05$ or were contained in interactions still in the model.

Dive data from SDRs were extracted using software provided by the manufacturer. An error-checking algorithm was used to validate messages. Histogram messages were sorted by date, period, and type, and duplicate messages were removed. In addition, this software extracted status messages which provided information about battery voltage and maximum depth of dive. Custom software was developed to sum dive information by month or a specified range of dates, and within months (or date range) by bin and by period.

Dive data from individual seals were graphed and visually examined for patterns relating to date, time of day, and location. In this report, we present some examples of the dive data that are available. However, these examples only describe the behavior of individual seals, and are of limited use in investigating more general patterns that may be related to age, sex, or geographic location. Statistical methods for the analysis of dive data are currently being developed. Conceptual approaches and accompanying methods for describing and analyzing patterns of seal diving behavior will be described in future reports.

RESULTS

Aerial Surveys

Molting period surveys of trend count sites were conducted in 1984 and 1988 (Pitcher 1986, 1989), and have been done annually since the spill (Frost and Lowry 1994*a*, *b*; Frost et al. 1995, 1996). In 1996, the trend sites were surveyed during 17-26 August, and up to eight replicate counts were made at each site (Table 3). The unadjusted mean count for the trend count area as a whole was 716 seals, which was 16% lower than the unadjusted mean count in August 1995 (854) and 6% higher than in 1994. Since 1989, the annual mean unadjusted counts have ranged from a high of 920 (1991) to a low of 678 (1994). Linear regression of the unadjusted counts indicates no significant trend over the past eight years ($R^2 = 0.1546$).

Factors Affecting when Seals are Hauled Out

The multivariate analysis developed in 1995 to model the effects of time of day, date, and time of low tide on seal counts during the molting period was rerun including 1996 data. Parameter estimates changed slightly with the incorporation of new data, but the general results remained the same. Time of day, date, and time relative to low tide all significantly affected the counts. Time of day entered the model first as the most significant factor, followed by date, and finally the time of counts relative to low tide ($P < 0.0001$ for all three). Tide height was not significant. Time of day was collapsed into five categories and time relative to low tide into four. Categories used in the model and parameter estimates are shown in Table 4.

The analysis for time of day indicated that the highest counts would be expected in the period 2-4 hours before midday, and the lowest counts 2-4 hours after midday (Figure 2a). The model indicated that 25% fewer seals would be counted 2-4 hours after midday than in the period 2-4 hours before midday. During late August, sunrise occurs at about 6:30 am local time and sunset at about 9:00 p.m., placing midday at approximately 1:40 p.m. Therefore, the highest counts would be expected before 11:40 a.m., intermediate counts between 11:40 a.m. and 3:40 p.m., and the lowest counts between 3:40 p.m. and 5:40 p.m.

The highest survey counts relative to tidal stage were from 1.0 hour before to 1.5 hours after low tide (Figure 2b). Maximum counts were for the periods 1.0 to 0.5 hour before low tide and from low tide to 0.5 hour after the tide. The model indicated that about 30% fewer seals would be counted more than 1.5 hour after the low tide than during peak times.

Dates for molting surveys during 1984-1994 ranged from 22 August to 16 September. Because the model developed from the 1984-1994 count data predicted that maximum counts would occur before 22 August, the 1995 and 1996 surveys began on 17 August, five days earlier than any previous molting surveys. When the 1995 and 1996 data were incorporated, the model again indicated that more seals would be counted during the earliest surveys, and that in fact the maximum number of seals would be expected still earlier in August (Figure 2c). Counts on 31 August are predicted to be 21% lower than counts made on 17 August, while counts on 16 September would be 29% lower than counts on 31 August and 44% lower than those on 17 August.

Sky conditions clearly had an effect on the number of seals counted ($P < 0.001$). The highest counts were under low overcast conditions. Counts were predicted to be 5%-6% lower when it was clear, cloudy, or high overcast, and 13% lower when it was raining. Although the model indicated that the effect of sky conditions on counts was significant, correcting for this effect made very little difference in the actual adjusted counts (Table 5; Figure 3). For any one year, adjusting for sky conditions changed the total adjusted count by 4-19 seals (<2%). For this reason, and because data on sky conditions were not available prior to 1992, we did not include sky conditions in the overall model to adjust counts for use in trend analysis.

Wind speed had no significant effect on the number of seals counted during surveys and therefore was not included in the model to adjust counts ($P = 0.271$).

Trend Analysis of Adjusted Counts

Using the model parameter estimates for time of day, date, and time relative to low tide, the expected counts for each site were calculated. Because incorporation of the 1996 data caused minor changes in all parameter estimates, new adjusted counts were produced for all years.

For molting period surveys, all counts were corrected to 15 August, 2-4 hours before midday, and 1.0 to 0.5 hour before low tide (Table 6). Once adjusted, the molting-period counts for the 25 trend sites combined indicated a very clear overall decrease in numbers from 1989-1996 ($P = 0.0014$; Figure 4). Adjusted counts in 1996 were 33% lower than counts in 1989 and 62% lower than those in 1984 (Table 7). Since 1994, there has been considerable annual variation in the adjusted as well as the unadjusted counts. The adjusted counts in 1996 were approximately 15% lower than 1995 counts and 3% lower than 1994 counts.

Capture and Tagging of Seals

In 1996 we captured 39 seals and attached 14 SDRs, 6 in spring and 8 in fall (Table 8). SDRs were attached to seals at Little Green Island (2 in spring), Applegate Rocks (1 in spring and 1 in fall), Seal Island (1 in spring), Port Chalmers (2 in spring and 2 in fall), Channel Island (4 in fall), and Stockdale Harbor (1 in fall).

Table 9 summarizes the age, sex, and seasonal distribution of all SDRs attached during 1992-1996 that operated for more than 30 days. A total of 51 tags have been attached, 22 in spring and 29 in fall. The greatest number of SDRs were attached to adult females, and about equal numbers to adult males, juvenile males, and juvenile females. Two pups were tagged.

Satellite-linked Depth Recorder Performance

In fall 1995 we attached a prototype 0.25-watt tag to subadult seal captured on 26 September. Thirteen locations were obtained during 26 September-9 October. No signals were received after 9 October until 27 October when a single and last transmission was received. We consider this tag a failure, and the limited data obtained is not included in this report.

Most of the 0.5-watt tags with version 3.10 software that we attached to seals in fall 1995 and spring 1996 worked well. An exception was a tag attached on 27 September that gave signals for only 42 days (Table 10). The other six fall tags lasted for 146-264 days (mean for all seven tags 204 days). Six tags attached in spring lasted 42-81 days (mean 64 days). As would be expected, for tags attached in the fall the percent of days on which seals were located was less for duty-cycled SDRs (31%-49%) than for SDRs that were not duty-cycled (70%-86%). Two adult females tagged in the spring were located on 97%-100% of the days tracked, while four subadults were located on 54%-98% of the days.

If duty-cycling is accounted for (i.e., the total days operational is divided by three), the average number of locations obtained per day for seals tagged in the fall was similar for all SDRs (2.3-4.2). Adult females tagged in spring gave many more locations per day (5.7-8.8) than did subadults (0.9-4.5).

Although the data have not yet been fully analyzed, it appears that most of the SDRs attached to seals in fall 1996 have worked properly. The experimental 0.25-watt transmitter with version 3.14 software transmitted until 23 December.

Movements and Haulout Behavior

The movements of seals tagged in September 1995 are shown in Figure 5 and are summarized in Table 11. Adult female 95-9 stayed in the Port Chalmers area for the entire tracking period, but all the other seals ranged quite widely. Movements of 94-8 were confined to PWS. It spent most of it's time in eastern PWS where it was tagged, but made three trips to the northern Sound as far as the head of College Fiord. Two seals (95-10 and 95-11) made 3-4 trips each to Middleton Island during the months of September through March. Seal 95-11 spent a considerable amount of time 20-90 km offshore in the area southwest of Montague Island. Seal 95-12 also spent time in this region but it did not range as far to the southwest. Four seals moved east out of PWS to the Copper River delta area. Adult female 95-12 moved to the delta on March 28 and remained there until transmissions stopped on May 10. Seal 95-10 was at the delta from March 14 through April 3, moved back to the north end of Montague Island during April 16-21, then returned to the delta for the remainder of the tracking period that ended May 17. Seal 95-7 was at the delta from October 5-8, moved back to eastern PWS for the period October 11-February 18, then returned to the delta on February 21 and stayed until the last fix on 16 June. Seal 95-13 was at the delta during October 15-November 5 and appeared to be moving toward PWS when transmissions stopped on November 8.

Movements of seals tagged in April 1996 are shown in Figure 6 and summarized in Table 12. Tagged seals mostly stayed in the vicinity of where they were captured. The longest movement was by 96-1 which spend May 3-19 at the south end of Knight Island Passage. Seals 96-1 and 96-2 were both captured at Little Green Island but for most of the time they were tracked they were at or near Applegate Rocks. Seals 96-5 and 96-6 were tagged at Port Chalmers. Both hauled out occasionally at Channel Island through the summer, and only there beginning on July 2.

Of the two seals tagged at Gravina Island in fall 1995, one (95-7) hauled out about equally at Gravina Island and the Copper River delta while the other (95-8) used mostly Gravina Island and sites in Port Fidalgo and northern PWS (Table 13). Of three seals tagged at Port Chalmers, one (95-9) hauled out mostly there, one (95-10) used mostly Port Etches, sites on Montague Island, and the Copper River delta, and one (95-13) did not haul out at all in the Port Chalmers area during the brief period that it was tracked. Two seals tagged at Little Green Island (95-11 and 95-12) used that haulout and a variety of other sites.

Both of the seals tagged at Little Green Island in spring 1996 (96-1 and 96-2) hauled out primarily at Applegate Rocks, as did seal 96-3 which was captured and tagged at Applegate (Table 14). Seal 96-4 tagged at Seal Island hauled out mostly there. Both seals tagged at Port Chalmers (96-5 and 96-6) hauled out primarily at Port Chalmers and secondarily at Channel Island.

The statistical model employed to analyze haulout use showed that the mean number of haulouts used each month declined over time from October through July ($p=0.021$; Figure 7). The number of haulouts used differed among age-sex classes ($p=0.015$), with adult females using the greatest number of sites, juvenile females the fewest, and juvenile males an intermediate number. However, samples sizes were small (especially for juvenile males) and there was considerable variability in the monthly mean values for all age-sex classes (Table 15). Maximum proportional use of the principal haulout showed an overall increase from October through July ($p=0.029$; Figure 8). However, using month as a covariate accounted for a relatively small proportion of the variation in this index ($r^2 = 0.12$). The factors period, age, and sex were not related to maximum proportional use.

We examined seasonal differences in the amount of time seals spent hauled out by comparing the percent of days per month that each seal hauled out based on land-sea sensor data reported by the SDRs (Table 16). During October through April, seals hauled out on 45%-63% of the days, compared to 71%-92% in May through July when pupping, breeding, and molting occur. The mean proportion of days hauled-out was compared for adult females and subadults (both sexes) and among months using a 2-way ANOVA (Table 17). (No adult males were tagged during this period.) There were differences between ages, among months, and there was an age by month interaction. Adult females hauled out on a higher proportion of days than did subadults (76% vs. 51%, $p<0.001$). Examination of monthly means shows that this pattern (adult females>subadults) held for all months except May. The proportion of days hauled out was more consistent across months for adult females than for subadults. For most of the year subadults hauled out at a much lower rate (Figure 9). However, from May through July subadult haulout rate increased and was much closer to the rate of adult females. The interaction of month by age in the ANOVA is likely due to the changing haulout pattern of the subadults.

Behavior at Sea

Depth of dive histogram information was received summarizing 239,216 dives made by seven seals tagged in September 1995 and 66,286 dives made by six seals tagged in April 1996. For the fall 1995 seals combined, 65% of the total dives were to depths of 20 m or less, and 74% to 50 m or less. Only 5% of the total dives were deeper than 150 m. For individual seals, 24%-96% of the total dives were shallower than 20 m, and 0%-15% were deeper than 150 m (Figure 10). A subadult male (95-11) feeding in the GOA during the winter made 15% of its dives to >150 m.

For the spring 1996 seals combined, 58% of the total dives were shallower than 20 m and 83% were shallower than 50 m. For individual seals, 33% to 93% of their dives in May-July were shallower than 20 m. For 5 of the 6 spring seals, almost no dives were deeper than 150 m. However, for one subadult male, almost 12 % of its dives were >150m (Figure 11).

Most of the seals tagged during fall 1995 did their deepest diving during December through late March or early April (Figure 10). The exception was an adult female that was spent the 4+ months it was tagged in Port Chalmers and never dove deeper than 40 m. Of the five seals that transmitted data into May, most made more shallow dives in April and May than during the winter. However, although seals spent the most amount of time at deeper depths during winter, there was no clear seasonal pattern in the maximum depth to which they dove on a particular day (Figure 12). At any time of year, maximum depths might exceed 200 m.

During winter 1995, 5 of the 7 tagged seals left PWS and traveled to the Copper River delta or the GOA to feed. Two of the three adult females spent considerable time in the GOA feeding in mid-winter. Both moved to the Copper River delta in March or April and remained there until May when their tags ceased to function. The third female spent the entire winter in Port Chalmers. Both subadult females spent time in the Copper River delta in October. One tag failed shortly thereafter, and the other animal returned to the Copper River delta again in late February and remained there until tag transmissions ceased in May. The subadult male spent the greatest amount of time in the GOA, hauling out at Middleton Island and making feeding trips to deeper water that lasted 5-19 days (average 11.6 days, n = 11). These trips were separated by periods of 4-11 days (average 6.5 days, n = 10) when the seals spent some time hauled out every day. This male returned to mid-PWS in April, after which the extended feeding trips ended. Although other seals made feeding trips into the GOA, none were so regular or so prolonged. Extended feeding trips are evident in Figure 12 by the complete gaps in the data during which seals were diving so intensively that no signals were received by the satellite for many consecutive days.

The daily maximum depth of dive for individual seals, as well as the time spent at different depths, varied by the geographic location in which the seals were feeding. For example, after April 1 adult female 95-12 fed and hauled out in the Copper River delta. Maximum depth of dive did not exceed 20 m and rarely exceeded 4 m. The same was true for seals 95-7 and 95-10 when they were in the Copper River delta. Figure 13 shows the time spent in different depth increments and the amount of time spent hauled out for seal 95-12. When in the Copper River delta 95-12 spent much time hauled out, almost all of her time spent underwater was at depths less than 20 m, and 20 m was the maximum depth of dive. In contrast, when near Danger Island she spent much less time hauled out, dove to maximum depths of about 75 m, and spent most of her time underwater at 50-100 m.

DISCUSSION

Aerial Survey Methods

In previous years as part of this project we constructed a model that considered the effects of various factors on the counts of seals in PWS (Frost et al. 1995, 1996). Primary factors included in the model were time of day, date, and time relative to low tide. The model generated parameter estimates for each of these factors, and the estimates were then used to adjust the actual counts of seals to optimal conditions. These adjusted data were used for annual comparisons and analyses of trend.

This year, the effects of sky conditions and wind speed were incorporated into the model for the first time. Wind was found to have no significant effect on seal counts, and therefore was not used to calculate adjusted count estimates. This is not surprising since surveys are not flown in extremely windy conditions when seal behavior is most likely to be affected.

Sky conditions were found to have a significant effect, with more seals counted when there was a low overcast. This is probably partially due to the hauling out behavior of the seals. Seals may be thermally stressed in very bright, clear, warm weather (Watts 1992, Hansen et al. 1995), and therefore haul out less often or for shorter periods of time. Also, higher counts may occur partly because the light is excellent for counting when the sky is overcast. In bright sunlight, seals dry out quickly, appear lighter colored, and are more difficult to detect due to glare. Although the analysis of sky conditions was informative relative to optimum counting conditions, we do not plan to include the effects of sky conditions in future estimations of adjusted counts.

The 1996 counts for the PWS trend sites were adjusted using the same factors that we used in the 1995 and 1996 analysis. Because there is such a large dataset (10 years) the parameter estimates, and therefore the predicted effect of parameters such as time, tide, and date, showed almost no change between 1995 and 1996. This suggests that the total dataset encompasses a representative sample of the environmental conditions likely to be encountered and that new data reinforce the existing model rather than causing large changes. As in previous analyses, the 1996 modeled data predicted the highest counts from 2 hr before midday to midday and from 1.5 hr before to 0.5 hr after low tide. Counts are predicted to decline steadily after the middle of August.

It is clear from these analyses that adjusting counts to take into account variation in survey conditions greatly improves our ability to detect trend. However, even this approach may not adequately estimate the variance associated with corrected counts. The current model for trend-monitoring use Poisson regression and linear regression uses a two-stage analysis. For the Poisson regression, a separate effect is fit for each site and year. With 10 years of data, 25 sites, and an average of 6 replicates per year we have approximately 1,500 observations. Our model estimates separate covariate effects for time of day, time relative to low tide, date, and weather. There are about 300 estimated parameters, and the ratio of parameters estimated to number of data points is 1/5. Under conditions such as this where hundreds of parameters are being estimated large variances and poor estimation properties may result.

For the second stage analysis, the mean effect for year and location are calculated from the Poisson regression parameter estimates for standardized states of the covariates, and then the sites are summed for each year. This sum is then used in linear regression to determine trend across years. This second stage does not formally include estimation variance from the Poisson regression, which is an additional concern.

We have considered variations to our model to eliminate the second stage regression analysis, but they also cause difficulties. For example, we could put the overall trend parameter in Poisson regression. However, this would cause all sites to have a common yearly mean. Another approach would be to allow each site to have a separate intercept with a common trend in the Poisson regression. However, it is clear that not all sites have a common trend. A final approach is to allow each site to have a separate trend slope and intercept in the Poisson regression model, but then it is unclear how to combine all 25 slope estimates into a single estimate of overall trend.

Ideally, we would like to weight each slope estimate by the abundance at each site, but computing the variance of such a method may not be possible.

The Poisson regression model has served a purpose in that it has: 1) incorporated covariates that allowed us to examine effects of survey variables on seal counts; 2) allowed us to adjust our counts to get better trend estimates; and 3) allowed us to do power analysis. However, as we acquire more data, we think that it is important to model effects separately for each site, and this makes the model much more complicated.

Given the problems listed above, one solution is to put more structure in the model. This can be done using a hierarchical model, where all the "parameters" above can be considered "variables" in their own right, coming from one or a few "prior" distributions. For example, rather than having 25 separate trend slope parameters (one for each site), we might consider all 25 slopes as coming from a common prior distribution. These prior distributions have only a few parameters that control their behavior. Thus, we would reduce a large set of hundreds of parameters to a set that contains relatively few. Also, because the 25 slope parameters would have a "distribution," it is conceptually easy to take a weighted sum and obtain the proper variance for an overall trend.

With a hierarchical modeling approach, we could develop a Bayesian statistical model that relates observed seal counts to a number of covariates. Covariates recorded at each observation include year, spatial coordinates, calendar day, time, height of low tide, time of low tide, and qualitative assessments of wind and sky conditions. Using modern Monte Carlo Markov Chain methods, we could assess the usefulness of any or all of these covariates in explaining and/or predicting the number of seals observed. An integral part of this modeling would be the development of a hierarchical Bayesian approach to trend monitoring. Ultimately, a separate trend might be occurring at each of the 25 haul-out sites in the Prince William Sound. We could consider a trend parameter, such as the slope of a regression through time, for each site. Bayesian hierarchical methods are ideally suited for combining these 25 trend parameters to get an overall trend indicator for all sites. This is the direction we will take in future years for trend analysis.

Trends in Numbers of Seals

The number of harbor seals counted on 25 trend count sites in PWS has declined more than 60% since 1984 when the first trend counts were made. This rate of decline is similar whether adjusted (-62%) or unadjusted (-60%) counts are used. That decline was exacerbated by the *Exxon Valdez* oil spill in 1989, when about 300 seals were estimated to have died (Frost et al. 1994). Since 1989, the number of seals on the trend count route in PWS has continued to show an overall decline (Table 7). Comparisons of adjusted trend count data from 1989 and 1996 indicate a 33% decline.

In the 1995 annual report for this project, we reported a 16% increase in the adjusted 1995 molting period counts. At that time we were unable to determine whether that increase represented the start of an increasing trend, between-year variation, or was a survey artifact. Modeling efforts using 1984-1994 data had predicted that higher counts would occur early in August. Therefore, we intentionally began the 1995 surveys five days earlier than in any previous year (17 August versus 22 August) in part to confirm the relationship between date and counts. We thought it was possible, considering the apparent increase in the 1995 counts, that either the effect of date was greater than the model had predicted using mostly data from later in August and September, or some other factor was responsible for the increased counts. During 1996, surveys again began on the 17th of August when counts were expected to be high. However, despite the early starting date, the adjusted mean count was lower than for any other year since surveys began. Unadjusted counts were also lower than for any year except 1994. Based on the 1996 counts, it appears that the declining trend is still continuing.

Satellite-linked Depth Recorder Performance

We continued to have very good performance from the 0.5 watt SDRs with version 3.10 software that we attached to seals during 1995-1996. Tags attached in late April 1996 transmitted until June-July, and the average number of days operational (64) was identical to that for 16 other tags we attached to seals in PWS in spring 1992-1995 (Frost et al. 1996). As has been the case previously, tags attached in September usually lasted much longer, although there have been some that failed prematurely. If those early failures are disregarded, the tags attached in fall 1995 transmitted longer on average (231 days) than did tags attached in fall 1993-1994 (185 days; Frost et al. 1996).

Small SDRs attached in September 1994 were duty-cycled one day on and one day off. Two of those units transmitted until December, one until February, and one until March (Frost et al. 1996). To try and increase longevity, we changed the duty-cycling for small SDRs attached in September 1995 to one day on and two days off. One of those tags failed in November, but the other three transmitted into May-June. The increased longevity of those small tags explains much of the improved overall operational period of the September 1995 tags. We concluded that one day on and two day off duty-cycling is the best for small SDRs, and that is how units attached in fall 1996 were programmed.

Movements and Haulout Behavior

Frost et al. (1996) presented a description of the movements of 30 seals satellite tagged in PWS from spring 1992 through spring 1995. Those results will be combined with data in this report and from SDRs currently operational for a complete analysis of movements by tagging location, season, and sex and age class for all 51 tagged seals (see Table 9). Results of that analysis will be presented in the final report for this project.

The restricted movements of seals tagged in April 1996 is consistent with data from seals previously tagged in spring (Frost et al. 1996). Of 22 seals tracked during April-July, only 3 have shown substantial movements out of PWS.

The situation with seals tagged in September and tracked during fall, winter, and spring appears more complex. Six seals tagged in central PWS in fall 1993 all stayed within the Sound, and only 2 of 8 tagged in southern PWS in fall 1994 spent considerable time offshore the GOA (Frost et al. 1996). In contrast, 5 of 7 seals tagged in fall 1995 moved out of PWS, going to either Middleton Island (1 animal), the Copper River delta (3 animals), or both (1 animal). Based on a preliminary look at the data, 7 of the 8 seals tagged in fall 1996 also left PWS to feed offshore in the GOA or the Copper River delta. As in the previous year, the feeding trips outside PWS occurred primarily during winter and spring.

Over the four years of this study there appears to have been a change in the feeding locations of seals during winter-spring. Prior to fall 1995, only 2 of 30 tagged seals had gone to the Copper River delta: a juvenile male tagged in May 1992 was at the delta from May 25-June 5 and June 12-July 18, and a juvenile female tagged in September 1994 was briefly at the delta in October while en route to Yakutat Bay (Frost et al. 1995, 1996). Since then, adult female and juvenile seals tagged in fall 1995 and adult females tagged in September 1996 spent a considerable amount of time at the Copper River delta, especially during March-June.

Prior to fall 1995, only two seals had left PWS and gone to Middleton Island: an adult male and an adult female (Frost et al. 1996). The animals tagged in fall 1995 that went to Middleton were an adult female and a juvenile male. Of animals tagged in 1996, adult females, subadults, and a pup went to the GOA/Middleton area.

As mentioned above, a full analysis of all movements data will not be done until the SDRs attached in fall 1996 have finished transmitting data. However, we have plotted results from the fall 1995 and spring 1996 tagging efforts separately for juvenile seals and adult females (Figures 14 and 15). The figures show a considerable similarity in the movements and areas used by these two age/sex classes, which suggests that the variability we have documented may be due mostly to a seasonal effect (see Figures 5 and 6).

Seals tagged in spring 1996 used only haulouts that were frequently used by tagged seals in past years. Seals tagged in fall hauled out at several known haulout areas that had not been used previously. Perhaps the most notable of those was Icy Bay in southwest PWS, a region that none of our previously tagged seals had visited although it is known to be a major seal haulout. Tagged seals also used some haulouts that had not been previously reported, including three sites in Port Fidalgo and two on the outer coast of Montague Island.

Frost et al. (1996) reported that 29 of 30 seals tagged during spring 1992 through spring 1995 were in PWS at the time they were last located. Of those 29, 24 were at or near the capture site or an adjacent haulout, while the other 5 were located 5-30 km away. Similar results were found for seals tagged in spring 1996 (Table 12). The situation was different for seals tagged in fall 1995, as 3 of 8 animals were outside of PWS in the Copper River delta when the last locations were received in May-June (Table 11).

Previously we analyzed the number of haulouts used and the maximum proportional use for 30 seals tagged in PWS during spring 1993 through spring 1995 (Frost et al. 1996). Generally, results were similar to those for the 13 seals analyzed in this report, with individual seals using 1.3-3.7 haulout sites per month, and usually hauling out at the principal site 60%-90% of the time. However, differences found over time and between age-sex groups were not the same. Results indicated that in the earlier tagged sample seals used more haulouts and showed a lower proportional use during May-July than during September through March, while data from seals tagged in fall 1995 and spring 1996 showed opposite trends. In the recent sample adult females used more haulouts in most months than did juveniles, while in the earlier sample juveniles used more haulouts than adult females during May-July. At present it is impossible to explain or interpret the possible significance of these differences. Patterns and differences in haulout behaviors should become more clear when data from all SDR tagged seals are analyzed together, as will be done for the final project report.

It is clear from these preliminary analyses that some harbor seals in PWS move considerable distances to feed during winter months. The distance from south-central PWS, where most seals were tagged, to the GOA (either near Middleton Island or the Copper River delta) is more than 100 km. This greater movement than has been reported for harbor seals in most other studies. Suryan (1995) used VHF radio telemetry to study use of three haulouts in the northern San Juan Islands, Washington. The greatest recorded movement was 28 km. Harvey (1987) attached VHF radiotags to 26 seals along the Oregon coast. Radiotagged seals moved as much as 280 km from the release site, but 92% of the time were located within 8 km. Working in the Channel Islands off southern California, Stewart and Yochem (1994) found some subadults moved further to other islands or the mainland, while satellite tagged adults mostly stayed near the island where they were tagged.

Land-sea sensor data for seals tagged during 1995-1996 show that PWS harbor seals haul out on a higher percentage of days during June-July than they do at other times of year (Figure 9). This was true for both adult females and subadults. Data presented in the 1996 annual report for 26 seals tagged between May 1992 and September 1995 showed the same pattern (Frost et al. 1996). This pattern is consistent with our aerial survey data, which also suggests that the number of seals hauled out is highest from late June through mid-August and decreases steadily in September. Harbor seal investigators in other areas also report that seals spend a greater percentage of their time hauled out in spring/summer when they pup, breed, and molt, than they do in winter (Harvey 1987, Thompson 1989, Moss 1992, Stewart and Yochem 1994). The percentage of days hauled out by PWS seals in summer (80%-100%) is considerably higher than was found on Sable Island, Nova Scotia (52%-57%; Godsell 1988).

Behavior at Sea

Seals tagged in 1995-1996, like those tagged previously (Frost et al. 1995, 1996), showed considerable individual variability in how deep they dove. However, it appears that PWS harbor seals spend little of their time deeper than 150 m. Of the 13 seals presented in this report, only 3 spent any significant amount of time deeper than 150 m. Two of those did most of their deep diving in the GOA during winter. The third made deep dives in Port Fidalgo area of PWS. In Norway, Bjørge (1995) found that seals fed near the bottom at 15-200 m in a diversity of habitats. Stewart and Yochem (1994) reported that seals in the California Channel Islands dove as deep as 446 m.

The seals tagged in September 1995 did not show a consistent seasonal pattern in how deep they dove. One adult female tagged in Port Chalmers spent the entire five months she was tagged diving to less than 50 m and usually to less than 20 m. Another adult female tagged in Port Chalmers spent February and early March in the GOA making many dives to more than 150 m, while for the rest of the year most dives were less than 20 m. A pup and a subadult male alternated periods of deep and shallow dives. Depth of dive appeared to be more correlated with location than with time of year. For example, three seals were in the shallow Copper River delta in March-May and almost all of there dives were shallow during this time. In contrast, two seals feeding near Danger Island spent most of their time in water deeper than 50 m. A female pup alternating between College Fiord and Port Fidalgo did more shallow diving (< 20 m) in College Fiord and more deep diving in Port Fidalgo. Similar variability was found in the diving and feeding behavior of seals tagged in previous years. It appears possible that each seal has an individual strategy that is determined by a combination of age, geographic location, prey availability, and perhaps other factors.

Two of the seals we tagged in September 1996 and two tagged the previous year made extended trips into the GOA to feed. In winter 1996, some of these trips lasted two weeks at sea without hauling out. When seals stayed within PWS, they appeared to make fewer extended trips to sea, and the trips were of shorter average duration. It appears that when a haulout is nearby, seals take advantage of it and haul out between bouts of feeding. However, they also travel far from haulouts to feed and remain in these areas for days and even weeks at a time. Most investigators have found that harbor seals make repeated feeding trips to the same areas, and that these areas are within 20-50 km of their haulouts (Bjørge 1995, Thompson and Miller 1990, Stewart and Yochem

1994). This allows them to haul out each day between feeding. Apparently, the long distances required to reach feeding areas in the GOA make it less energetically efficient to return to a haulout each day.

Foods and Trophic Relationships

In 1994 we began a study using fatty acid analyses to investigate food web relationships of harbor seals in PWS. To date, we have been able to analyze the fatty acid composition of blubber from 218 seals sampled in PWS, near Kodiak Island, and in southeast Alaska. In addition, we have analyzed the fatty acid composition of 528 prey collected in PWS, representing 16 taxa (capelin, flathead sole, rex sole, yellowfin sole, unidentified flatfish, herring, octopus, Pacific cod, pink salmon (adults and smolt), pollock, rainbow smelt, copper rockfish, sandlance, shrimp, squid, and tomcod). The primary goals of these analyses have been: a) to build a library of prey species fatty acid signatures that is large enough to allow in-depth assessment of the influence of size-class, location, and season on signatures; b) to build our sample of harbor seals both within PWS and elsewhere in the GOA; c) to begin to assess whether harbor seals differ in diet according to age-class or sex; and d) to begin to assess whether there have been differences in the diets of harbor seals over a three year period. The results of this study are described in detail in Appendix A.

Prey species in PWS differed notably in fatty acid composition and could be readily distinguished from one another. Species such as herring, pollock, capelin, squid and tomcod could be distinguished by size class and location within PWS, depending on species. Data suggest that size class and location are the most important factors influencing differences in fatty acid composition within prey species, with season having little effect. In contrast, fat content is strongly affected by season, with most species highest in fat in the fall and lowest after the wintering period.

Data from harbor seal blubber fatty acid signatures, as well as from satellite telemetry data, suggest strongly that seals not only haul out site-specifically, but also forage site-specifically. Within PWS over a spatial scale of about 80 km or less, large differences were observed in fatty acid patterns of seals, indicating differences in feeding over small spatial scales. The diets of seals from northern and eastern PWS were very different from those in southern PWS. On a broader geographical scale of 400-800 km in the GOA, seals also differed in fatty acid signatures and thus in foraging. Seals from Kodiak shared some characteristics with those from southern PWS, which is not surprising considering that some of the PWS seals travel to the GOA to feed, and that some prey species also move in and out of PWS seasonally.

In addition to differences among locations, there was a strong indication that diets of seals changed over the three years of study (especially in 1996). The difference in diets of 1996 seals are consistent with results from satellite-tagged seals which indicate that more seals traveled to and fed in the Copper River delta and the GOA during the winter of 1995-1996 than in previous years. The blubber samples taken in spring 1996 would represent diet during the 1995-1996 winter.

Lastly, evidence indicates that diets differ with demographic characteristics of the seals. Although not all age classes are available from all areas, it is clear that the diets of adult males tend to differ from that of adult females and from subadults.

Although the use of fatty acid signatures in blubber to directly identify the prey eaten is precluded by the complexity of the data, it is nonetheless possible to examine prevalence of particular fatty acid components and make some suggestions about likely components of the diet. Based on such an approach, it is likely that capelin was present in the diet of both adult and juvenile seals in PWS, but especially juveniles. Sandlance and small herring likely also contributed to the fatty acid signatures found in juveniles. Signatures of adult males and females suggest a variety of prey species. Larger sizes of pollock, herring, and yellowfin sole were likely components of the adult diet, but it is unlikely that these sizes of prey were consumed by juveniles.

CONCLUSIONS

1. Trend count surveys showed that the number of harbor seals in PWS has continued to decline since the *Exxon Valdez* oil spill. A statistically significant decline occurred in molting period counts from 1989 through 1996. Adjusted molting period counts were 33% lower in 1996 than in 1989.

2. The 1996 molting period counts were 15% lower than 1995 counts and 3% lower than 1994 counts, indicating some annual variability in counts.

3. The generalized linear model used to adjust counts reduces variation due to date, time of day, and time relative to low tide. Analyses showed that wind speed had no significant effect but that sky conditions did have a small effect on seal counts. However, sky conditions will not be incorporated into the model in the future because the effect is so small and because historical data sets do not contain this information.

4. Ongoing studies using SDRs continue to provide a wealth of information on harbor seal movements and behavior. During 1995-1996, average duration of operation was 64 days for SDRs attached in April and 231 days for SDRs attached in September. By comparison, the average duration of operation for previous years was 64 days for May attachments and 153 days for September attachments. Duty cycling of small tags has significantly improved their useful life. The majority of seals tracked during spring-summer have stayed within PWS and hauled out principally at the capture location and adjacent haulout sites.

5. Prior to 1995, only a few seals made trips outside of PWS. A few individuals made trips to tidewater glaciers in northern PWS, or moved out into the GOA. In 1995, this appeared to change. Twelve of 15 seals instrumented in September of 1995 and September 1996 left PWS to feed during the winter-spring, traveling either to offshore waters of the GOA, to the Copper River delta, or both.

7. Fatty acid signature analysis of 528 potential seal prey representing 16 taxa showed differences between species, collection areas, and seasons. Analysis of fatty acid signatures from 218 seal blubber samples indicated differences in the diets of seals from PWS, southeast Alaska, and the Kodiak area. Within PWS there were differences between seals sampled near Montague Island and those from the northern and eastern Sound. Seals from southern PWS were more similar to seals from Kodiak. Fatty acid signatures indicated that diets of adult males are different than diets of adult females and juveniles.

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Table 1. Prince William Sound harbor seal trend count route.

Site #	Site Name	Latitude	Longitude	Oiling Status
1	Sheep Bay	60° 37 N	146° 0 1 W	unoiled
2	Gravina Island	60° 38.4 N	146° 17.5 W	unoiled
3	Gravina Rocks	60° 39.8 N	146° 15.8 W	unoiled
4	Olsen Bay	60° 43 N	146° 11 W	unoiled
5	Porcupine Point	60° 43 N	146° 41 W	unoiled
6	Fairmount Island	60° 51.5 N	147° 26.5 W	unoiled
7	Payday	60° 54.3 N	147° 30 W	unoiled
8	Olsen Island	60° 51.1 N	147° 34 W	unoiled
9	Point Pellew	60° 50.5 N	147° 40.5 W	unoiled
10	Little Axel Lind Island	60° 48.5 N	147° 40 W	unoiled
11	Storey Island	60° 44 N	147° 23 W	oiled
12	Agnes Island	60° 37 N	147° 23 W	oiled
13	Little Smith Island	60° 31 N	147° 25.5 W	oiled
14	Big Smith Island	60° 31.5 N	147°19 W	oiled
15	Seal Island	60° 25.5 N	147° 19 W	oiled
16	Applegate Rocks	60° 21 N	147° 23.5 W	oiled
17	Green Island	60° 18.5 N	147° 23 W	oiled
18	Channel Island	60° 14.5 N	147° 23 W	unoiled
19	Little Green Island	60° 12 N	147° 31 W	unoiled
20	Port Chalmers	60° 15 N	147° 14.5 W	unoiled
21	Stockdale Harbor	60° 18 N	147° 12 W	unoiled
22	Montague Point	60° 22 N	147° 04 W	unoiled
23	Rocky Bay	60° 21 N	147° 01.5 W	unoiled
24	Schooner Rocks	60° 18.2 N	146° 54 W	unoiled
25	Canoe Passage	60° 31.6 N	146° 09.5 W	unoiled

Table 2. Factors considered in Poisson regression analysis of the number of seals hauled out during aerial surveys.

Factor	Type	Description
Location	categorical	25 sites
Year	categorical	10 years, 1984 and 1989-1996 for molting surveys
Time of day	categorical	before (midday - 4 hours) (midday - 4 hours) to (midday - 2 hours) (midday - 2 hours) to (midday) (midday) to (midday +2 hours) (midday + 2) to (midday + 4 hours) after (midday + 4 hours)
Date	continuous, scaled	day/10 since August 15 $(\text{day}/10)^2$ since August 15
Time relative to low tide	categorical	before (lowtide - 1.5 hours) (lowtide - 1.5 hours) to (lowtide - 1 hour) (lowtide - 1 hour) to (lowtide - 0.5 hour) (lowtide - 0.5 hour) to (lowtide) (lowtide) to (lowtide + 0.5 hour) (lowtide + 0.5 hour) to (lowtide + 1 hour) (lowtide + 1 hour) to (lowtide + 1.5 hours) after (lowtide + 1.5 hours)
Tide height	continuous	deviations from low tide, in feet
Wind	categorical	CA = calm LB = light breeze LW = light wind WI - windy
Sky conditions	categorical	CL = cloudy HO = high overcast LO = low overcast or fog PC = partly cloudy RN = rain or drizzle

Table 3. Repetitive counts of harbor seals on selected haulout sites in Prince William Sound, August 1997. Dashes indicate that no count was made.

	Date (August)								
	17	18	19	21	22	23	24	26	mean
Sheep Point	0	0	0	0	0	0	0	1	0.1
Gravina Island	21	33	21	25	9	30	28	22	23.6
Gravina Rocks	48	53	54	40	18	45	18	31	38.4
Olsen Bay	116	129	103	111	113	59	100	79	101.3
Porcupine	0	0	0	--	0	0	0	0	0
Fairmount	0	0	0	--	0	--	0	--	0
Payday	0	0	0	--	0	--	0	--	0
Olsen Island	0	0	0	--	0	--	0	--	0
Point Pellew	8	6	7	--	9	--	7	--	7.4
Little Axel Lind	0	0	0	--	0	--	0	--	0
Storey Island	0	0	0	--	0	0	0	--	0
Agnes Island	48	53	54	--	18	33	26	26	36.9
Little Smith Island	26	22	22	--	22	13	22	7	19.1
Big Smith Island	27	26	43	--	31	13	27	4	24.4
Seal Island	39	42	42	--	36	42	37	24	37.4
Applegate Rocks	172	158	203	--	123	84	103	29	124.6
Green Island	11	16	11	--	15	10	13	0	10.9
Channel Island	65	88	69	--	37	0	0	7	38.0
Little Green Island	45	36	10	--	41	18	14	30	27.7
Port Chalmers	80	90	75	--	99	50	85	28	72.4
Stockdale Harbor	37	42	38	--	48	42	39	27	39.0
Montague Point	0	0	0	--	0	0	1	0	0.1
Rocky Bay	50	59	58	--	51	48	45	22	47.6
Schooner Rocks	33	33	40	--	24	17	34	26	29.6
Canoe Passage	58	24	39	29	40	38	36	38	37.7

Table 4. Parameter estimates for factors affecting molt period counts of hauled out seals made during aerial surveys of Prince William Sound, August-September 1984-1996.

		Parameter estimate		
			1992-96	
Factor	Category	1984-96	No sky	With Sky
Time of day	before (midday - 4 hr)	-0.0509	-0.0534	-0.0465
	(midday - 4 hr) to (midday - 2 hr)	0.0000	0.0000	0.0000
	(midday - 2 hr) to midday	-0.1137	-0.0929	-0.0908
	midday to (midday + 2 hr)	-0.1681	-0.1785	-0.1566
	(midday + 2 hr) to (midday + 4 hr)	-0.2862	-0.2667	-0.2570
	after (midday + 4 hr)	-0.1681	-0.1785	-0.1566
Date	day/10 since August 15	-0.1350	-0.1945	-0.2159
	$(\text{day}/10)^2$ since August 15	-0.0171	-0.0190	-0.0145
Time of tide	more than 1.5 hr before low tide	-0.1293	-0.1603	-0.1573
	1.5 hr before low tide to 1.0 hr before low	-0.1293	-0.1603	-0.1573
	1 hr before low tide to 0.5 hr before low	0.0000	0.0000	0.0000
	0.5 hr before low tide to low tide	-0.0575	-0.0592	-0.0623
	low tide to 0.5 hr after low tide	0.0000	0.0000	0.0000
	0.5 hr after low tide to 1.0 hr after low	-0.0575	-0.0592	-0.0623
	1.0 hr after low tide to 1.5 hr after low	-0.0575	-0.0592	-0.0623
	more than 1.5 hr after low tide	-0.3534	-0.2810	-0.2853
Sky	Low overcast			0.0466
	High overcast			0.0000
	Partly cloudy			-0.0094
	Clear			-0.0106
	Rain			-0.0935

Table 5. Adjusted mean counts of harbor seals on selected haulout sites in Prince William Sound, August-September 1992-1996, with and without adjustments for sky conditions.

	1992		1993		1994		1995		1996	
	with	w/o	with	w/o	with	w/o	with	w/o	with	w/o
Sheep Point	1	<1	7	7	0	0	<1	<1	0	0
Gravina Island	43	41	26	26	17	17	23	23	32	32
Gravina Rocks	55	53	68	68	98	96	75	75	53	54
Olsen Bay	73	71	123	123	82	80	145	146	147	148
Porcupine	13	12	4	4	1	1	0	0	0	0
Fairmount	21	20	30	30	4	4	23	23	0	0
Payday	<1	<1	<1	<1	<1	<1	0	0	0	0
Olsen Island	7	7	4	4	8	7	0	0	0	0
Point Pellew	21	21	16	16	<1	<1	5	5	9	9
Little Axel Lind	11	11	4	4	0	0	0	0	0	0
Storey Island	<1	<1	<1	<1	0	0	<1	<1	0	0
Agnes Island	75	73	36	35	64	62	73	72	49	49
Little Smith Island	55	54	40	39	47	46	53	53	29	29
Big Smith Island	73	72	58	57	73	71	35	35	38	38
Seal Island	85	84	66	65	70	69	41	41	50	50
Applegate Rocks	107	104	87	87	102	101	186	186	185	185
Green Island	64	62	45	45	42	41	15	15	16	16
Channel Island	137	134	189	189	105	104	131	132	63	62
Little Green Island	97	95	77	77	46	45	51	51	35	35
Port Chalmers	111	108	192	189	121	120	116	117	103	102
Stockdale Harbor	76	74	24	23	55	55	45	46	51	51
Montague Point	17	17	2	2	11	11	1	1	<1	<1
Rocky Bay	43	42	36	36	66	65	85	85	68	67
Schooner Rocks	102	100	107	107	56	56	40	40	40	39
Canoe Passage	45	46	37	36	69	67	45	45	51	50
TOTAL	1332	1303	1278	1271	1137	1118	1188	1192	1019	1014

Table 6. Adjusted mean counts of harbor seals on selected haulout sites in Prince William Sound, August-September 1984-1996.

	Year									
	1984	1988	1989	1990	1991	1992	1993	1994	1995	1996
Sheep Point	64	25	0	<1	1	<1	7	0	<0	0
Gravina Island	37	24	37	9	19	37	24	15	22	31
Gravina Rocks	62	82	63	38	39	48	62	88	73	52
Olsen Bay	208	146	79	126	112	63	112	73	143	144
Porcupine	42	6	13	1	20	11	4	1	0	0
Fairmount	136	73	61	38	23	18	28	3	23	0
Payday	16	3	3	7	6	<1	<1	<0	0	0
Olsen Island	55	21	13	17	13	6	3	7	0	0
Point Pellew	32	35	44	38	31	19	15	<0	5	9
Little Axel Lind	39	33	42	25	14	10	4	0	0	0
Storey Island	16	9	5	4	<1	<1	<1	0	<0	0
Agnes Island	114	67	63	61	52	66	33	56	71	48
Little Smith Island	109	56	39	50	33	49	36	42	52	28
Big Smith Island	136	140	72	49	45	65	53	64	34	37
Seal Island	158	130	65	65	86	76	60	63	39	48
Applegate Rocks	318	276	162	198	142	94	81	92	181	180
Green Island	88	79	32	42	33	57	42	38	15	15
Channel Island	424	161	172	64	139	123	176	95	128	60
Little Green Island	85	95	57	51	21	86	71	41	50	34
Port Chalmers	109	136	122	169	144	99	173	109	113	99
Stockdale Harbor	55	88	82	82	61	68	21	50	45	49
Montague Point	77	61	65	63	36	15	2	10	1	<0
Rocky Bay	61	21	35	19	27	38	33	60	81	65
Schooner Rocks	18	125	111	78	74	91	100	51	38	38
Canoe Passage	24	74	39	41	70	41	34	60	42	47
TOTAL	2583	1966	1476	1335	1241	1180	1174	1018	1156	984

Table 7. Adjusted mean counts and annual percent change for harbor seals at oiled and unoiled trend count sites in Prince William Sound, based on surveys during August-September 1984-1996.

	Oiled (n=7)		Unoiled (n=18)		All (n=25)	
Year	mean	annual % change	mean	annual % change	mean	annual % change
1984	939		1644		2583	
1988	757	-19	1209	-26	1966	-24
1989	438	-42	1038	-14	1476	-25
1990	469	+ 7	866	-17	1335	-10
1991	391	-17	850	-2	1241	- 6
1992	407	+ 4	773	-9	1180	- 6
1993	305	-25	869	+11	1174	- 1
1994	355	+14	663	-24	1018	-12
1995	392	+9	764	+13	1156	+16
1996	356	-9	628	-18	984	-15
Overall changes						
1984-1996		-62		-62		-62
1988-1996		-53		-48		-48
1989-1996		-19		-39		- 33

Table 8. Harbor seals captured, sampled, and tagged with satellite-linked depth recorders in Prince William Sound, April - September 1996.

Specimen Number	Capture Date	Capture Location	Sex	Age Class	SDR Number	Standard Length (cm)	Axillary Girth (cm)	Weight (kg)
PWSHS-01-96	4/28/96	Little Green Isl, PWS	F	Pup	-	94	77	28.7
PWSHS-02-96	4/28/96	Little Green Isl, PWS	F	Sub	2094	94	85	39.2
PWSHS-03-96	4/28/96	Little Green Isl, PWS	F	Sub	2093	112	89	38
PWSHS-04-96	4/30/96	Applegate Rocks, PWS	F	Sub	2095	109	76	31.9
PWSHS-05-96	4/30/96	Applegate Rocks, PWS	M	Ad	-	140	118	84.2
PWSHS-06-96	4/30/96	Seal Island, PWS	M	Sub	2096	113	84	38.7
PWSHS-07-96	4/30/96	Seal Island, PWS	M	Ad	-	147	104	74.6
PWSHS-08-96	4/30/96	Seal Island, PWS	M	Ad	-	117	96	51
PWSHS-09-96	4/30/96	Stockdale Harbor, PWS	M	Sub	-	114	88	44
PWSHS-10-96	4/30/96	Stockdale Harbor, PWS	M	Ad	-	157	111	91.8
PWSHS-11-96	4/30/96	Port Chalmers, PWS	F	Ad	2282	143	112	84.2
PWSHS-12-96	4/30/96	Port Chalmers, PWS	F	Ad	2097	138	117	93.8
PWSHS-13-96	4/30/96	Port Chalmers, PWS	M	Ad	-	156	115	88.6
PWSHS-14-96	5/1/96	Port Chalmers, PWS	F	Sub	-	112	89	37.4
PWSHS-15-96	5/1/96	Channel Island, PWS	M	Ad	-	116	95	49.7
PWSHS-16-96	5/1/96	Little Green Isl, PWS	M	Ad	-	122	93	54.2
PWSHS-17-96	5/1/96	Little Green Isl, PWS	F	Ad	-	119	99	51.7
PWSHS-18-96	5/1/96	Little Green Isl, PWS	M	Sub	-	111	93	45.1
PWSHS-19-96	5/1/96	Olsen Bay, PWS	M	Pup	-	99	85	31.5
PWSHS-20-96	5/1/96	Olsen Bay, PWS	M	Ad	-	149	109	86.2
PWSHS-21-96	5/2/96	Olsen Bay, PWS	M	Sub	-	107	82	33.6

Table 8. Continued.

Specimen Number	Capture Date	Capture Location	Sex	Age Class	SDR Number	Standard Length (cm)	Axillary Girth (cm)	Weight (kg)
PWSHS-22-96	5/2/96	Olsen Bay, PWS	M	Ad	-	130	94	54
PWSHS-23-96	9/26/96	Channel Island, PWS	F	Sub	2280	113	83	43.5
PWSHS-24-96	9/26/96	Port Chalmers, PWS	F	Pup	2287	95	74	25.1
PWSHS-25-96	9/27/96	Port Chalmers, PWS	F	Ad	2098	142	115	101.7
PWSHS-26-96	9/27/96	Stockdale Harbor, PWS	M	Sub	2283	125	93	52.9
PWSHS-27-96	9/27/96	Channel Island, PWS	M	Ad	-	150	107	77.3
PWSHS-28-96	9/27/96	Channel Island, PWS	M	Sub	2284	114	95	47.7
PWSHS-29-96	9/27/96	Channel Island, PWS	M	Sub	2285	112	92	42.3
PWSHS-30-96	9/27/96	Channel Island, PWS	F	Ad	2286	136	102	70.5
PWSHS-31-96	9/27/96	Seal Island, PWS	F	Ad	-	131	107	71
PWSHS-32-96	9/27/96	Seal Island, PWS	F	Ad	-	132	97	58.3
PWSHS-33-96	9/27/96	Seal Island, PWS	M	Pup	-	106	76	28.6
PWSHS-34-96	9/28/96	Seal Island, PWS	F	Sub	-	108	76	28.9
PWSHS-35-96	9/28/96	Applegate Rocks, PWS	F	Sub	2281	124	92	47.6
PWSHS-36-96	9/28/96	Applegate Rocks, PWS	M	Sub	-	107	86	40.6
PWSHS-37-96	9/28/96	Applegate Rocks, PWS	F	Sub	-	104	66	24.6
PWSHS-38-96	9/28/96	Port Chalmers, PWS	F	Sub	-	98	71	27.2
PWSHS-39-96	9/28/96	Port Chalmers, PWS	M	Ad	-	150	118	103.5

Table 9. Summary of the number of satellite-linked depth recorders attached to harbor seals in Prince William Sound during 1992-1996 by age/sex class and season. Only animals whose tags operated properly for 30 days or more are included.

	Spring	Fall	Total
Females			
Adults	6	9	15
Juveniles	5	6	11
Pups	0	2	2
Males			
Adults	6	6	12
Juveniles	5	6	11
Pups	0	0	0
TOTAL	22	29	51

Table 10. Performance of satellite-linked depth recorders attached to harbor seals in Prince William Sound, 1995-1996. Does not include units with versions 3.11 or 3.13 software.

SDR	ID Number	Age\ Sex[a]	Date Attached	Date of Last Transmission	Total Days Operational	No. Days w/ Locations	Total No. Locations
1995 - fall							
2283[b]	95-7	JF	9/25/95	6/16/96	264	130	307
2286[b]	95-8	JF	9/25/95	5/21/96	238	101	249
2285	95-9	AF	9/26/95	2/9/96	146	125	614
2280	95-10	AF	9/26/95	5/17/96	243	172	623
2287[b]	95-11	JM	9/26/95	5/29/96	255	104	303
2281	95-12	AF	9/26/95	5/16/96	242	169	561
2284[b]	95-13	JF	9/27/95	11/8/95	42	13	35
1996 - spring							
2094	96-1	JF	4/28/96	7/18/96	81	51	264
2093	96-2	JF	4/28/96	7/2/96	65	51	219
2095	96-3	JF	4/30/96	6/11/96	42	41	191
2096	96-4	JM	4/30/96	6/28/96	59	32	56
2282	96-5	AF	4/30/96	7/5/96	66	66	582
2097	96-6	AF	4/30/96	7/8/96	69	67	392
1996 - fall							
2280[c]	96-7	JF	9/26/96				
2287[c]	96-8	PF	9/26/96				
2098[c]	96-9	AF	9/27/96				
2283[c]	96-10	JM	9/27/96				
2284[c]	96-11	JM	9/27/96				
2285[c]	96-12	JM	9/27/96				
2286[c]	96-13	AF	9/27/96				
2281[c]	96-14	JF	9/28/96				

[a] AF = adult female; AM = adult male; JF = juvenile female; JM = juvenile male; PF=pup female

[b] These SDRs were duty-cycled one day on and two days off (see methods)

[c] Location data for these SDRs have not yet been analyzed, and will be presented in the 1997 annual report

Table 11. Summary of movements of satellite tagged harbor seals in Prince William Sound, September 1995-June 1996.

ID no.	Age/ sex[a]	Location and Date Tagged	Other Major Areas and Dates of Use	Location and Date of Last Location Fix
95-7	JF	Gravina Island 9/25/95	Port Etches 10/3; Sheep Bay 1/1-2/18 Copper River Delta 10/5-8; 2/21-6/16	Copper River Delta 6/16/96
95-8	JF	Gravina Island 9/25/95	Little Smith I. 10/9; Seal I. 10/15-30 College Fiord 11/8-12, 2/12-19, 4/27-5/12 Port Fidalgo 12/23-2/10, 2/22-4/25, 5/16-21	Port Fidalgo 5/21/96
95-9	AF	Port Chalmers 9/26/95		Port Chalmers 2/9/96
95-10	AF	Port Chalmers 9/26/95	Middleton I. 9/30-10/7, 11/6-13, 12/5-7, 2/10-14 Port Etches 10/14-11/3, 11/15-30,12/11-1/28, 3/12 SE Montague I. 2/2, 2/18-3/8; Rocky Bay 4/16-21 Copper River Delta 3/14-4/3, 4/22-5/17	Copper River Delta 5/17/96
95-11	JM	Little Green I. 9/26/95	Danger I. 10/2,11/6-19, 11/30-12/22 Middleton I. 10/8-26, 12/24-1/3, 2/10-3/24 Icy Bay 5/4-8	Little Green Island 5/29/96
95-12	AF	Little Green I. 9/26/95	Columbia Bay 10/10-17, 11/14, 11/23 Danger I. 12/27-3/24; Copper River Delta 3/28-5/10	Copper River Delta 5/10/96
95-13	JF	Port Chalmers 9/27/95	SE Montague 10/6; Copper River Delta 10/15-11/5	Orca Inlet 11/8/95

[a] AF = adult female; AM = adult male; JF = juvenile female; JM = juvenile male

Table 12. Summary of movements of satellite tagged harbor seals in Prince William Sound, April-July 1996.

ID no.	Age/ sex[a]	Location and Date Tagged	Other Major Areas and Dates of Use	Location and Date of Last Location Fix
96-1	JF	Little Green I. 4/28/96	Applegate Rocks 4/30-5/2, 5/20-7/18 Squire I. 5/3-19	Applegate Rocks 7/18/96
96-2	JF	Little Green I. 4/28/96	Applegate Rocks 5/3-7/2	Applegate Rocks 7/2/96
96-3	JF	Applegate Rks. 4/30/96		Applegate Rocks 6/11/96
96-4	JM	Seal Island 4/30/96		Seal Island 6/27/96
96-5	AF	Port Chalmers 4/30/96	Channel I. 5/14,25, 6/1,2,13,30, 7/2-5	Channel Island 7/5/96
96-6	AF	Port Chalmers 4/30/96	Channel I. 5/21, 6/9,16,21,26,28, 7/2-8	Channel Island 7/8/96

[a] AF = adult female; AM = adult male; JF = juvenile female; JM = juvenile male

Table 13. Use of haulout sites by satellite tagged harbor seals in Prince William Sound, September 1995-June 1996. Numbers indicate the number of haulout bouts that occurred at each site based on location and land-sea sensor data.

	ID Number and Tagging Site (age/sex[a])						
Location	95-7 (JF) Gravina I.	95-8 (JF) Gravina I.	95-9 (AF) Pt. Chalmers	95-10 (AF) Pt. Chalmers	95-11 (JM) L. Green I.	95-12 (AF) L. Green I.	95-13 (JF) Pt. Chalmers
Port Chalmers	--	--	70	9	--	4	--
Channel Island	--	--	7	--	--	--	--
Stockdale Harbor	--	--	2	4	--	--	--
Little Green Island	--	--	--	--	22	21	--
Green Island	--	--	1	--	--	--	--
Little Smith Island	--	2	--	--	--	--	--
Seal Island	--	4	--	--	--	--	--
Schooner Rocks	--	--	--	1	--	--	--
Rocky Bay	--	--	--	8	--	--	--
Port Etches	--	--	--	49	--	--	--
Gravina Island	24	11	--	--	--	--	--
Hells Hole	3	--	--	--	--	2	--
Two Moon Bay	--	2	--	--	--	--	--
Upper Port Fidalgo	--	8	--	--	--	--	--
Landlocked Bay	--	2	--	--	--	--	--
Columbia Bay	--	2	--	--	--	12	--
L. Axel Lind Island	--	2	--	--	--	--	--
Harriman Fiord	--	3	--	--	--	--	--
College Fiord	--	7	--	--	--	--	--
Icy Bay	--	--	--	--	3	--	--

Table 13. Continued.

	ID Number and Tagging Site (age/sex[a])						
Location	95-7 (JF) Gravina I.	95-8 (JF) Gravina I.	95-9 (AF) Pt. Chalmers	95-10 (AF) Pt. Chalmers	95-11 (JM) L. Green I.	95-12 (AF) L. Green I.	95-13 (JF) Pt. Chalmers
Danger Island	--	--	--	--	7	72	--
Latouche Island	--	--	--	--	--	3	--
Copper River Delta	26	--	--	17	--	19	5
Middleton Island	--	--	--	20	24	--	--
Box Point	--	--	--	17	--	--	--
Wooded Islands	--	--	--	--	--	--	1
TOTAL KNOWN	53	43	80	125	56	133	6
Unknown	1	--	8	4	1	8	--

[a] AF = adult female; AM = adult male; JF = juvenile female; JM = juvenile male

Table 14. Use of haulout sites by satellite tagged harbor seals in Prince William Sound, April-July 1996. Numbers indicate the number of haulout bouts that occurred at each site based on location and land-sea sensor data.

	ID Number and Tagging Site (age/sex[a])					
Location	96-1 (JF) Little Green I.	96-2 (JF) Little Green I.	96-3 (JF) Applegate Rks.	96-4 (JM) Seal Island	96-5 (AF) Pt. Chalmers	96-6 (AF) Pt. Chalmers
Applegate Rocks	40	50	31	1	--	--
Seal Island	1	--	--	13	--	--
Little Green Island	1	--	1	--	--	--
Squire Island	10	--	--	--	--	--
Unnamed cove	--	--	--	2	--	--
Port Chalmers	--	--	--	--	73	67
Stockdale Harbor	--	--	--	--	2	--
Channel Island	--	--	--	--	13	14
Green Island	--	--	--	--	--	1
TOTAL KNOWN	52	50	32	16	88	82
Unknown	2	2	6	2	--	4

[a] AF = adult female; AM = adult male; JF = juvenile female; JM = juvenile male

Table 15. Monthly use of haulouts by harbor seals tagged with satellite-linked depth recorders in Prince William Sound, October 1995-July 1996. Values shown are monthly means for each age-sex class, with the sample size and range given in parentheses.

Month	Adult Female	Juvenile Female	Juvenile Male
October	3.7 (3, 3-4)	2.7 (3, 2-3)	1.0 (1, ---)
November	3.3 (3, 2-5)	2.0 (2, ---)	2.0 (1, ---)
December	2.7 (3, 2-4)	1.5 (2, 1-2)	2.0 (1, ---)
January	2.7 (3, 2-3)	3.0 (2, 2-4)	2.0 (1, ---)
February	2.8 (3, 1-3)	1.0 (2, ---)	1.0 (1, ---)
March	3.5 (2, 3-4)	1.5 (2, 1-2)	1.0 (1, ---)
April	3.0 (2, 1-5)	1.3 (4, 1-2)	1.0 (1, ---)
May	2.5 (4, 1-4)	2.4 (5, 1-4)	3.0 (2, ---)
June	3.0 (2, ---)	1.5 (4, 1-2)	3.0 (2, ---)
July	2.5 (2, 2-3)	1.5 (2, 1-2)	---

Table 16. Percent of days hauled out by month for harbor seals satellite tagged in Prince William Sound, October 1995-July 1996.

SDR	Age	Sex	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
95-7	Sub	F	45	33	17	43	21	50	63	87	100	
95-8	Pup	F	56	20	44	33	13	38	35	60		
95-9	Ad	F	64	69	71	68	50					
95-10	Ad	F	60	54	54	76	72	77	79	58		
95-11	Sub	M	43	60	44	38	24	57	57	81		
95-12	Ad	F	50	67	63	94	90	77	81	57		
95-13	Sub	F	54	50								
96-1	Sub	F								77	100	100
96-2	Sub	F								73	62	67
96-3	Sub	F								87	83	
96-4	Sub	M								53	65	
96-5	Ad	F								74	97	100
96-6	AD	F								77	100	100
mean			53.1	50.4	48.8	58.7	45.0	59.8	63.0	71.3	86.7	91.8
std. deviation			7.67	18.04	18.86	24.36	31.05	17.11	18.71	12.27	16.99	16.50

Table 17. Comparison of the proportion of days hauled out by month for adult female and subadult harbor seals satellite tagged in Prince William Sound, September 1995-July 1996.

	All Seals			Adult Females			Subadults		
Month	N	Mean	SD	N	Mean	SD	N	Mean	SD
1	6	0.59	0.2436	3	0.79	0.1331	3	0.38	0.0500
2	6	0.45	0.3105	3	0.71	0.2003	3	0.19	0.0569
3	5	0.60	0.1711	2	0.77	0.0000	3	0.48	0.0961
4	5	0.63	0.1871	2	0.80	0.0141	3	0.52	0.1474
5	11	0.71	0.1227	4	0.67	0.1047	7	0.74	0.1313
6	7	0.87	0.1699	2	0.99	0.0212	5	0.82	0.1829
7	4	0.92	0.1650	2	1.00	0.0000	2	0.84	0.2333
10	7	0.53	0.0767	3	0.58	0.0721	4	0.50	0.0645
11	7	0.50	0.1804	3	0.63	0.0814	4	0.41	0.1776
12	6	0.49	0.1886	3	0.63	0.0850	3	0.35	0.1559
Total	54	0.63	0.1597	27	0.76	0.1452	37	0.52	0.2140

	df	F	P
AGE	1,63	49.08	0.0001
MONTH	9,63	8.83	0.0001
AGE*MONTH	9,63	3.17	0.0049

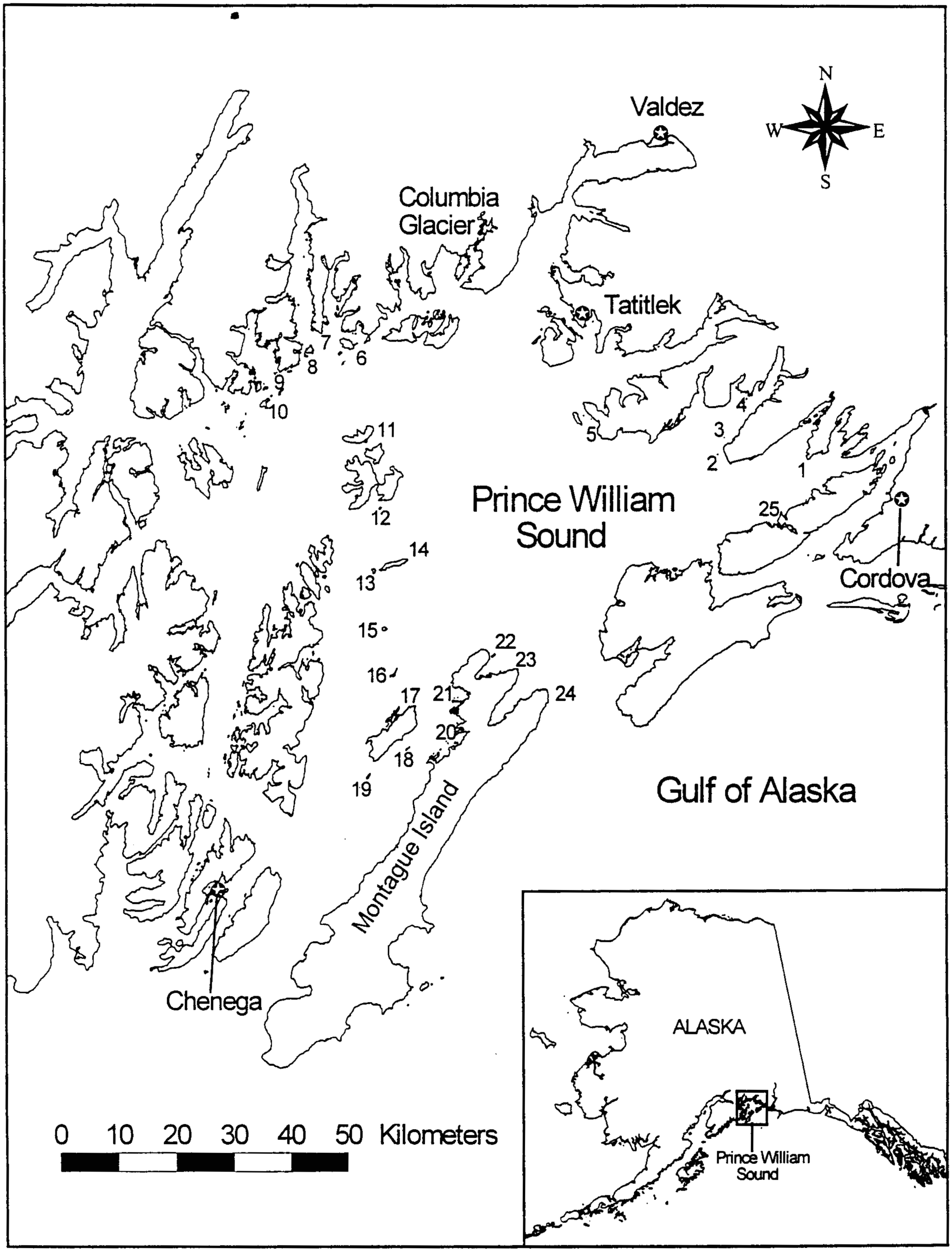


Figure 1. Map of the Prince William Sound study area showing trend count sites.

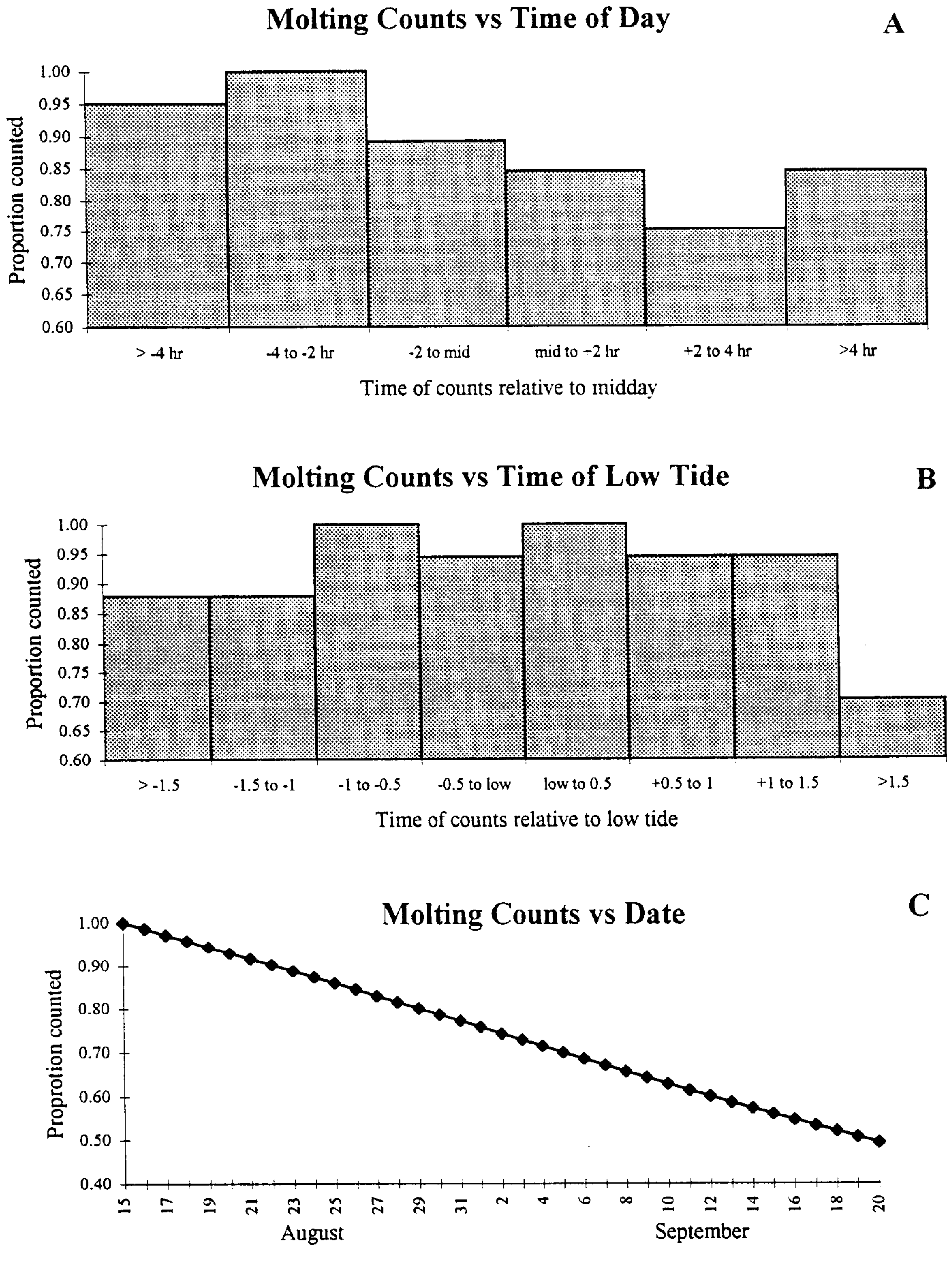


Figure 2. Effect of time of day (A), time relative to low tide (B), and date (C) on counts of harbor seals in Prince William Sound, August-September 1984-1996.

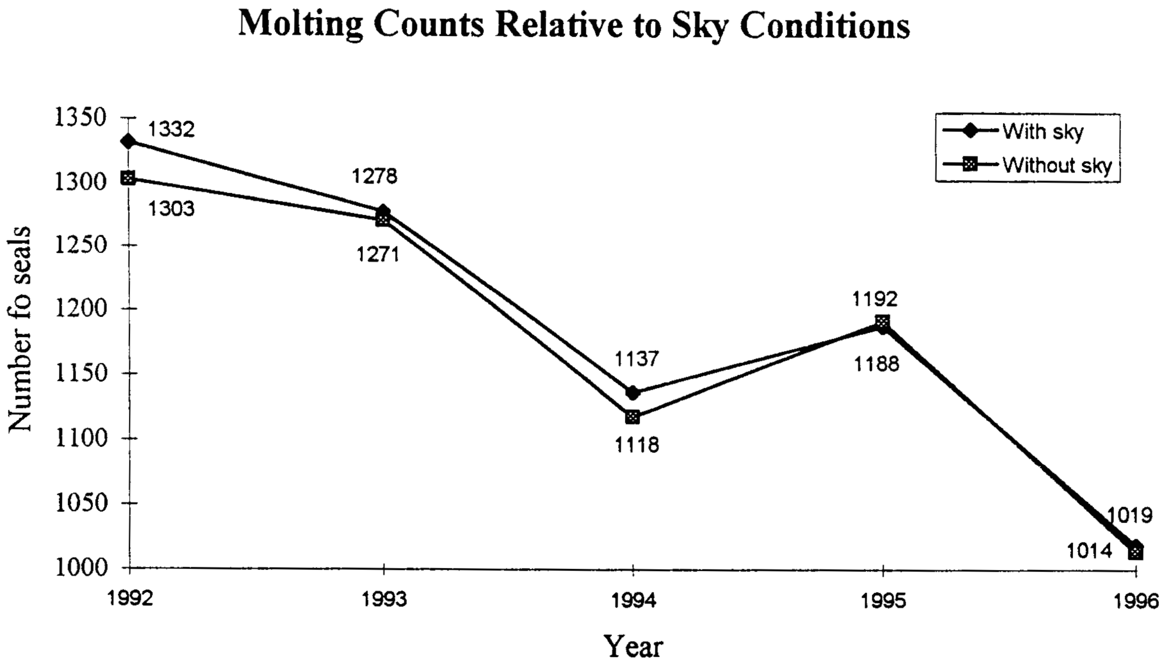


Figure 3. Effect of sky conditions on counts of harbor seals in Prince William Sound, August-September 1992-1996.

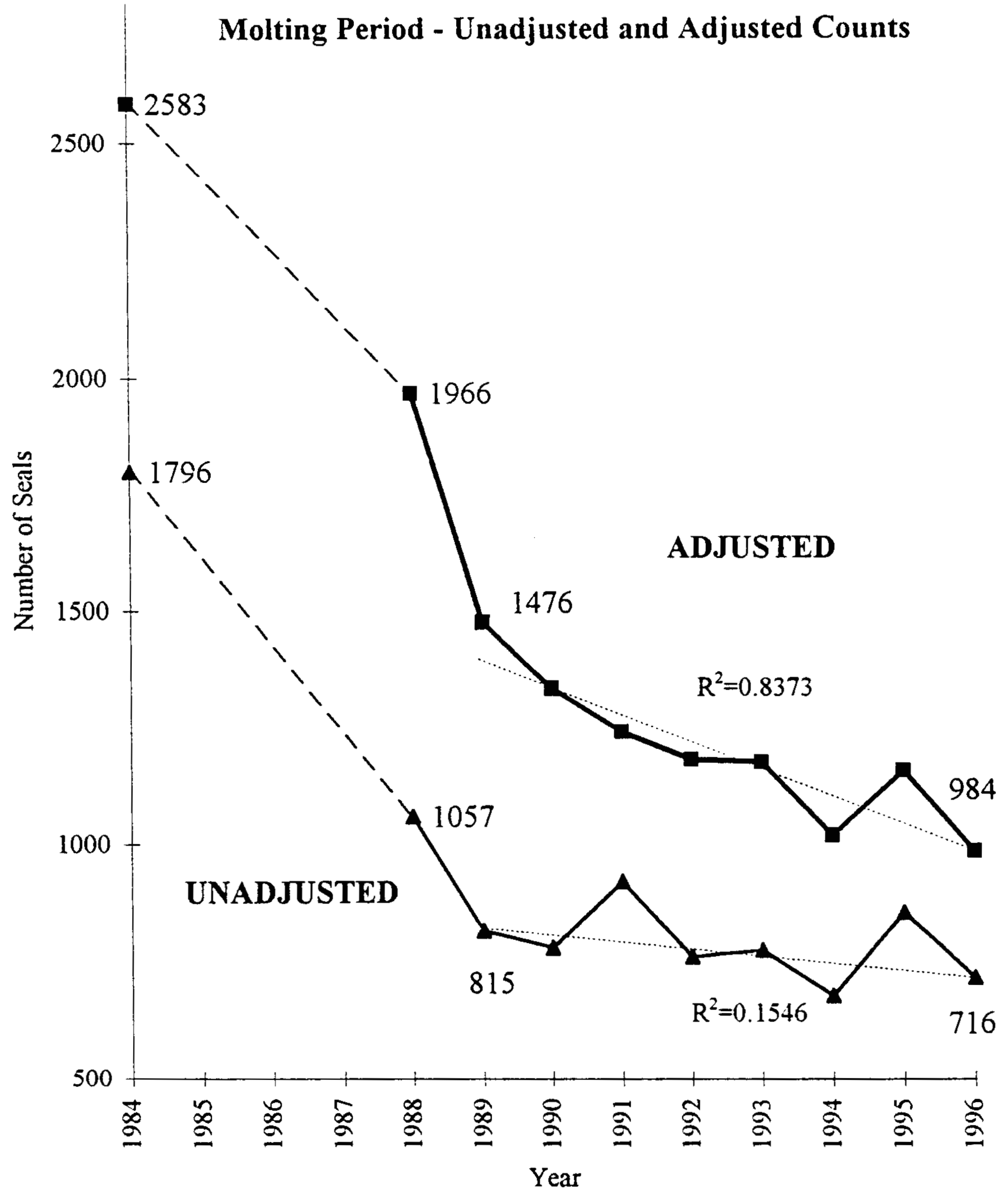


Figure 4. Trend in number of harbor seals in Prince William Sound based on unadjusted and adjusted counts made during August-September 1984-1996

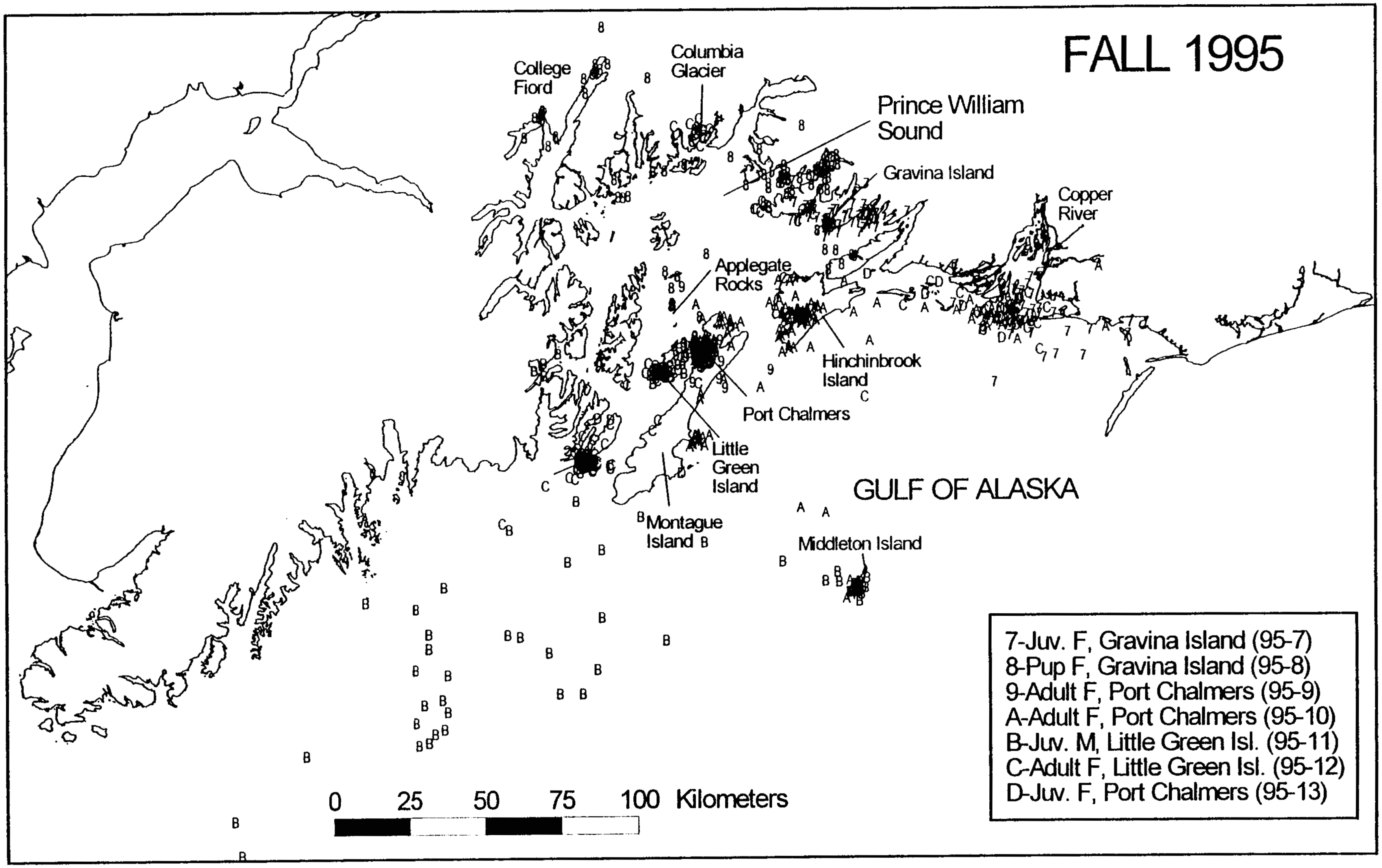


Figure 5. Map of Prince William Sound and the Gulf of Alaska showing average daily locations of satellite tagged seals during September 1995-June 1996.

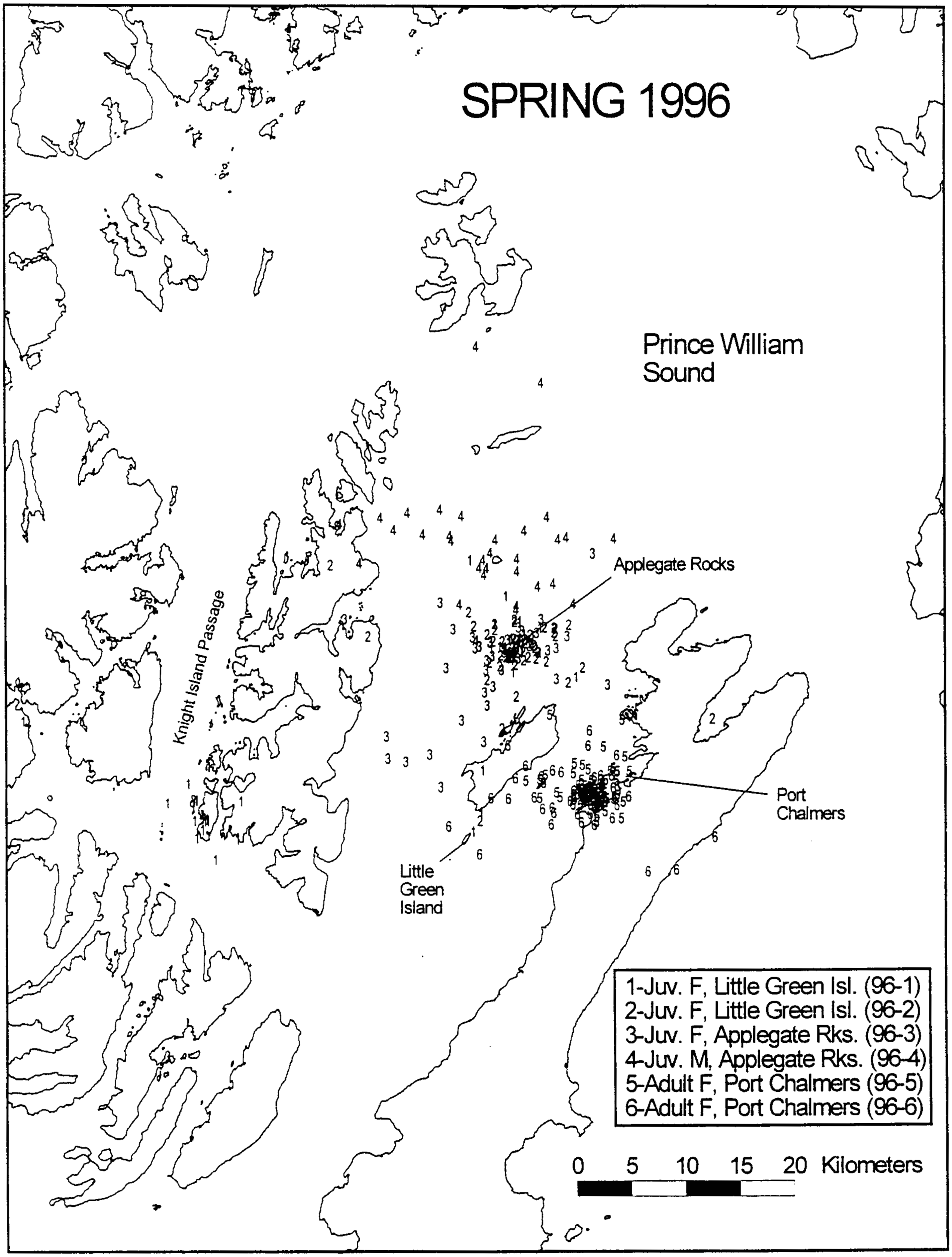


Figure 6. Map of Prince William Sound showing average daily locations of satellite tagged seals during May-July 1996.

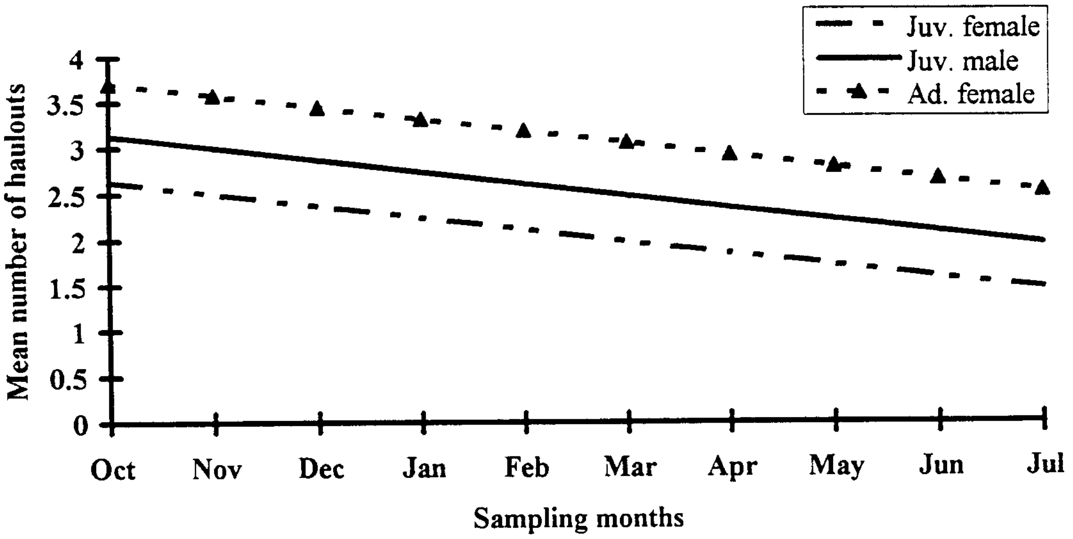


Figure 7. Number of haulouts used per month for each age-sex class of harbor seals in Prince William Sound, October 1995-June 1996.

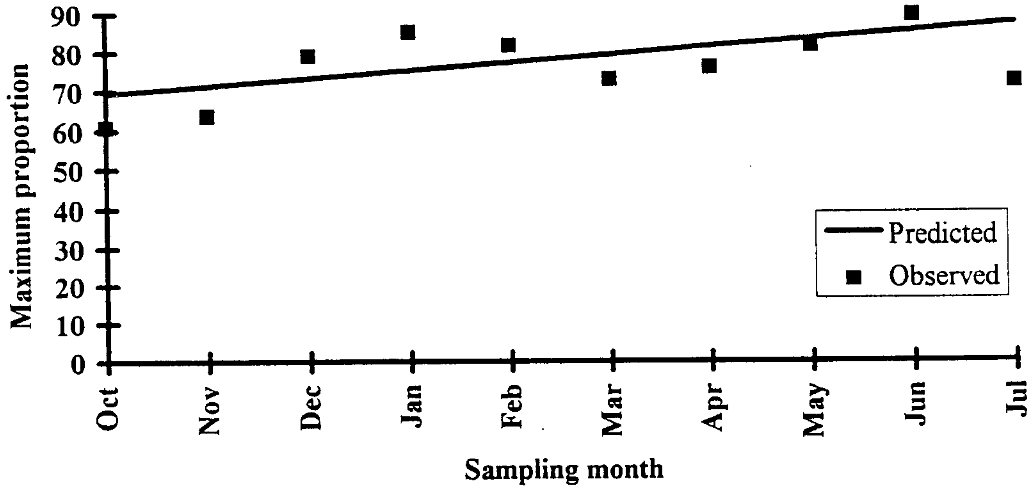
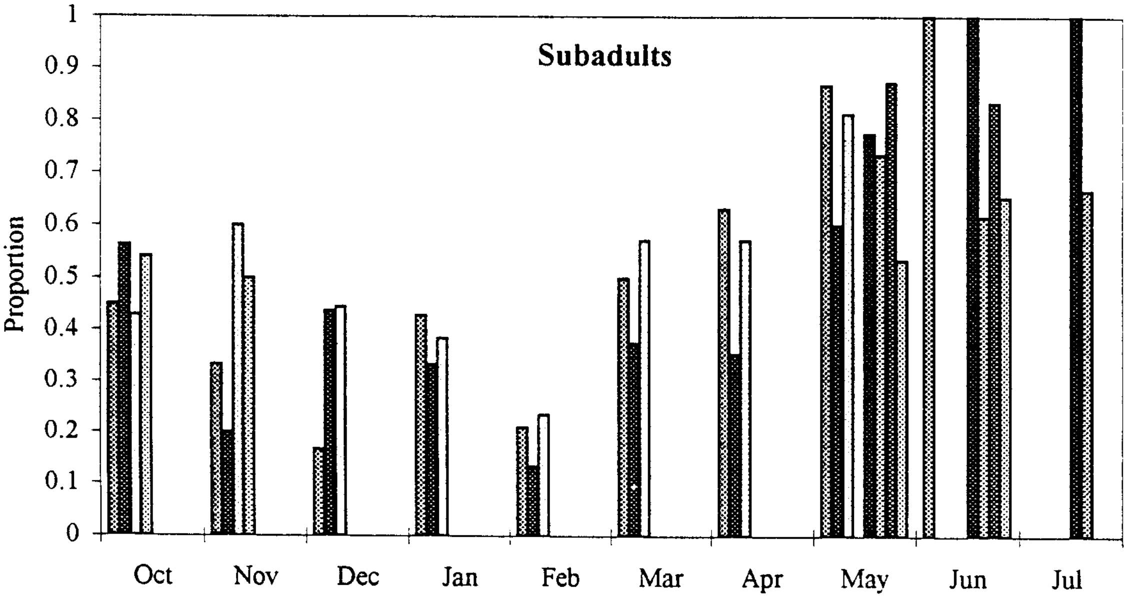


Figure 8. Change in maximum proportional use of haulouts over time for harbor seals in Prince William Sound, October 1995-July 1996.



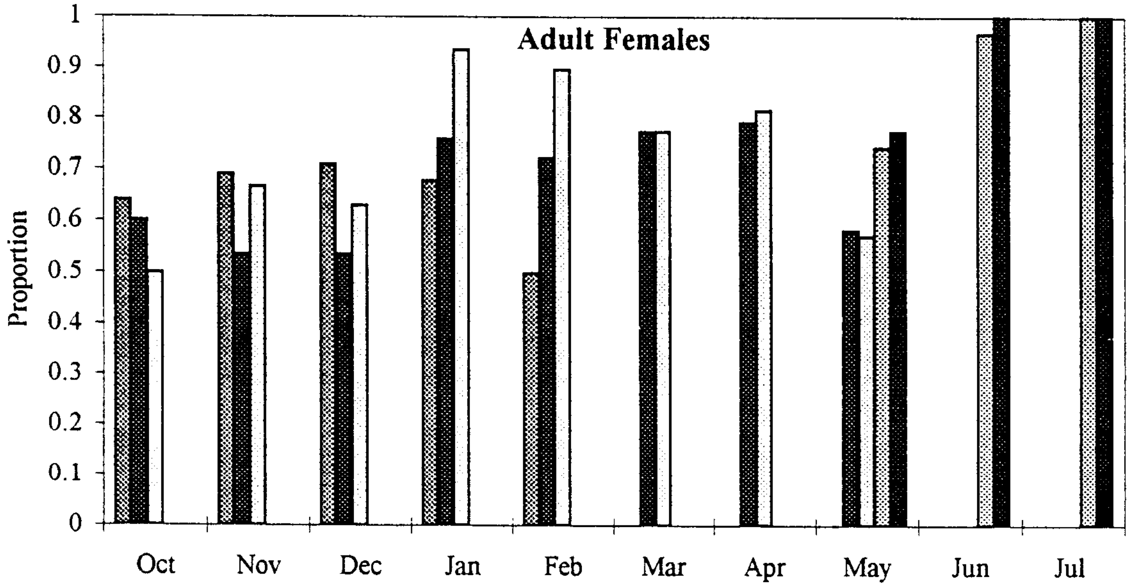


Figure 9. Percent of days hauled out each month, based on land-sea sensor data, for subadult and adult female harbor seals in Prince William Sound, September 1995-July 1996.

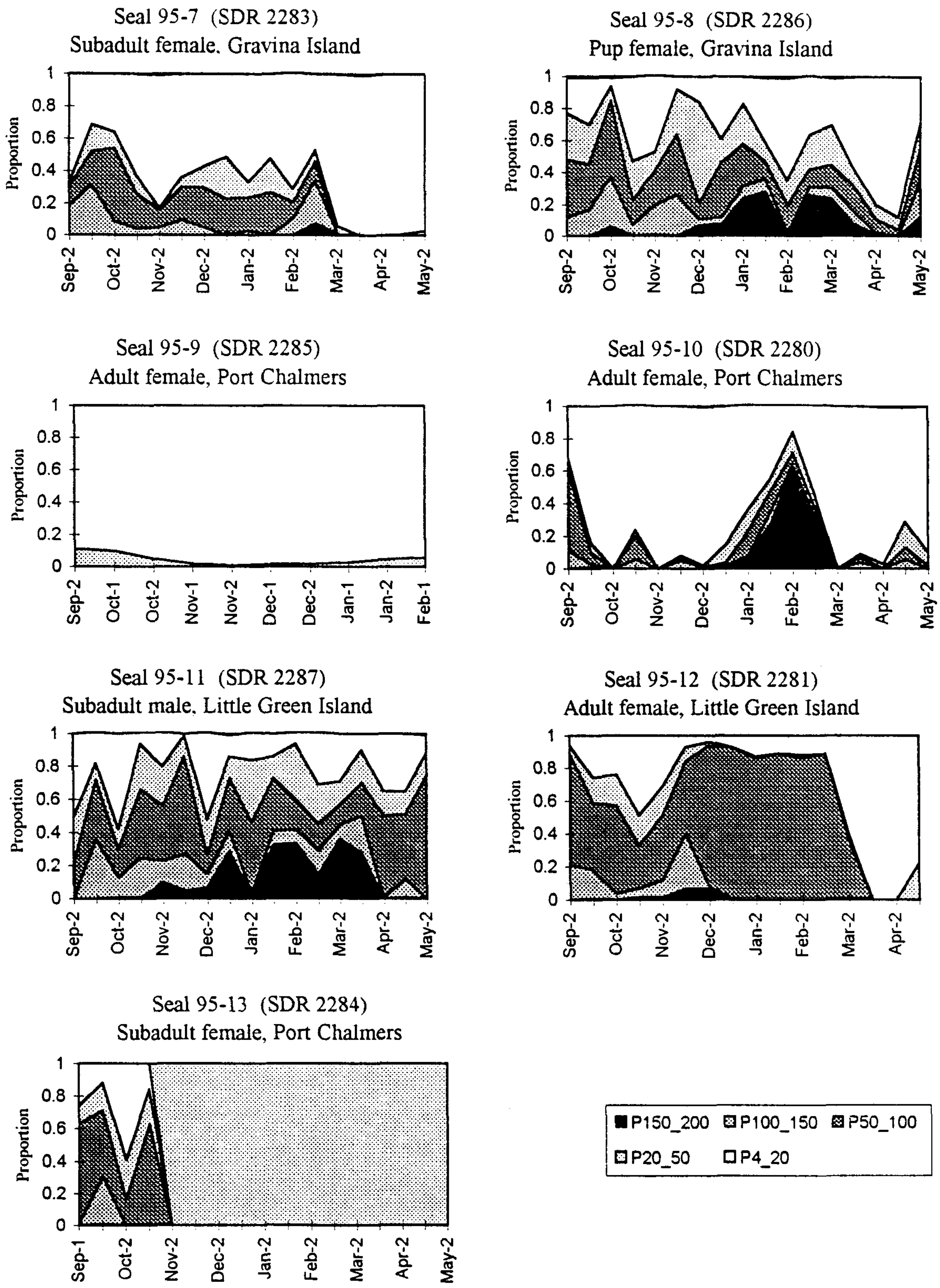
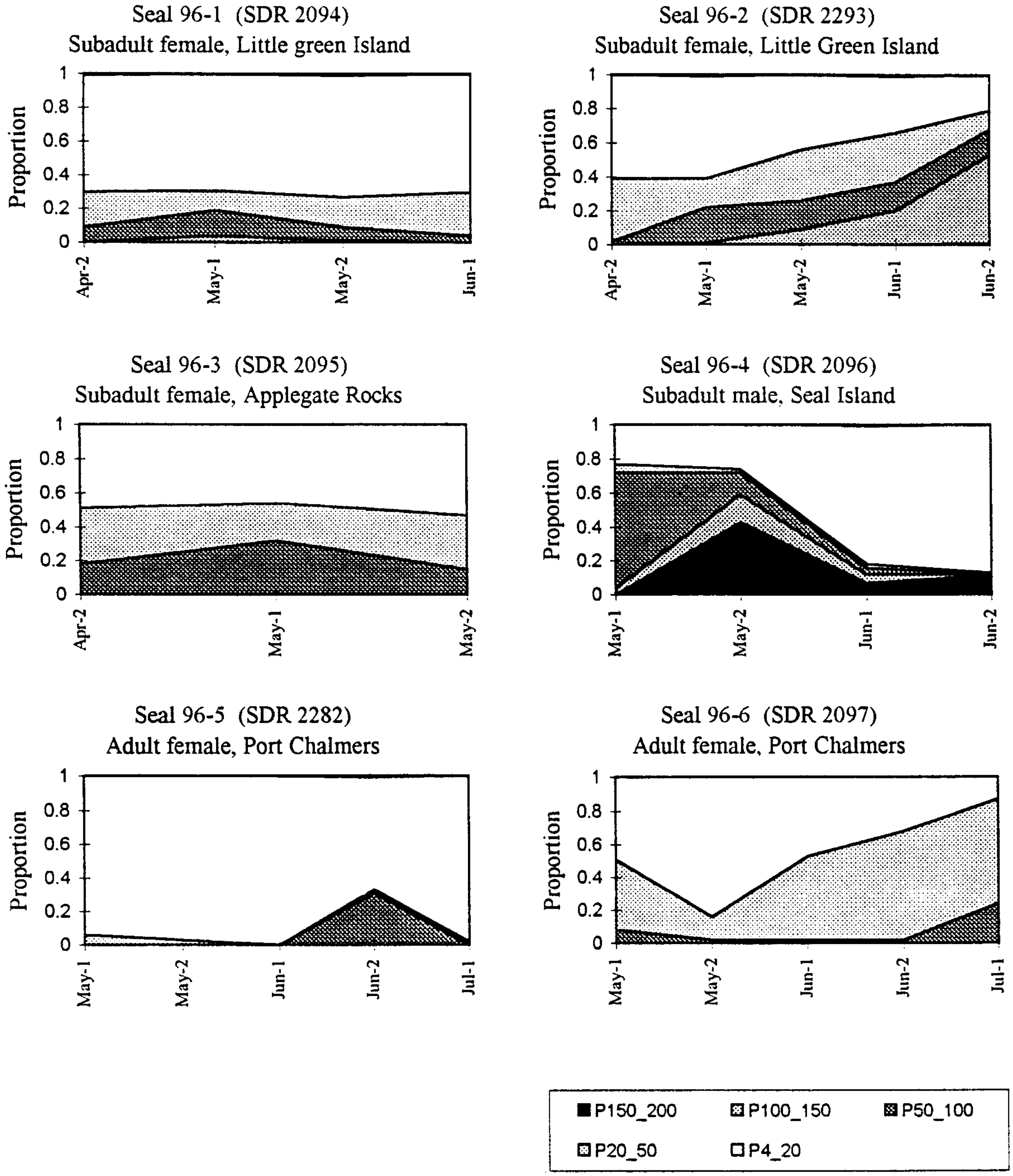


Figure 10. Monthly distribution of dives by depth (m) for seven satellite tagged harbor seals in Prince William Sound, September 1995-May 1996.


Seal 96-1 (SDR 2094)
Subadult female, Little green Island

Seal 96-2 (SDR 2293)
Subadult female, Little Green Island

Seal 96-3 (SDR 2095)
Subadult female, Applegate Rocks

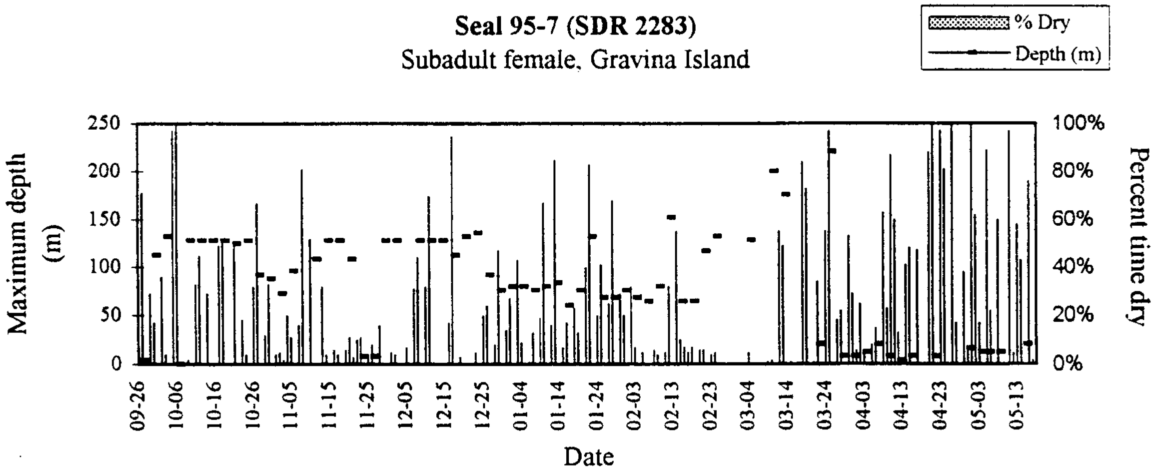
Seal 96-4 (SDR 2096)
Subadult male, Seal Island

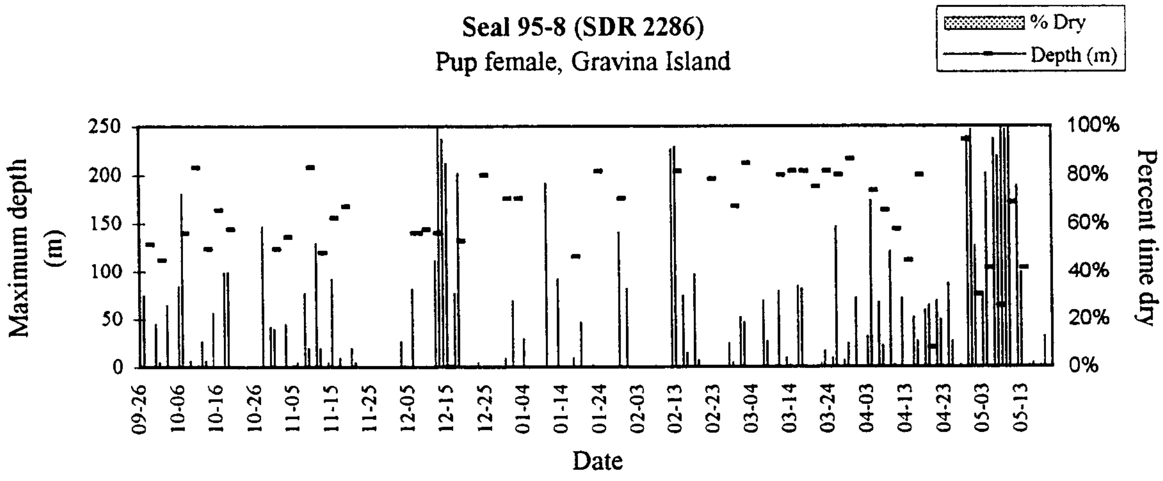
Seal 96-5 (SDR 2282)
Adult female, Port Chalmers

Seal 96-6 (SDR 2097)
Adult female, Port Chalmers

Figure 11. Monthly distribution of dives by depth (m) for six satellite tagged harbor seals in Prince William Sound, May-July 1996.

Maximum Depth of Dive and Percent Time Dry


Seal 95-7 (SDR 2283)
Subadult female, Gravina Island


Seal 95-8 (SDR 2286)
Pup female, Gravina Island

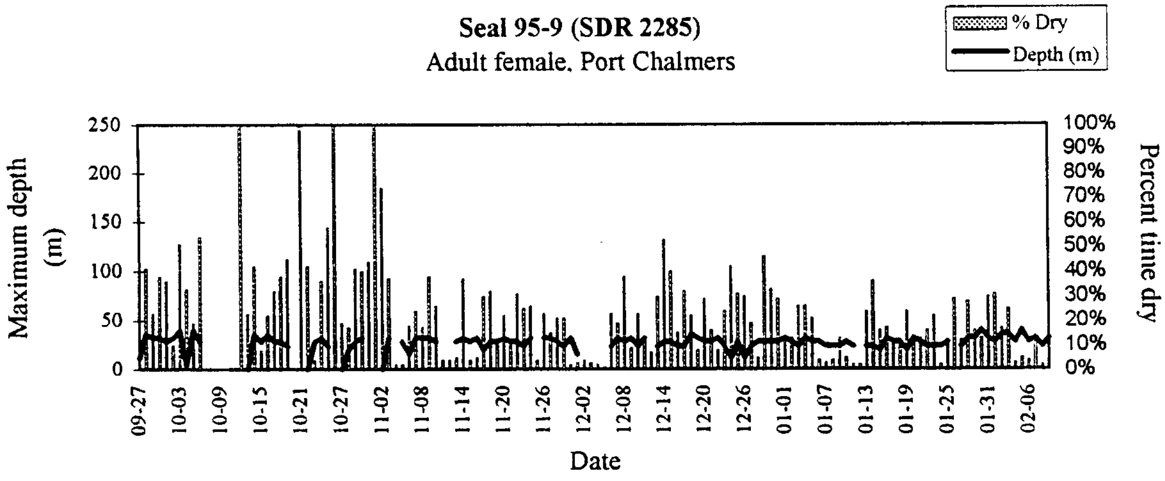
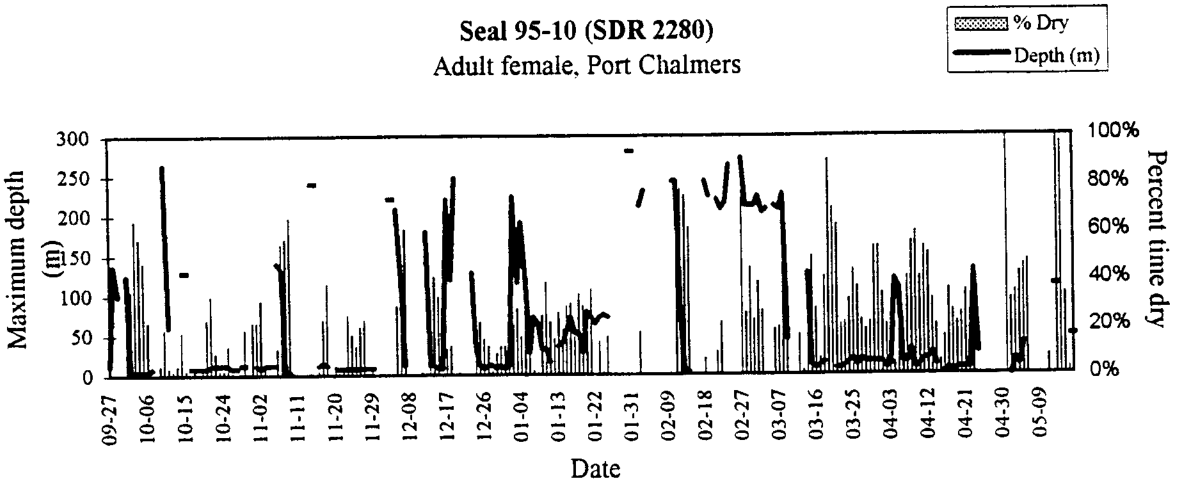
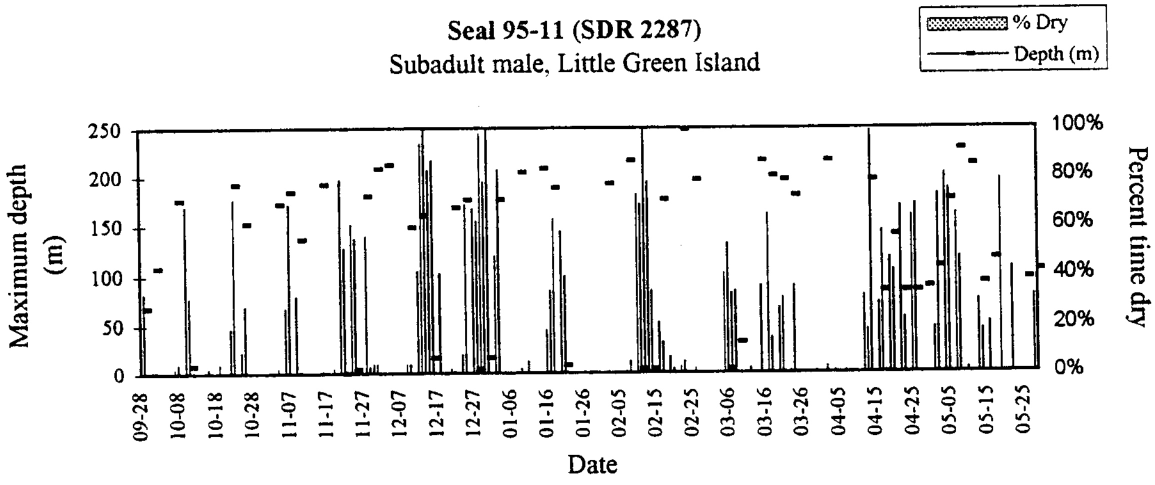

Seal 95-9 (SDR 2285)
Adult female, Port Chalmers

Figure 12. Maximum depth of dive and proportion of time spent dry for seven satellite tagged harbor seals in Prince William Sound, September 1995-May 1996.

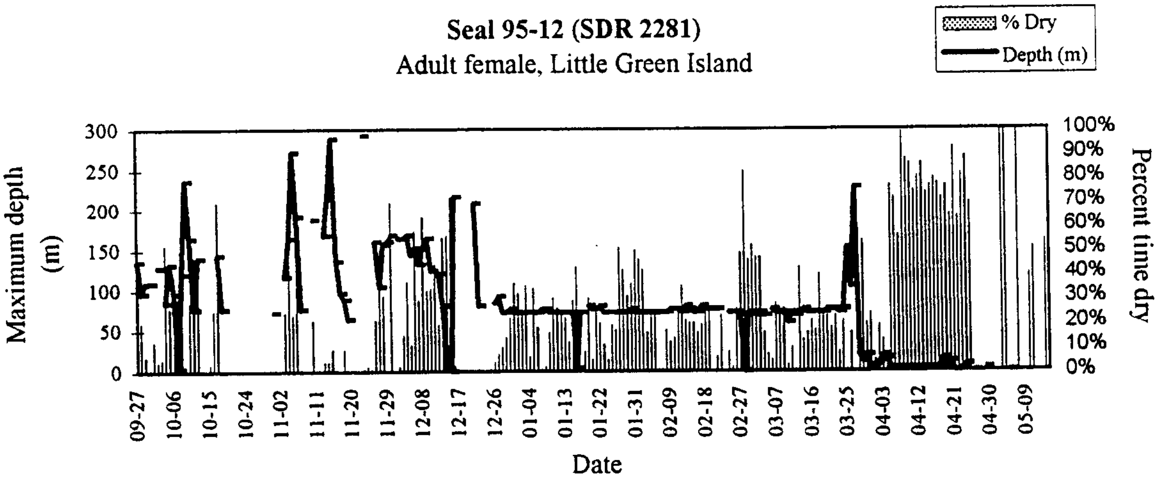
Maximum Depth of Dive and Percent Time Dry



Seal 95-10 (SDR 2280)
Adult female, Port Chalmers



Seal 95-11 (SDR 2287)
Subadult male, Little Green Island



Seal 95-12 (SDR 2281)
Adult female, Little Green Island

Figure 12. Continued.

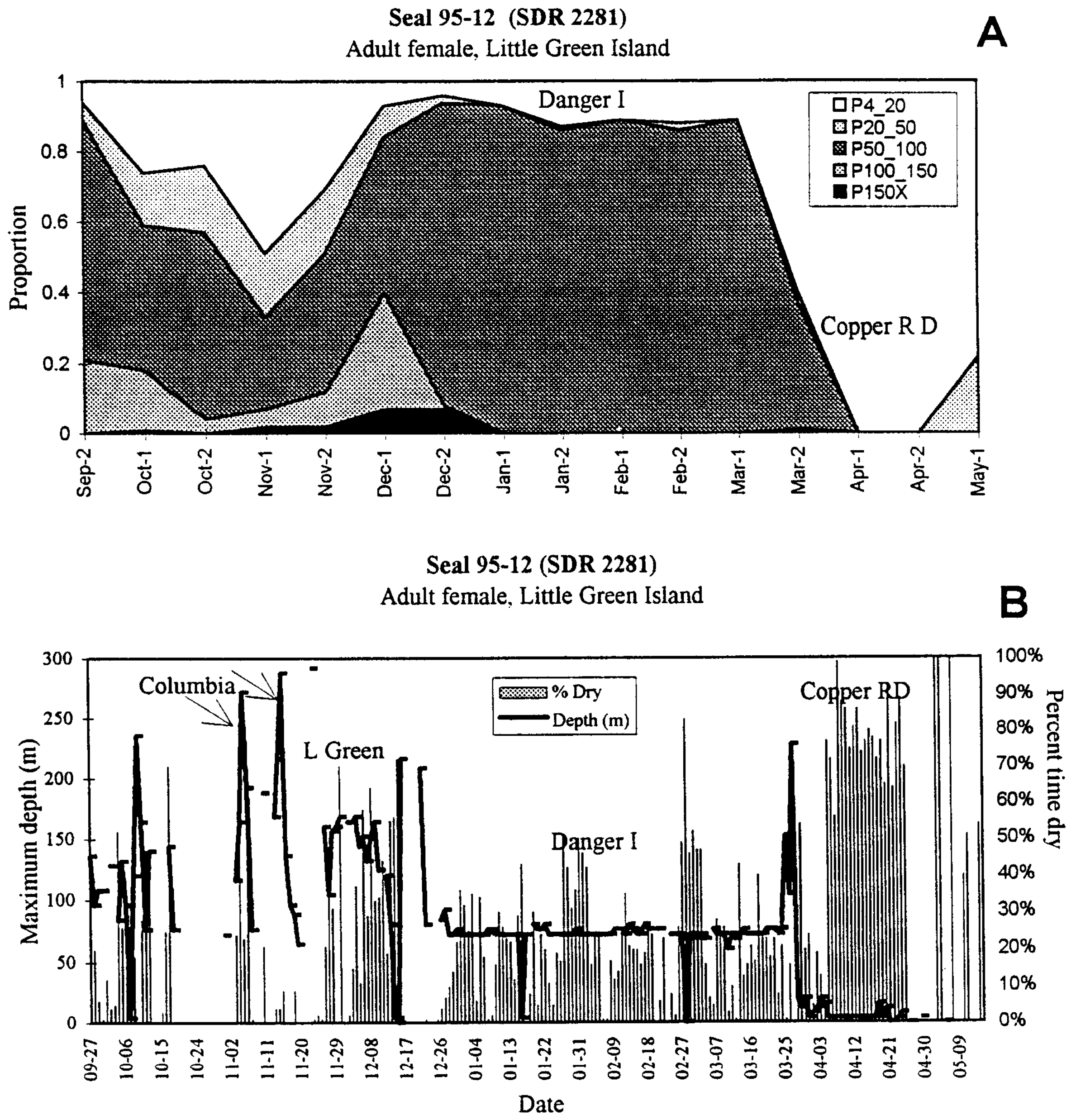


Figure 13. Monthly distribution of dives by depth (A) and maximum depth of dive and proportion of time spent dry (B) for seal 95-12, an adult female tagged in Prince William Sound, September 1995.

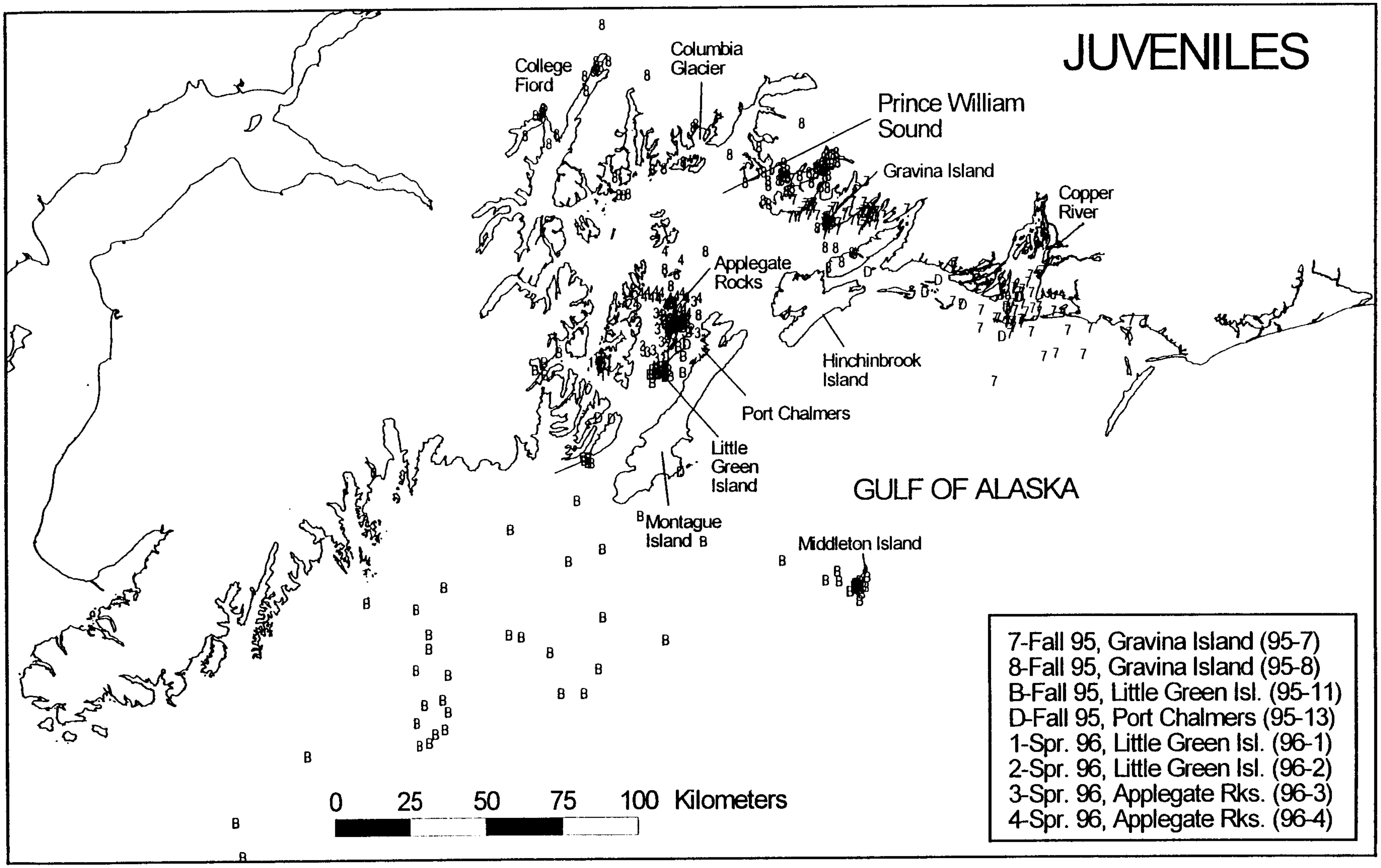


Figure 14. Map showing average daily locations of juvenile harbor seals that were satellite taggged in southern Prince William Sound, September 1995-July 1996.

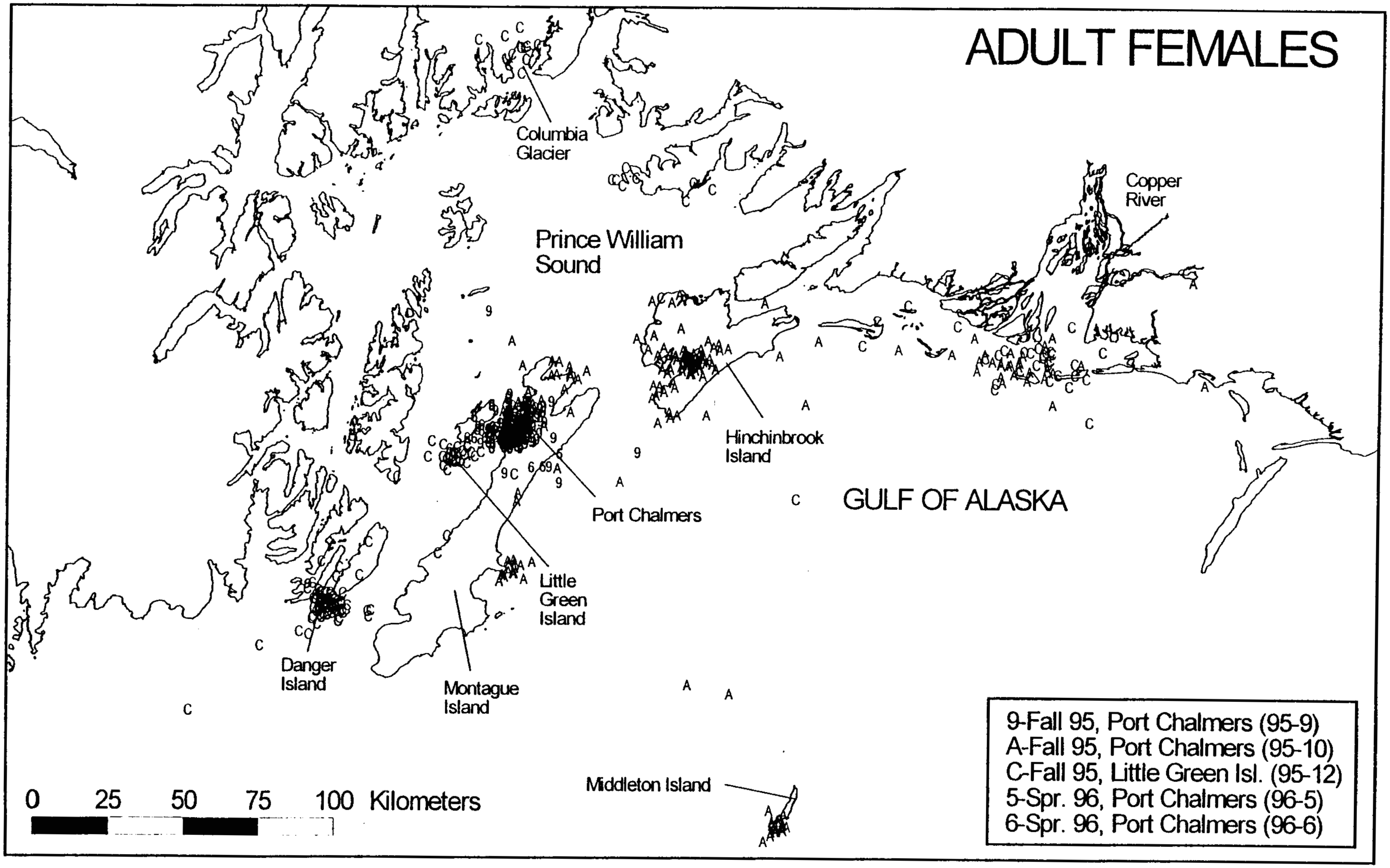


Figure 15. Map showing average daily locations of adult female harbor seals satellite tagged in eastern and western Prince William Sound, September 1995- July 1996.

Appendix A.

The Use of Fatty Acid Signatures to Investigate Foraging Ecology and Food Webs in Prince William Sound, Alaska: Harbor Seals and their Prey

Part of:
Monitoring, Habitat Use, and Trophic Interactions of Harbor Seals
in Prince William Sound, Alaska

Exxon Valdez Oil Spill
Restoration Study Number 96064
1997 Annual Report

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SUMMARY

In the present study, we report on part of a longer term research project to investigate both harbor seals and their prey in Prince William Sound (PWS) and the Gulf of Alaska (GOA) using fatty acid signature analysis. The primary goals of our current analyses were: to continue to build a library of prey species fatty acid signatures and with a stronger assessment of the influence of factors such as size-class, geographical location, season, and eventually year, on species signatures; to continue to build our sample of the harbor seal population both within areas of PWS as well as elsewhere in the GOA; to begin to assess whether harbor seals differ in diet according to age-class or sex; and to begin to assess whether there have been differences in the diets of harbor seals over a three year period. A total of 528 individual PWS prey representing 16 taxa [capelin, flathead sole, rex sole, unidentified flatfish sp., yellowfin sole, Pacific herring, octopus, Pacific cod, pink salmon (adults and smolts), walleye pollock, rainbow smelt, copper rockfish, sandlance, shrimp, squid, and tomcod] were analyzed for total fat content and fatty acid composition. Blubber from a total of 218 harbor seals from PWS and the GOA was sampled in 1994, 1995 and 1996, and analyzed for fatty acid composition. Prey species in PWS differed notably in fatty acid composition and were readily distinguished from one another. Additionally, not only could species such as herring, pollock, capelin, squid and tomcod be differentiated from one another using fatty acid signatures, but they could also be distinguished by size-class and location within PWS, depending on the species. Data suggest that size-class and location are the most important factors influencing differences in fatty acid composition within prey species. In contrast, fat content is strongly affected by season, with most species being highest in fat in the fall and lowest in fat after the wintering period, consistent with evidence feeding is reduce or ceased during the winter months. Data from harbor seal blubber fatty acid signatures, as well as from satellite telemetry data, suggest strongly that animals not only haul out site-specifically, but also forage and feed site-specifically. Within PWS over a spatial scale of about 80 km or even smaller, large differences were observed in fatty acid patterns of harbor seals indicating differences in feeding habits over small spatial scales. On a broader geographical scale of 400-800 km in the GOA, seals also differed in fatty acid signatures and thus in foraging. In addition to general differences among locations, there was a strong indication that diets of seals changed over the 3 years of study (especially in 1996) and that diets differ with demographic groups: i.e., diets differ between adult males, adult females, and subadults. Small forage fish species such as capelin and sandlance may be particularly important to juvenile seals, and may be an integral factor in the decline of some Alaskan pinniped populations. The ability to detect relationships between and within predators and prey on small spatial scales indicates that fatty acid signature analysis could begin to address such hypotheses.

INTRODUCTION

Marine mammals and seabirds are apex predators in ecosystems in which fishes and cephalopods are important prey. As such, a strong relationship would be expected between predator populations and fish stock abundances, a relationship that is likely influenced by factors such as commercial fisheries and ecosystem changes (e.g., Beddington, Beverton & Lavigne 1985; Springer 1993). In many parts of the world pinniped populations have increased as predicted after protection from over-exploitation (e.g., Olesiuk, Bigg & Ellis 1990; Shelton et al. 1995). However, large declines in populations of harbor seals (*Phoca vitulina richardsi*) and Steller sea lions (*Eumetopias jubatus*) have been documented in the Bering Sea and the Gulf of Alaska, especially Prince William Sound (PWS) (Pitcher 1990; Loughlin, Perlov & Vladimirov 1992). Likewise, since the 1970's numerous species of seabirds have also declined in PWS. These unanticipated declines have prompted monitoring and assessment of marine mammal, seabird, and fish population trends, and perhaps most importantly, have furthered the idea of using predators as samplers of forage fish abundances (Duffy 1996; Roseneau & Byrd 1996). The latter aspect may provide the most useful information towards addressing the question of "Is it food?", since the mean abundance of prey at large spatial scales, as determined from fisheries surveys, may not be relevant to the scale at which seals and seabirds forage (e.g., Duffy 1996; NRC 1996).

In PWS, harbor seals are one of the most abundant and widely distributed marine mammals, hauling out and/or breeding at more than 50 sites. Since 1984 harbor seal numbers in PWS have declined by about 60%, with only part of this decline attributable to the 1989 *Exxon Valdez* oil spill (Frost & Lowry 1994). The decline in harbor seals has not been limited to PWS, but has also occurred in adjacent parts of the Gulf of Alaska (Pitcher 1990). A change in the trophic structure of the ecosystem, and hence the availability of prey, is among the hypothesized causes for this observed decline, as well as that of other apex predators. Thus, understanding the diet of harbor seals and how they may depend on seasonal or area-specific concentrations of prey is not only needed in the management of harbor seals as a resource, but also as important indicators of other marine resources, namely forage fishes and other prey.

Unfortunately, methods of stomach content and fecal analysis, which are routinely used to determine diets in free-ranging pinnipeds, suffer from a number of inherent limitations and potential biases which may affect conclusions about the diets of a population (e.g., Jobling & Brieby 1986; Olesiuk 1993; Bowen & Harrison 1996). Due to the rapid passage of food from the gut, stomachs collected from killed seals are often empty (Harwood & Croxall 1988; Bowen, Lawson & Beck 1993), and those which contain food may yield biased information. For instance, cephalopod beaks may be retained for long periods in stomachs and hence result in an overestimation of their importance in the diet (Bigg & Fawcett 1985). In contrast, the heads of large fish may not be consumed, precluding otolith recovery in stomachs or scats. Fragile otoliths from small fish, such as herring, may be completely digested and hence underrepresented in scat hard parts. Lastly, collections of stomachs and feces are usually restricted to nearshore haul-out sites and hence may not represent what the population feeds upon offshore. Past studies of harbor seal diets in PWS and the Gulf of Alaska (GOA) have recognized these limitations (Pitcher 1980a and 1980b), nevertheless, the use of stomach content analysis may have biased conclusions towards an overestimation of octopus and an underestimation of herring.

Recently, the use of fatty acid signature analysis (Iverson 1993) has been advanced to study marine food webs and pinniped diets (Iverson 1995). Fatty acids are the largest constituent of lipids and those of carbon chain length 14 or greater are often deposited in animal tissue with minimal modification from diet. Lipids in the marine food web are exceptionally complex and diverse. Owing to various restrictions and specificities in the biosynthesis and modification of fatty acids among different taxonomic groups (e.g., Paradis & Ackman 1976; Ackman 1980; Cook 1985; Fraser et al. 1989), many components appear which can be traced to a general or even specific ecological origin. Certain "indicator" fatty acids (Iverson 1993) exist which are particularly useful in food web studies since they can arise only or mostly from the diet. In seals, ingested fatty acids appear to be deposited directly into adipose tissue, such that blubber may be a mirror of diet when a seals is rapidly fattening on a high fat diet (Iverson et al. 1995), or may reflect an integration of diet over a period of time when not rapidly fattening (Kirsch, Iverson & Bowen 1995). By sampling a core of blubber from a free-ranging seal, one may relatively non-invasively obtain information about diet that is not dependent on prey with hard parts, nor limited to nearshore influences. Similarly, these patterns extend to fish as predators, in that body lipids strongly reflect the influences of their dietary lipids (Kirsch et al., in review).

Although methods of fatty acid signature analysis are still being developed, the technique has been used both to identify general trophic level of diets and to detect major and minor shifts in diet within populations (Iverson, Arnould & Boyd 1997; Smith, Iverson & Bowen 1997). Of the two most comprehensive ecosystem studies which have ever been conducted in this area (Iverson, Frost & Lowry 1997; Iverson, Bowen & Ackman, unpublished data), work in the Gulf of Alaska and funded by the Trustee Council has come the farthest in advancing the development of this method. In the first 1.5 years of study in PWS [Frost et al. 1996: (Iverson & Frost Appendix)], fatty acid signatures indicated that fine-scale structure of foraging distribution of harbor seals could be discerned, and that this was likely due not only to localized feeding patterns in seals, but also to specific differences in prey species with size and location or habitat within PWS (Iverson, Frost & Lowry 1997).

In the present study, we report on part of a longer term research project to investigate both harbor seals and their prey in PWS and the Gulf of Alaska using fatty acid signature analysis. These analyses of harbor seals and prey species in PWS and the GOA are continuing and therefore some of the results presented in this report are preliminary; this report includes all data analyzed from our previous 1996 report (1994-1995: prey, n = 163; seals, n = 84) as well as that analyzed since. The primary goals of our present analyses were:
1) to continue to build a library of prey species fatty acid signatures and with a stronger assessment of the influence of factors such as size-class, geographical location, season, and eventually year, on species signatures; 2) to continue to build our sample of the harbor seal population both within areas of PWS as well as elsewhere in the GOA; 3) to begin to assess whether harbor seals differ in diet according to age-class or sex; and 4) to begin to assess whether there have been differences in the diets of harbor seals over a three year period. Our ultimate goal is to link the prey species to observed differences in seal fatty acids and to determine percentage species composition of seal diets. However, at the current stage in this research, our last aim was to infer possible influences and general importance of various prey species in overall diets of seals, with the aim of future modeling efforts to carry these interpretations further.

METHODS

Sample Collection

Figure 1 depicts a map of PWS showing major locations of harbor seals and prey species sampled for this study, which should be referred to throughout this report. For the purpose of analyses, PWS locations were divided into regions as follows: central (C), northeast (NE), northwest (NW), southcentral (SC), southeast (SE), and southwest (SW) PWS (see Fig. 1). Prey species were collected from fishing trawls and as opportunity provided in PWS at various locations and seasons during 1994, 1995, and 1996 and stored frozen until analysis. A total of 528 individual prey representing 16 taxa [capelin, flathead sole, rex sole, unidentified flatfish sp., yellowfin sole, Pacific herring, octopus, Pacific cod, pink salmon (adults and smolts), walleye pollock, rainbow smelt, copper rockfish, sandlance, shrimp, squid, and tomcod] were analyzed for total fat content and fatty acid composition for the present report. The most detailed sampling, by region within PWS and over size classes, still remained for herring (n = 153) and pollock (n = 142), however reasonably large samples sizes are becoming available for other species such as capelin, flatfish, pink salmon, sandlance, squid and tomcod.

Blubber from a total of 218 harbor seals was sampled in 1994, 1995 and 1996, and analyzed for fatty acid composition. Most of the seals were caught by entanglement in nets deployed near haulout sites. Blubber core samples were collected from the pelvic region of each seal using sterile 6 mm biopsy punches and immediately placed in chloroform containing BHT (butylated hydroxytoluene) as an antioxidant and stored frozen (-20°C) until analysis. Blubber cores (5-7 cm) were consistently taken through the full depth of the blubber layer, excluding that directly nearest (0.3 cm) to the skin; these deeper areas comprise all the metabolically active sites where deposition of fatty acids occur during periods of fattening (Koopman, Iverson & Gaskin 1996; Iverson unpublished data). Some blubber samples were also obtained from Alaska Native subsistence hunters in PWS as part of a biosampling program designed to make specimen material from harvested seals available to researchers. Blubber samples obtained in this manner were frozen in airtight plastic bags until they could be shipped to a laboratory where they were placed in chloroform/BHT and frozen. Seals were sampled in PWS (n = 152) which was further divided into the same general locations as prey collections (see above and Fig. 1), and from other areas of the GOA: at Kodiak Island (n = 18 from Uganik Passage), in Southeast Alaska (SEA, n = 37) from areas of Stephen's Passage, Sitka, and Peril Straight, and from Yakutat (n = 11). Not all areas were sampled in all years, precluding some direct comparisons.

Sample Analysis

After recording length and mass of each whole prey, each was ground individually and lipids were quantitatively extracted in duplicate aliquots using a modified Bligh & Dyer method (Bligh & Dyer 1959); fat content was expressed as an average of the two duplicates. In some cases when prey were too small to analyze separately, several or more individuals were combined for total fat content and fatty acid measurements; in these cases all group analyses were considered to be equal to a sample size of one (n = 1). Lipid was extracted from harbor seal blubber samples according to the method of Folch, Lees & Sloane-Stanley (1957) as modified by Iverson (1988; Smith et al. 1997).

Fatty acid methyl esters were prepared directly from 100 mg of the pure extracted lipid (filtered and dried over anhydrous sodium sulfate), using 1.5 ml 8% boron trifluoride in methanol (w/w) and 1.5 ml hexane, capped under nitrogen, and heated at 100°C for 1 hour. Fatty acid methyl esters were extracted into hexane, concentrated, and brought up to volume (50 mg/ml) with high purity hexane. This method of transesterification, as employed in our lab with fresh reagents, was routinely tested and found to produce identical results to that using Hilditch reagent (0.5 N H_2SO_4 in methanol).

Duplicate analyses of fatty acid methyl esters were performed on samples using temperature-programmed gas liquid chromatography according to Iverson (1988) and Iverson, Sampugna & Oftedal (1992), on a Perkin Elmer Autosystem II Capillary FID gas chromatograph fitted with a 30m x 0.25 mm id. column coated with 50% cyanopropyl polysiloxane (0.25µ film thickness; J&W DB-23; Folsom, CA) and linked to a computerized integration system (Turbochrom 4 software, PE Nelson). Identifications of fatty acids and isomers were determined from the following sources: known standard mixtures (Nu Check Prep., Elysian, MN), silver-nitrate (argentation) chromatography (Iverson 1988), and several secondary external reference standard mixtures composed of natural mixtures of fatty acids from several fish and seal oils which had been identified by chemical degradative and spectroscopic procedures including hydrogenation and GC-mass spectrometry performed in the laboratory of R. G. Ackman (Iverson et al. 1997). Individual fatty acids are expressed as weight percent of total fatty acids after employing mass response factors relative to 18:0. Theoretical relative response factors were used for this purpose, with minor adjustments made after tests with accurate quantitative standard mixtures (Nu Check Prep., Elysian, MN). GC columns were kept in good condition throughout the study by changing septa daily, cleaning the injector liner regularly, and by use of a guard column. All sample chromatograms and identifications were individually checked daily and freshly made quantitative standard mixtures were rerun several times weekly to determine any column deterioration or re-programming of GC necessary. Fatty acids are expressed as weight percent of total fatty acids and are designated by shorthand IUPAC nomenclature of carbon chain length:number of double bonds and location (n-x) of the double bond nearest the terminal methyl group.

Data analysis and interpretation

Fat content and fatty acid data were analyzed using both analysis of variance (ANOVA) and methods of classification and regression trees (CART) in S-plus according to methods described in Iverson et al. (1997) and Smith, et al. (1997). In overview, CART uses an algorithm which automatically selects the "best" variable to split data into two named groups ("nodes") that are as different as possible. The deviance of a node is then a measure of the homogeneity of the observations which fall into each side of that node. The CART algorithm begins at the root node by considering all possible ways to split the data, i.e. all variables (fatty acids) and all possible splitting points within each variable, and chooses that split which maximizes the difference at that node. The observations (seals or prey) in that split are then sent down one of two branches. This splitting is continued in a tree-like form and occurs until one of two stopping criteria (based on a minimum number of observations in a node or a minimum deviance of a node relative to the root node) is met. Tree growth (splitting) ends at a terminal node where a classification is made and the associated misclassification rate (number of observations not correctly classified in the node) is given. A restriction on CART analyses is that group sizes less than 4 cannot be classified, thus groups with sample sizes of 3 or less were excluded from any of the CART analyses.

Since the fatty acids and splitting points in the tree are selected algorithmically by maximizing the change in deviance between the root node and subsequent nodes, we also examined which, if any, other fatty acids might have been nearly as close to being selected using charts of deviances. We then forced the algorithm to select specific major fatty acids known to be indicative of diet differences for the split and compared these to the original tree. However, because of the extent and complexity of the present data set, in general only the final classification trees are presented and discussed in this report. Application of the SPLUS software is described in Clark & Pregibon (1992) and Venables & Ripley (1994).

All data are presented as mean ± SEM, unless otherwise indicated.

RESULTS

Prey Species - Fat Content

Collection, morphometric measurement, and fat content data for prey species collected and analyzed in PWS are summarized in Table 1. Because several species analyzed occurred over a large size range and differences with size were expected (Iverson et al. 1997), several within-species size classes were created: the length distributions available for herring and pollock were divided into three: for herring, small, medium, and large corresponded to lengths of 8.0-14.0 cm, 14.1-20.1 cm, and 20.2-27.0 cm, respectively; for pollock, small, medium, and large corresponded to lengths of 5.0-11.9 cm, 12.0-18.9 cm, and 19.0-25.9 cm, respectively. Squid and tomcod were divided into two size classes of small and large each (Table 1).

Herring had the highest fat content of any species analyzed (7.4%), but this ranged widely (0.6 - 19.1%). The fat content of most other species averaged 5% or less. Flatfish species (other than yellowfin sole) and pink salmon smolt had the lowest fat contents at generally less than 1%. Within species, fat content appeared to vary mostly with season, but possibly also size. Confounding of collection distributions (i.e. all one size class from one season) precluded strict analysis of this in most species, however, in herring and pollock several trends were apparent (Fig. 2). In both herring and pollock, fat content was lowest in the spring (March, April, May) and highest in the fall (Sept., Oct., Nov., $P < 0.0001$) with moderate trends during summer months (June, July, Aug.). Larger size classes tended to be significantly higher in fat in the fall than smaller size classes in the fall: for instance medium and large herring averaged 10.0 and 9.5% fat, respectively, while small herring averaged 3.2% fat in the fall ($P < 0.0001$). The single exception to both of the above trends were animals from the NW areas in any season. In both herring and pollock, individuals from the NW were consistently high in fat content regardless of season or size class. This can be clearly seen in pollock, where all individuals sampled in spring were from the NW and averaged 4.2% fat (Fig. 2).

In other species for which data could be tested by season, the same trends were apparent. Capelin was significantly higher in fat in the fall (2.4± 0.44%) versus the spring (1.1 ± 0.09%) except for the only two individuals from the NW, which were collected in spring and were particularly high in fat at 2.9%. Sandlance (2.8% vs. 1.2%), squid (2.2% vs. 1.3%) and tomcod (1.1% vs. 0.9%) all appeared to be higher in fat in fall than in spring or summer, respectively, but these conclusions were somewhat confounded by separate size classes from separate seasons and regions.

Prey Species - Fatty Acids

Approximately 70 fatty acids and isomers were routinely identified in all prey species (Table 2). Two additional components were formed from the ratio of two sets of important isomers as suggested by Iverson et al. (1997): ratio of 20:1n-11 to 20:1n-9 (R20:1) and ratio of 22:1n-11 to 22:1n-9 (R22:1). Differences between prey species in many components were apparent and are illustrated by several of the important indicator/dietary fatty acids and these ratios (Fig. 3). For instance, capelin, yellowfin sole, large herring and pollock, and sandlance were all notable for high yet differing levels of the monounstaurates 20:1n-11 and 22:1n -11 and their ratios, whereas pink salmon smolt were most notable for high levels of 22:6n-3. In general, yellowfin sole differed greatly from all other flatfish in most of the indicator fatty acids presented. Indeed, despite variations within species (see below), differences between prey species were readily distinguished using CART analysis, which compares all 70 fatty acids simultaneously across all species of prey (excluding prey with sample sizes less than 4). Using the algorithmically chosen variable 22:5n-3, the resulting classification tree correctly identified 93.1% of all prey species in PWS by their fatty acid signatures (Fig. 4). Despite apparent differences among the flatfish species (Fig. 3 and above), all flatfish (including yellowfin sole) traveled down the right node of the tree and only 3 out of 50 were misclassified. Adult salmon and smolt salmon, though quite different in some respects (Fig. 3), initially traveled together and later were correctly separated. Squid were also readily separated. In general capelin, herring, pollock, sandlance and tomcod required more splits and fatty acids in order to be correctly classified and appeared at several points, mostly on the right-hand side of the tree (Fig. 4).

As stated previously, differences were expected among size classes of species and hence for herring, pollock, squid and tomcod, several size classes were distinguished (see Table 1). When these were included in the CART analysis a largely correct, but more complex tree was grown (Fig. 5). Only the final classifications and at the appropriate rank in the tree are presented for ease of viewing. In this case, a slightly lower classification rate resulted (88.8%), however, size classes could be distinguished between large and small tomcod (87.5%), large and small squid (85.7%), and among large, medium and small herring (89.5%) and pollock (88.0%), respectively (Fig. 5). It should be noted, however, that these size classes were not necessarily represented across all areas of PWS and groups could be confounded by location - perhaps resulting in some of the misclassifications between size classes. As an illustration of this, two indicator fatty acids can be compared in herring and pollock across size-classes and different locations within PWS (Fig. 6). Although the trend for larger herring and larger pollock to be distinguished from smaller herring and pollock is apparent, a notable exception were individuals of both herring and pollock from NW PWS. In NW animals, small individuals as well as large were all high in the fatty acids 20:1n-11 and 22:1n-11, components which are usually directly related to larger sizes (e.g., Iverson et al. 1997). This can also be illustrated by showing the individual relationship between body length (size) and level of 20:1n-11 in herring with location (Fig. 7a). While all individuals demonstrated a curvilinear increase in this component with size regardless of location ($P < 0.0001$), NW individuals deviated significantly from this relationship. The same (Fig. 7a) was true for pollock, with NW individuals deviating from the general pattern.

Hence, while size was an important factor, so also appeared to be collection location. CART analysis of both herring and pollock samples by location and size class confirmed these findings. In herring and pollock, 88.1% and 86.7%, respectively, could be correctly classified to size-class and location using fatty acid signatures (Figs. 8 and 9). Although only the full herring tree is presented (Fig. 8), the pollock tree (summarized in Fig. 9) is actually far less complex, with all NW animals (small, medium and large) traveling down the right hand node, all other small size-class individuals traveling down the left hand node, and the rest (medium and large) traveling down an internal middle node.

Seasonal data was not able to be tested across all locations or within many species, however, herring from SC and SE PWS ($n = 133$) could be investigated (Fig. 7b). Season appeared to have little or no influence on fatty acid content once body size and location were taken into account. Thus, given this finding and a lack of further unconfounded data to date, season was not assumed to influence fatty acid signatures greatly, although this will need to be further tested. Differences among years is not yet able to be tested for similar reasons. Other species for which data could be subjected to CART analysis were capelin and flatfish. Capelin could be differentiated correctly (98.3%) by location (Fig. 10). Although these location differences were also confounded by season, this may not be an issue other than for total fat content (see above). Flatfish were also readily distinguished (89.6%) by species using fatty acid signatures (Fig. 11). Unfortunately, species groups are currently confounded by single locations, so location differences vs. species differences could not yet be tested.

In summary, although within species differences were apparent and usually predictable with both size class and collection location (Figs. 5-11), species could still be readily differentiated from one another across species as a whole (Fig. 4) using fatty acid signatures.

Harbor Seal Fatty Acids

Table 3 summarizes the collection data for blubber samples from harbor seals in areas of PWS as well as the GOA. Additionally, data on age-class and sex were available for most animals sampled. In some cases where age-class was not noted but measurements were available, an equation using body length and mass was used to estimate age-class. A summary of these demographic groups is also presented in Table 3. Where possible, differences between locations, years, and age groups were tested, although again not all age groups were available from all locations and all locations were not available from all years.

The same approximately 70 fatty acids and isomers found in PWS prey were routinely identified in all harbor seal blubber samples (Table 4). The largest sample size of individuals was available from SC-PWS (n = 97), and thus data were divided into demographic groups for illustration. Variations between groups of seals by location alone were apparent, as well as among demographic groups in SC-PWS, especially in indicator fatty acids (generally those starting with 20:1n-11, Table 4).

Differences among locations can be tested using CART which compares all 70 fatty acids. The results of CART analyses confirmed the observations of differences between general locations both within PWS as well as elsewhere in the GOA (Fig. 12). The ratio of 20:1n-11/n-9 was algorithmically selected by CART for the initial separation and classified 89% of seals to their general location using their blubber fatty acid signatures. Kodiak animals tended to misclassified by location alone more frequently than other groups, perhaps reflecting the similarity in diet between these individuals and those in SC-PWS (see Iverson et al. 1997). This CART analysis tested only for differences among locations, without consideration of any other factors such as year or age-class. Within PWS, on a slightly finer-scale designation of locations, CART classified individuals to location with 91% accuracy, again using the ratio of 20:1n-11/n-9 (not presented). Within other areas of the GOA alone, and again on slightly finer-scale designation of locations within SEA, CART correctly identified 89.4% of seals to location using fatty acids (Fig. 13). The results of these analyses indicated differences between seals within SEA among areas of Stephen's Passage, Sitka, and Peril Straight, although these may have reflected year influences as well (Peril Straight animals were all collected in 1996, while the others were collected in 1995). Ten of 11

Yakutat animals and 17 of 18 Kodiak animals were clearly distinguished from SEA animals (Fig. 13).

Again, the above analyses considered only location as the classifying variable. Seals were sampled across 3 years and differences could potentially occur in diets between years. Indeed, when the factor of year was incorporated along with general locations (in PWS and GOA), the result was a somewhat complex tree which classified seals by year and location with 85% accuracy (Fig. 14). Each year class was clearly separated from each other within the tree, suggesting that differences had occurred in seal diets over the 3 years of study. These changes can be illustrated using two important indicator fatty acids, 20:1n-11 and 22:1n-11, over the 3 years of study (Fig. 15). Some trends were apparent in that both 20:1n-11 and 22:1n-11 tended to increase in most areas of PWS from 1994 to 1996, especially in 1996. Indeed, ANOVA revealed significant year effects ($P < 0.0001$) between 1996 and the other two years. Since sampling across all years occurred only within PWS, these were analyzed separately (Fig. 16). Again, results of CART analysis suggested that dietary differences in seals were both a function of location within PWS and with year (Fig. 16).

Differences in diet could be assessed among animals within PWS as a function of age-class. Age-classes were divided into adult males, adult females (20 out of 28 known to be pregnant), subadults and pups. Across PWS as a whole, ANOVA revealed significant differences ($P = 0.01$ to < 0.0001) in many indicator fatty acids among these demographic groups. Yet clearly, different locations would also likely influence these results. This can be illustrated using several of the important indicator/dietary fatty acids and ratios among demographic groups by location within PWS (Fig. 17). NE and NW animals were excluded from analyses due to small sample sizes of groups. Within SC and SE PWS, location effects were found for 20:1n-11, ratio 20:1, and ratio 22:1 ($P < 0.0003$), while demographic group effects were found for 20:1n-11, ratio 20:1, ratio 22:1, 14:0 and 22:6n-3 ($P < 0.01$). Adult males almost always differed from adult females, and subadults differed from either adult males or adult females depending upon the fatty acid and the location (Fig. 17). CART analysis correctly distinguished between 85 and 91% of individuals by age group and location within PWS (not presented).

The findings of location differences in fatty acid signatures between individuals (i.e., diet differences by location), suggest that individual harbor seals tend to forage and feed fairly site-specifically. This can to some extent be tested using data from satellite-tagged seals (Frost et al. 1996). A number of harbor seals were satellite-tagged in PWS at the time of blubber sampling. Unfortunately, due to logistic constraints, these animals are tagged and followed after they are sampled for fatty acids, but if we assume that in general seals may behave similarly after tagging as they did before tagging, we can look at distribution of these animals during the year following tagging and compare to information from their fatty acid signatures. Since these animals ($n = 14$)

are all from the initial group of seals sampled in 1994 and 1995, only these are included in the CART trees. Not a single satellite-tagged animal was missclassified in any of the CART analyses (Figs. 18-20). On a large scale of PWS and GOA, all animals tagged in NW, E, or SC PWS remained at or near the original location of capture (Fig. 18). Only one left PWS for any period of time (94-1) and went to Yakutat. However, again, it is not known whether this individual behaved similarly prior to fatty acid sampling. On several finer-scale resolutions, these seals not only remained in the general region of initial capture in PWS (Fig. 19), but most remained close to the specific haul-out site at which they were tagged throughout the study period (Fig. 20). These results suggest that difference in fatty acid signatures of seals from different locations, reflect specific foraging in each location.

DISCUSSION

Prince William Sound is a large, complex estuarine system that also has characteristics of a small inland sea (Niebauer, Royer & Weingartner 1994). Localized habitats have differing depths (up to 700 m), temperatures, and salinities, and levels and patterns of glacial, fresh and saltwater input (Walters, Josberger & Driedger 1988; Niebauer et al. 1994) which are likely to result in different food web structures (e.g., Lalli & Parsons 1993). Since fatty acid signatures are significantly affected by spatial or temporal heterogeneity in habitats and food webs (Sargent et al. 1988; Iverson 1993; St. John & Lund 1996), analyses of fatty acids in harbor seals and their prey should provide an opportunity to study the spatial scales of foraging and habitat use. Our findings support the notion of differences in habitat use and foraging on small spatial scales in both harbor seals and their prey in PWS, and at larger spatial scales elsewhere in the Gulf of Alaska.

Prey species in PWS differed notably in fatty acid composition and continue to be readily separated from one another using CART (Fig. 4). Additionally, not only could herring and pollock be differentiated from one another using fatty acid signatures, but they could also be distinguished by size-class and location within PWS (Figs. 5-9). Other prey species such as capelin, squid and tomcod could also be identified by location or size class (Figs. 5 and 10). The finding that the fatty acid composition of species changes with body size indicates that the diets of these fish change with size and age. Indeed, fish such as pollock begin life feeding on small zooplankton, copepods eggs and nauplii, followed by larger zooplankton, and finally becoming piscivores as adults (Pereyra 1976; Frost & Lowry 1981; Lalli & Parsons 1993). Herring are thought to occupy lower trophic levels feeding mainly on zooplankton, but including small fishes as they get older (NRC 1996). Differences in fatty acid signatures in herring and pollock within size classes also suggested localized habitat and feeding differences of these species within areas of PWS. These conclusions about size/age and geographic differences in herring and pollock diets based on fatty acid analysis are supported by the results of extensive stomach content analysis of these species in PWS. Sturdevant (1996) found substantial differences in the diets of pollock and herring from northern and southern PWS, and between small and large fish. Sturdevant (1996) also found that the diet of small pollock was more like that of small herring than large herring, and that diets of larger pollock were more similar to that of large herring. The fact that within-species differences in fish fatty acid composition are apparent and directly related to diet has been demonstrated in captive or controlled feeding studies (studied and reviewed in Kirsch et al., in review). However despite this, prey are still able to be distinguished by species as a whole (this study; Kirsch et al. in review).

Although our data among seasons for all prey species are currently limited, data for herring suggests that size-class and location are the most important factors influencing differences in fatty acid composition (Fig. 7a,b). In contrast, fat content is strongly affected by season, with most species being highest in fat in the fall and lowest in fat after the wintering period (e.g., Fig. 2 and results). These findings are consistent with evidence that prey reduce or cease feeding during the winter months (e.g., Sturdevant 1996), resulting in a reduction of fat content. The fact that fatty acid composition does not appear to change as a consequence of this may support the notion that, even during poor feeding conditions, the original food web signature is retained in the existing lipid stores of the prey (Martin, Wright & Means 1984; St. John & Lund 1996). This will need to be further explored, but has important and favorable consequences for using fatty acid signature analysis. One result of such findings would be that given a fatty acid composition of an unknown herring or pollock or other species, one could essentially determine its size-class and location within the study area with reasonable certainty (e.g., Figs. 5-11). This could provide an important tool for studying foraging ecology and stock structure of fish species. Also, these prey characteristics should enhance the power of using fatty acids for examining foraging and feeding behavior in predators such as harbor seals within PWS, since they likely explain the different blubber fatty acid patterns of seals feeding in one area versus another.

A particularly unique pattern appears to occur in prey species located in NW PWS. Fatty acid signature trends with size-classes in NW PWS do not tend to fit with other areas (e.g., Fig 7a and results) and prey appear to be quite high in fat content at all times of year (e.g., Fig. 2 and results). These patterns would likely arise from differences in primary production in that area and need to be further explored.

Our data from harbor seal blubber fatty acid signatures, as well as from satellite telemetry data (Frost et al. 1996), suggests strongly that our initial conclusions were correct: that animals not only haul out site-specifically, but also forage and feed site-specifically. Within PWS over a spatial scale of about 80 km, the large differences observed in fatty acid patterns between harbor seals sampled in the SC, NE, NW, vs. SE areas indicate that these groups had different diets.

Seals differed in fatty acid signatures, and hence likely feeding habits, even within small areas, such as Port Fidalgo and Port Gravina (see Fig. 1) separated by about 25 km in eastern PWS, or over a finer scale of 9-15 km in various bays and islands around Montague Island. Our results suggest that seals sampled at a particular haulout location had foraged and fed nearby or at least on the same general prey sources. Misclassifications in the CART trees could represent those seals which were simply more wide-ranging in their foraging patterns or that had highly individual feeding habits. These conclusions are supported by data on movements of satellite-tagged seals (Figs. 18-20). Of 30 harbor seals tagged in PWS between 1992 and 1995, only five left PWS for any time, and most remained close to the specific location at which they were tagged throughout the study period (Frost et al. 1995, 1996). Overall, findings from fatty acid signature analysis and satellite telemetry suggest that harbor seals in PWS may depend on a very localized prey base.

Data on harbor seals have become increasingly available from other parts of Alaska, and fatty acid signature analysis also indicated differences in feeding on a broader geographical scale of 400-800 km in the GOA. Seals from other areas of the GOA (SEA, Yakutat and Kodiak) were distinguished from one another and from PWS animals (Fig.12), and within smaller areas of SEA (Fig. 13). Kodiak seals continued to share some characteristics with those from southern PWS, and some difficulty in separating them probably results from a more common diet.

In addition to general differences among locations, there was a strong indication that diets of seals changed over the 3 years of study (Fig. 14, 15). The most data is available for PWS seals and these data suggest that diets in 1996 had shifted from those in 1994 and 1995 (Figs. 15, 16 and results). Although available fisheries data are preliminary, there has been a suggestion that capelin may have increased substantially in 1996 (E. Brown, pers. comm.), which could well account for some of the changes observed. Lastly, evidence indicates that the diets of demographic groups of seals differ. Although not all age-classes are available from all areas, it is clear that the diets of adult males tend to differ from that of adult females and from subadults (e.g. Fig. 17). In the future, it will be important in the future to document diet differences among age-groups in the declining PWS harbor seal population, as well as differences which occur in the same age-groups but in areas where the population is stable. It will also be important to compare this information with data available from time periods of lesser declines (1970's and 1980's) since we can clearly detect year differences (e.g., Figs. 14-16). Juveniles in particular are thought to be significantly affected by reduced prey availability at relevant scales to the nutrition of individuals (NRC 1996). Thus, there could be several indications about stresses on juveniles through understanding diets. Small forage fish species such as capelin and sandlance have long been an important part of pinniped diets and a decline in these prey species may have affected the seal populations which depend upon them. If a reduction in these prey are apparent in the diets of adult seals in areas of decline, this would suggest a lower abundance of these prey in general. If indeed juveniles are found to be dependent on and limited to smaller size prey, this would coincide with the above finding. If juveniles are feeding on smaller but different prey than the small prey in adult diets, this might indicate competition with large animals for available food and further indication of low abundance of important forage fish species. Satellite data on pregnant females may help to shed light on the habits or possible limits to their foraging and why adult females appear to feed differently than adult males.

The eventual aim of fatty acid signature analysis will be to link specific prey species to observed differences in seals. Although the degree of complexity of the data at this point precludes simple comparisons as a means to assess direct prey species influences, an initial view of one or two components in seals and their prey illustrates some similarities (Fig. 21). The ratios of 20:1 and 22:1 can be used for this purpose, although it is reiterated that these are single-point comparisons and thus do not include all varying fatty acids. For simplicity, seals are not separated by region or year in this presentation, both of which are factors that may have a large impact. The ratio of 20:1n-11/n-9 suggests capelin may be an important component of the diet of both adults but especially juveniles. Larger sizes of herring and pollock, as well as yellowfin sole, could contribute similar influences in adults, however, it is unlikely that these sizes of prey would be consumed by juveniles. The ratio of 22:1n-11/n-9 in juveniles could be contributed strongly by capelin, sandlance and smaller size classes of herring, whereas in adult males and females levels could suggest a variety of prey species or sizes.

The use of fatty acids to elucidate diet and trophic relationships has proceeded considerably in its developmental stages and now, especially with the degree of complexity of the data, requires a mathematical modeling component in order to use it quantitatively. Using fatty acids to determine the diet of seals is facilitated by the fact that seals go through bi-annual periods of extensive blubber fat depletion followed by intensive fattening and that 2-4 prey species often account for most of the diet. Nevertheless, in free-ranging seals, fatty acid composition of lipid stores will rarely, if ever, match that of their prey because dietary fatty acids will be integrated into the seal's fatty acid signature. The time course of these changes will depend on the rate of food intake and the extent to which lipids are stored seasonally. Finally, biosynthesis of some fatty acids will take place, thus altering their representation in the signature. Thus, the next stage in using fatty acids to estimate diet composition, must be the development of a mathematical model which takes all possible prey species signatures and computes the most-likely mixture of signatures (species and levels) to create the closest signature (a maximum-likelihood estimate) to that of the predator and which includes an error component in the estimation. Such a statistical program must incorporate information on a wide range of potential prey signatures and the variability in these signatures with size-class and geographical location, as well as season if applicable. The mathematical model must also incorporate a relative weighting of prey signatures that reflects the proximate fat content of each prey and size-class, and finally, a weighting on individual fatty acids as a function of their ability to be biosynthesized by the predator.

Since harbor seals are likely to adjust their foraging patterns to changes in abundance of local prey (Olesiuk 1993; Tollit & Thompson 1996), this suggests that determining diets or changes in diets of harbor seals over time using fatty acid signatures may provide clues not only to changes in foraging patterns, but also to differences in local prey availability, predominant species size classes, and species abundance at the spatial and temporal scales that are essential to the nutrition of individual animals. It has been proposed that one cause for the decline in some Alaskan pinniped populations may have been a change in community structure over time that resulted in an ecosystem dominated by large predatory pollock, thus making small forage fish less available to pinnipeds, especially juveniles (NRC 1996). Thus, the ability to detect relationships between and within predators and prey on a small spatial scale indicates that fatty acid signature analysis could begin to address such hypotheses.

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Table 1. Collection Data and Fat Content of PWS Prey Species Analyzed (n = 528)

						LENGTH (cm)		MASS (g)		FAT CONTENT (%)	
Species		n	Locations	Years	Seasons	Mean ± SEM	range	Mean ± SEM	range	Mean ± SEM	range
Capelin		62	C,NE,NW,SC	1995	all	12.9 ± 0.13	8.6-14.4	13.9 ± 0.61	4.1-25.8	1.3 ± 0.10	0.5-4.2
Flatfish	FlatheadSole	14	NW,SC,SE	1995	Su,Fa	19.6 ± 0.82	15.5-26.2	63.4 ± 9.96	26.4-168.8	0.9 ± 0.07	0.6-1.4
Flatfish	RexSole	4	SE	1995	Fall	20.7 ± 0.85	18.9-23.0	46.0 ± 7.15	31.7-64.4	1.0 ± 0.13	0.7-1.4
Flatfish	unknown sp.	24	NE	1995	Fall	19.7 ± 0.57	15.6-26.2	61.8 ± 6.78	23.2-168.3	0.9 ± 0.08	0.4-1.6
Flatfish	YellowfinSole	8	SC	1994	Fall	28.6 ± 0.89	25.6-33.1	291.6 ± 32.03	188.1-436.8	3.2 ± 0.54	1.5-5.3
Herring	Large	52	SC,SE	1994-1996	all	22.3 ± 0.20	20.2-26.7	115.9 ± 4.56	62.7-208.0	5.5 ± 0.46	1.1-13.2
Herring	Medium	59	SC,SE	1994-1996	all	17.7 ± 0.22	14.5-20.1	58.0 ± 2.58	8.5-101.6	7.4 ± 0.55	1.7-19.1
Herring	Small	42	C,NE,NW,SC,SE	1994,1995	all	10.5 ± 0.22	8.4-13.9	9.7 ± 0.79	3.9-25.9	3.5 ± 0.25	0.6-10.7
Octopus		6	NE,SC	1994-1996	Su,Fa	47.6 ± 6.52	33.0-71.6	722.0 ± 290.51	159.1-1858.0	1.1 ± 0.10	0.8-1.5
PacificCod		10	SE	1994	Sum	19.3 ± 0.34	17.3-20.6	57.5 ± 6.32	42.2-109.2	2.3 ± 0.25	0.9-3.6
Pinksalmon	Adult	5	NE	1996	Sum	47.8 ± 0.48	46.7-49.4	1438.9 ± 90.42	1238.7-1776.2	2.4 ± 0.35	1.7-3.4
Pinksalmon	Smolt	20	C,NE	1996	Sum	8.3 ± 0.23	6.7-10.4	5.2 ± 0.40	2.5-8.6	0.7 ± 0.03	0.5-1.2
Pollock	Large	36	all	1995	Su,Fa	20.4 ± 0.20	19.0-24.5	64.0 ± 2.61	40.9-112.2	1.7 ± 0.11	0.7-3.6
Pollock	Medium	71	all	1995	all	16.4 ± 0.21	12.6-18.9	33.5 ± 1.04	14.1-52.8	2.0 ± 0.14	0.6-4.8
Pollock	Small	35	all	1994,1995	all	8.3 ± 0.41	5.2-11.3	4.5 ± 0.54	0.9-12.1	1.5 ± 0.17	0.6-4.5
RainbowSmelt		4	n/a	1994	n/a	20.5 ± 0.55	19.6-21.5	73.4 ± 14.21	52.1-108.4	2.5 ± 0.60	1.8-4.1
Rockfish		1	NE	1995	Fall	20.2		173.9		1.7	
Sandlance		21	C,SE	1994,1995	Sp,Su	11.3 ± 0.26	8.7-13.3	7.8 ± 0.53	1.8-11.4	2.2 ± 0.21	0.8-3.9
Shrimp		2*	SE	1994	Fall	n/a		n/a		1.6 ± 0.92	0.8-3.1
Squid	Large	8	SC	1994,1995	Fall	49.2 ± 4.81	28.4-72.8	148.7 ± 35.74	18.0-345.4	2.2 ± 0.29	1.0-3.2
Squid	Small	20	NW	1996	Spr	18.4 ± 0.68	13.5-25.4	31.4 ± 3.78	9.7-78.1	1.3 ± 0.05	1.0-1.7
Tomcod	Large	14	NE	1995,1996	Su,Fa	20.2 ± 0.90	16.2-29.1	70.2 ± 13.16	33.9-214.8	1.1 ± 0.09	0.7-1.8
Tomcod	Small	10	n/a	1996	Sum	8.8 ± 0.31	7.3-10.6	5.3 ± 0.74	2.3-10.8	0.6 ± 0.06	0.4-1.0

All values were derived from whole prey that were ground and analyzed individually. In cases where prey were too small to be analyzed separately, several individuals were combined for analysis and considered to be an n of 1. See Fig.1 for definition of locations (C, NE, NW, SC, SE, SW). Seasons included spring (Sp), summer (Su or Sum), and fall (Fa).

*Each sample consisted of 23 inidividual shrimp ground together.

Table 2. Fatty Acid Composition of PWS Prey Species

	Capelin	**Flatfish**			
		Flathead Sole	**Rex Sole**	**unknown sp.**	**Yellowfin Sole**
n	62	14	4	24	8
12:0	0.45 ± 0.050	0.00 ± 0.002	0.00 ± 0.000	0.01 ± 0.002	0.04 ± 0.003
13:0	0.01 ± 0.002	0.02 ± 0.002	0.03 ± 0.005	0.02 ± 0.002	0.03 ± 0.001
Iso14	0.02 ± 0.001	0.02 ± 0.006	0.02 ± 0.004	0.03 ± 0.003	0.03 ± 0.003
14:0	4.30 ± 0.326	2.17 ± 0.150	1.90 ± 0.234	2.17 ± 0.124	4.49 ± 0.246
14:1n-9	0.13 ± 0.013	0.14 ± 0.027	0.05 ± 0.029	0.24 ± 0.033	0.29 ± 0.022
14:1n-7	0.00 ± 0.001	0.03 ± 0.003	0.05 ± 0.008	0.03 ± 0.004	0.04 ± 0.004
14:1n-5	0.04 ± 0.005	0.05 ± 0.009	0.03 ± 0.009	0.03 ± 0.004	0.13 ± 0.013
Iso15	0.08 ± 0.008	0.13 ± 0.007	0.18 ± 0.025	0.11 ± 0.007	0.26 ± 0.020
Anti15	0.02 ± 0.003	0.04 ± 0.004	0.06 ± 0.014	0.04 ± 0.004	0.11 ± 0.013
15:0	0.21 ± 0.011	0.41 ± 0.021	0.70 ± 0.012	0.40 ± 0.019	0.53 ± 0.015
15:1n-8	0.00 ± 0.000	0.00 ± 0.002	0.01 ± 0.005	0.02 ± 0.006	0.01 ± 0.001
15:1n-6	0.00 ± 0.001	0.01 ± 0.002	0.01 ± 0.009	0.03 ± 0.005	0.02 ± 0.004
Iso16	0.20 ± 0.012	0.61 ± 0.028	0.74 ± 0.081	0.79 ± 0.039	0.17 ± 0.027
16:0	15.77 ± 0.256	15.43 ± 0.128	14.58 ± 0.330	14.98 ± 0.183	12.84 ± 0.424
16:1n-11	0.37 ± 0.015	0.51 ± 0.016	0.79 ± 0.035	0.44 ± 0.008	0.94 ± 0.043
16:1n-9	0.17 ± 0.030	0.35 ± 0.010	0.36 ± 0.022	0.37 ± 0.015	0.37 ± 0.016
16:1n-7	2.24 ± 0.162	4.90 ± 0.392	7.05 ± 2.039	5.11 ± 0.461	6.43 ± 0.438
7Me16:0	0.24 ± 0.010	0.35 ± 0.029	0.34 ± 0.010	0.30 ± 0.009	0.23 ± 0.034
16:1n-5	0.09 ± 0.005	0.29 ± 0.022	0.48 ± 0.036	0.23 ± 0.010	0.15 ± 0.008
16:2n-6	0.02 ± 0.004	0.02 ± 0.005	0.04 ± 0.021	0.03 ± 0.006	0.31 ± 0.023
Iso17	0.17 ± 0.026	0.19 ± 0.016	0.27 ± 0.037	0.15 ± 0.013	0.06 ± 0.009
16:2n-4	0.18 ± 0.013	0.17 ± 0.034	0.23 ± 0.106	0.23 ± 0.029	0.77 ± 0.036
16:3n-6	0.14 ± 0.006	0.37 ± 0.025	0.78 ± 0.067	0.40 ± 0.025	0.30 ± 0.020
17:0	0.13 ± 0.012	0.12 ± 0.026	0.10 ± 0.095	0.28 ± 0.023	0.31 ± 0.022
16:3n-4	0.16 ± 0.010	0.28 ± 0.045	0.19 ± 0.104	0.21 ± 0.036	0.18 ± 0.018
17:1	0.03 ± 0.007	0.18 ± 0.052	0.43 ± 0.034	0.31 ± 0.037	0.43 ± 0.025
16:3n-1	0.08 ± 0.004	0.14 ± 0.008	0.11 ± 0.015	0.11 ± 0.005	0.11 ± 0.003
16:4n-1	0.30 ± 0.031	0.49 ± 0.030	0.38 ± 0.046	0.72 ± 0.042	0.20 ± 0.027
18:0	2.72 ± 0.091	4.38 ± 0.179	5.07 ± 0.428	4.94 ± 0.155	2.75 ± 0.199
18:1n-13	0.02 ± 0.003	0.08 ± 0.016	0.41 ± 0.010	0.10 ± 0.018	0.16 ± 0.014
18:1n-11	0.59 ± 0.028	0.22 ± 0.034	0.16 ± 0.037	0.16 ± 0.012	0.62 ± 0.050
18:1n-9	6.74 ± 0.314	10.65 ± 0.266	6.28 ± 0.429	8.68 ± 0.287	11.25 ± 0.603
18:1n-7	2.24 ± 0.097	4.99 ± 0.223	5.93 ± 0.130	4.57 ± 0.173	3.63 ± 0.158
18:1n-5	0.53 ± 0.013	0.61 ± 0.050	0.43 ± 0.037	0.34 ± 0.016	0.56 ± 0.040
18:2d5,7	0.01 ± 0.002	0.03 ± 0.004	0.02 ± 0.002	0.02 ± 0.003	0.08 ± 0.024
18:2n-7	0.00 ± 0.001	0.02 ± 0.006	0.01 ± 0.009	0.00 ± 0.003	0.04 ± 0.004
18:2n-6	0.78 ± 0.029	0.77 ± 0.022	0.62 ± 0.038	0.77 ± 0.025	0.94 ± 0.028
18:2n-4	0.15 ± 0.004	0.12 ± 0.007	0.15 ± 0.019	0.14 ± 0.015	0.22 ± 0.015
18:3n-6	0.02 ± 0.003	0.10 ± 0.009	0.21 ± 0.011	0.13 ± 0.006	0.08 ± 0.007
18:3n-4	0.05 ± 0.002	0.08 ± 0.012	0.13 ± 0.042	0.10 ± 0.011	0.15 ± 0.009
18:3n-3	0.57 ± 0.044	0.42 ± 0.038	0.21 ± 0.029	0.26 ± 0.026	0.59 ± 0.035
18:3n-1	0.10 ± 0.004	0.15 ± 0.019	0.24 ± 0.034	0.23 ± 0.016	0.23 ± 0.010
18:4n-3	1.09 ± 0.122	0.72 ± 0.138	0.66 ± 0.300	0.78 ± 0.111	0.94 ± 0.066
18:4n-1	0.14 ± 0.007	0.03 ± 0.006	0.07 ± 0.023	0.04 ± 0.006	0.11 ± 0.005
20:0	0.13 ± 0.006	0.11 ± 0.004	0.17 ± 0.021	0.08 ± 0.003	0.14 ± 0.008

Table 2. Fatty Acid Composition of PWS Prey Species

	Capelin	**Flatfish**			
		Flathead Sole	**Rex Sole**	**unknown sp.**	**Yellowfin Sole**
20:1n-11	6.15 ± 0.513	1.26 ± 0.150	1.28 ± 0.120	1.30 ± 0.112	7.17 ± 0.761
20:1n-9	1.59 ± 0.100	1.20 ± 0.051	1.23 ± 0.150	1.08 ± 0.045	1.94 ± 0.103
R20:1	3.69 ± 0.154	1.04 ± 0.098	1.08 ± 0.157	1.27 ± 0.139	3.64 ± 0.252
20:1n-7	0.19 ± 0.013	0.72 ± 0.049	2.02 ± 0.040	1.07 ± 0.134	1.47 ± 0.098
20:1n-5	0.06 ± 0.004	0.10 ± 0.010	0.09 ± 0.004	0.06 ± 0.004	0.16 ± 0.007
20:2n-6	0.18 ± 0.006	0.29 ± 0.013	0.60 ± 0.044	0.20 ± 0.007	0.39 ± 0.012
20:3n-6	0.02 ± 0.002	0.06 ± 0.003	0.10 ± 0.003	0.08 ± 0.002	0.14 ± 0.043
20:4n-6	0.69 ± 0.062	3.54 ± 0.341	4.72 ± 0.822	5.05 ± 0.312	2.15 ± 0.196
20:3n-3	0.06 ± 0.004	0.12 ± 0.012	0.28 ± 0.026	0.08 ± 0.009	0.15 ± 0.009
20:4n-3	0.47 ± 0.018	0.37 ± 0.039	0.38 ± 0.065	0.32 ± 0.026	0.46 ± 0.023
20:5n-3	12.47 ± 0.343	12.56 ± 0.271	15.39 ± 0.399	12.14 ± 0.325	9.21 ± 0.398
22:1n-11	5.57 ± 0.578	0.83 ± 0.143	0.37 ± 0.083	0.62 ± 0.074	4.05 ± 0.532
22:1n-9	0.32 ± 0.024	0.23 ± 0.027	0.18 ± 0.029	0.15 ± 0.013	0.43 ± 0.029
R22:1	16.39 ± 0.947	3.71 ± 0.420	2.08 ± 0.245	4.53 ± 0.492	9.28 ± 0.863
22:1n-7	0.06 ± 0.005	0.17 ± 0.010	0.40 ± 0.036	0.17 ± 0.011	0.15 ± 0.026
22:2n-6	0.00 ± 0.001	0.04 ± 0.005	0.07 ± 0.019	0.09 ± 0.012	0.06 ± 0.006
21:5n-3	0.34 ± 0.007	0.23 ± 0.019	0.28 ± 0.054	0.22 ± 0.016	0.26 ± 0.050
22:4n-6	0.08 ± 0.007	0.33 ± 0.034	0.70 ± 0.039	0.47 ± 0.031	0.45 ± 0.040
22:5n-6	0.18 ± 0.008	0.45 ± 0.031	0.55 ± 0.031	0.57 ± 0.022	0.34 ± 0.024
22:4n-3	0.02 ± 0.002	0.05 ± 0.008	0.04 ± 0.006	0.09 ± 0.012	0.11 ± 0.008
22:5n-3	1.44 ± 0.045	2.51 ± 0.096	3.68 ± 0.185	2.48 ± 0.059	3.03 ± 0.164
22:6n-3	26.89 ± 0.966	22.53 ± 0.764	15.72 ± 1.049	22.68 ± 0.889	14.78 ± 0.815
24:1n-11	0.32 ± 0.022	0.11 ± 0.019	0.05 ± 0.053	0.17 ± 0.025	0.13 ± 0.013
24:1n-9	1.00 ± 0.031	0.82 ± 0.045	0.45 ± 0.075	1.02 ± 0.051	0.64 ± 0.033

Table 2. Fatty Acid Composition of PWS Prey Species

	Herring			**Octopus**	**PacificCod**
	Large	**Medium**	**Small**		
n	52	59	42	6	10
12:0	0.11 ± 0.016	0.08 ± 0.006	0.06 ± 0.005	0.04 ± 0.008	0.02 ± 0.002
13:0	0.02 ± 0.001	0.03 ± 0.001	0.04 ± 0.003	0.01 ± 0.004	0.01 ± 0.001
Iso14	0.02 ± 0.001	0.02 ± 0.001	0.03 ± 0.002	0.04 ± 0.006	0.01 ± 0.002
14:0	7.61 ± 0.158	6.71 ± 0.131	6.49 ± 0.375	1.55 ± 0.148	2.17 ± 0.249
14:1n-9	0.22 ± 0.006	0.31 ± 0.014	0.36 ± 0.019	0.12 ± 0.041	0.11 ± 0.022
14:1n-7	0.01 ± 0.001	0.02 ± 0.003	0.03 ± 0.004	0.02 ± 0.009	0.02 ± 0.002
14:1n-5	0.10 ± 0.003	0.09 ± 0.002	0.08 ± 0.005	0.06 ± 0.009	0.04 ± 0.005
Iso15	0.15 ± 0.004	0.20 ± 0.007	0.21 ± 0.015	0.09 ± 0.008	0.07 ± 0.005
Anti15	0.04 ± 0.002	0.07 ± 0.003	0.08 ± 0.007	0.05 ± 0.012	0.02 ± 0.002
15:0	0.27 ± 0.008	0.36 ± 0.010	0.51 ± 0.039	0.32 ± 0.048	0.27 ± 0.013
15:1n-8	0.01 ± 0.001	0.01 ± 0.001	0.01 ± 0.001	0.00 ± 0.003	0.00 ± 0.002
15:1n-6	0.01 ± 0.002	0.02 ± 0.004	0.01 ± 0.003	0.04 ± 0.022	0.01 ± 0.003
Iso16	0.05 ± 0.005	0.06 ± 0.003	0.11 ± 0.014	0.87 ± 0.124	0.21 ± 0.017
16:0	14.00 ± 0.274	17.43 ± 0.295	20.20 ± 0.363	15.16 ± 0.702	14.50 ± 0.461
16:1n-11	0.40 ± 0.017	0.49 ± 0.023	0.50 ± 0.025	0.42 ± 0.041	0.44 ± 0.018
16:1n-9	0.14 ± 0.005	0.17 ± 0.006	0.26 ± 0.018	0.18 ± 0.029	0.38 ± 0.036
16:1n-7	4.76 ± 0.188	5.82 ± 0.139	6.13 ± 0.255	2.53 ± 0.635	3.84 ± 0.220
7Me16:0	0.20 ± 0.014	0.27 ± 0.013	0.19 ± 0.016	0.20 ± 0.065	0.17 ± 0.021
16:1n-5	0.07 ± 0.008	0.10 ± 0.010	0.16 ± 0.016	0.33 ± 0.093	0.14 ± 0.013
16:2n-6	0.10 ± 0.006	0.11 ± 0.009	0.13 ± 0.010	0.11 ± 0.062	0.17 ± 0.013
Iso17	0.07 ± 0.010	0.22 ± 0.036	0.28 ± 0.058	0.12 ± 0.024	0.03 ± 0.008
16:2n-4	0.36 ± 0.030	0.26 ± 0.031	0.31 ± 0.030	0.10 ± 0.053	0.47 ± 0.042
16:3n-6	0.29 ± 0.030	0.27 ± 0.038	0.27 ± 0.039	0.07 ± 0.026	0.19 ± 0.032
17:0	0.13 ± 0.012	0.16 ± 0.009	0.15 ± 0.021	0.79 ± 0.110	0.22 ± 0.021
16:3n-4	0.30 ± 0.020	0.26 ± 0.020	0.25 ± 0.029	0.11 ± 0.039	0.11 ± 0.043
17:1	0.15 ± 0.011	0.17 ± 0.011	0.22 ± 0.027	0.09 ± 0.022	0.31 ± 0.034
16:3n-1	0.09 ± 0.004	0.08 ± 0.006	0.13 ± 0.012	0.05 ± 0.027	0.16 ± 0.030
16:4n-1	0.45 ± 0.054	0.55 ± 0.041	0.75 ± 0.133	0.42 ± 0.178	0.16 ± 0.058
18:0	1.57 ± 0.051	1.78 ± 0.043	2.33 ± 0.115	4.44 ± 0.485	3.85 ± 0.160
18:1n-13	0.05 ± 0.006	0.02 ± 0.003	0.05 ± 0.007	0.42 ± 0.066	0.31 ± 0.043
18:1n-11	0.60 ± 0.029	0.29 ± 0.021	0.16 ± 0.012	0.18 ± 0.036	1.09 ± 0.143
18:1n-9	10.87 ± 0.483	14.05 ± 0.454	11.67 ± 0.371	3.65 ± 0.839	15.51 ± 0.711
18:1n-7	2.20 ± 0.098	2.44 ± 0.070	2.51 ± 0.125	4.24 ± 0.402	4.03 ± 0.174
18:1n-5	0.55 ± 0.010	0.65 ± 0.024	0.56 ± 0.023	0.46 ± 0.030	0.43 ± 0.021
18:2d5,7	0.02 ± 0.002	0.05 ± 0.004	0.04 ± 0.004	0.02 ± 0.005	0.04 ± 0.005
18:2n-7	0.02 ± 0.002	0.03 ± 0.003	0.03 ± 0.004	0.08 ± 0.018	0.02 ± 0.004
18:2n-6	0.79 ± 0.026	0.99 ± 0.026	1.07 ± 0.068	0.64 ± 0.035	0.70 ± 0.049
18:2n-4	0.11 ± 0.005	0.14 ± 0.004	0.18 ± 0.010	0.14 ± 0.030	0.15 ± 0.017
18:3n-6	0.05 ± 0.003	0.06 ± 0.003	0.08 ± 0.004	0.10 ± 0.028	0.05 ± 0.005
18:3n-4	0.05 ± 0.002	0.06 ± 0.003	0.09 ± 0.005	0.09 ± 0.020	0.10 ± 0.004
18:3n-3	0.60 ± 0.042	1.01 ± 0.063	1.09 ± 0.106	0.22 ± 0.057	0.44 ± 0.053
18:3n-1	0.05 ± 0.003	0.07 ± 0.003	0.10 ± 0.008	0.08 ± 0.023	0.15 ± 0.010
18:4n-3	1.44 ± 0.110	2.30 ± 0.161	2.51 ± 0.167	0.32 ± 0.091	0.56 ± 0.099
18:4n-1	0.15 ± 0.009	0.17 ± 0.007	0.18 ± 0.023	0.10 ± 0.018	0.09 ± 0.028
20:0	0.23 ± 0.006	0.14 ± 0.007	0.12 ± 0.008	0.22 ± 0.042	0.07 ± 0.008

Table 2. Fatty Acid Composition of PWS Prey Species

	Herring			Octopus	PacificCod
	Large	**Medium**	**Small**		
20:1n-11	11.51 ± 0.452	4.31 ± 0.399	2.19 ± 0.481	1.70 ± 0.600	2.53 ± 0.316
20:1n-9	2.82 ± 0.087	3.00 ± 0.208	1.38 ± 0.095	3.55 ± 0.213	2.10 ± 0.210
R20:1	4.29 ± 0.201	1.60 ± 0.161	1.47 ± 0.286	0.47 ± 0.146	1.22 ± 0.123
20:1n-7	0.22 ± 0.007	0.24 ± 0.010	0.23 ± 0.019	0.99 ± 0.285	0.52 ± 0.087
20:1n-5	0.09 ± 0.004	0.07 ± 0.003	0.09 ± 0.007	0.10 ± 0.057	0.06 ± 0.008
20:2n-6	0.14 ± 0.005	0.18 ± 0.006	0.19 ± 0.015	0.60 ± 0.035	0.31 ± 0.022
20:3n-6	0.03 ± 0.002	0.03 ± 0.003	0.04 ± 0.004	0.07 ± 0.012	0.08 ± 0.006
20:4n-6	0.38 ± 0.020	0.43 ± 0.020	0.54 ± 0.048	5.73 ± 0.576	2.14 ± 0.174
20:3n-3	0.06 ± 0.013	0.08 ± 0.005	0.09 ± 0.010	0.53 ± 0.036	0.12 ± 0.012
20:4n-3	0.42 ± 0.019	0.65 ± 0.034	0.62 ± 0.037	0.26 ± 0.043	0.61 ± 0.049
20:5n-3	6.88 ± 0.209	9.60 ± 0.186	10.95 ± 0.190	17.91 ± 0.648	11.84 ± 0.689
22:1n-11	13.98 ± 0.562	6.66 ± 0.503	2.91 ± 0.497	1.12 ± 0.600	1.38 ± 0.212
22:1n-9	0.60 ± 0.023	0.45 ± 0.021	0.30 ± 0.020	0.75 ± 0.116	0.30 ± 0.023
R22:1	24.32 ± 1.055	14.29 ± 0.794	10.41 ± 1.936	1.18 ± 0.526	4.69 ± 0.651
22:1n-7	0.17 ± 0.004	0.14 ± 0.005	0.14 ± 0.007	0.21 ± 0.019	0.09 ± 0.013
22:2n-6	0.03 ± 0.021	0.01 ± 0.003	0.01 ± 0.002	0.16 ± 0.084	0.04 ± 0.013
21:5n-3	0.22 ± 0.013	0.29 ± 0.010	0.30 ± 0.010	0.46 ± 0.086	0.26 ± 0.035
22:4n-6	0.09 ± 0.021	0.04 ± 0.003	0.07 ± 0.005	0.55 ± 0.084	0.19 ± 0.029
22:5n-6	0.10 ± 0.004	0.14 ± 0.005	0.18 ± 0.012	0.44 ± 0.062	0.23 ± 0.013
22:4n-3	0.08 ± 0.025	0.05 ± 0.006	0.05 ± 0.005	0.04 ± 0.007	0.04 ± 0.004
22:5n-3	0.84 ± 0.023	0.75 ± 0.020	0.83 ± 0.053	2.28 ± 0.310	2.69 ± 0.208
22:6n-3	10.54 ± 0.464	13.01 ± 0.371	16.34 ± 1.048	20.97 ± 0.926	21.16 ± 0.654
24:1n-11	0.25 ± 0.022	0.12 ± 0.013	0.28 ± 0.189	0.05 ± 0.032	0.06 ± 0.010
24:1n-9	0.67 ± 0.026	0.80 ± 0.015	0.97 ± 0.047	0.19 ± 0.048	0.82 ± 0.044

Table 2. Fatty Acid Composition of PWS Prey Species

	Pinksalmon		**Pollock**		
	Adult	**Smolt**	**Large**	**Medium**	**Small**
n	5	20	36	71	35
12:0	0.04 ± 0.006	0.02 ± 0.002	0.01 ± 0.002	0.14 ± 0.037	0.05 ± 0.023
13:0	0.03 ± 0.004	0.02 ± 0.002	0.01 ± 0.001	0.01 ± 0.001	0.01 ± 0.003
Iso14	0.02 ± 0.002	0.02 ± 0.002	0.01 ± 0.001	0.01 ± 0.001	0.02 ± 0.004
14:0	2.96 ± 0.155	1.96 ± 0.077	3.89 ± 0.190	4.15 ± 0.203	2.78 ± 0.219
14:1n-9	0.05 ± 0.006	0.05 ± 0.003	0.21 ± 0.012	0.15 ± 0.005	0.20 ± 0.013
14:1n-7	0.02 ± 0.001	0.03 ± 0.003	0.01 ± 0.002	0.02 ± 0.002	0.01 ± 0.002
14:1n-5	0.07 ± 0.005	0.00 ± 0.002	0.07 ± 0.004	0.06 ± 0.003	0.04 ± 0.006
Iso15	0.15 ± 0.007	0.16 ± 0.009	0.13 ± 0.004	0.11 ± 0.004	0.11 ± 0.008
Anti15	0.06 ± 0.002	0.08 ± 0.008	0.03 ± 0.002	0.02 ± 0.001	0.04 ± 0.006
15:0	0.42 ± 0.039	0.67 ± 0.025	0.28 ± 0.009	0.25 ± 0.007	0.31 ± 0.013
15:1n-8	0.00 ± 0.001	0.01 ± 0.002	0.01 ± 0.001	0.01 ± 0.001	0.00 ± 0.001
15:1n-6	0.00 ± 0.000	0.00 ± 0.002	0.01 ± 0.003	0.02 ± 0.003	0.00 ± 0.000
Iso16	0.15 ± 0.005	0.56 ± 0.013	0.15 ± 0.015	0.10 ± 0.010	0.28 ± 0.016
16:0	12.65 ± 0.530	18.40 ± 0.147	14.88 ± 0.421	14.25 ± 0.335	17.76 ± 0.295
16:1n-11	0.39 ± 0.028	0.55 ± 0.020	0.36 ± 0.007	0.36 ± 0.010	0.44 ± 0.021
16:1n-9	0.27 ± 0.014	0.48 ± 0.016	0.18 ± 0.006	0.15 ± 0.006	0.22 ± 0.010
16:1n-7	3.79 ± 0.172	2.57 ± 0.136	5.15 ± 0.303	5.33 ± 0.212	3.34 ± 0.289
7Me16:0	0.32 ± 0.034	0.28 ± 0.008	0.30 ± 0.009	0.31 ± 0.011	0.22 ± 0.040
16:1n-5	0.23 ± 0.023	0.30 ± 0.011	0.13 ± 0.010	0.11 ± 0.007	0.14 ± 0.010
16:2n-6	0.03 ± 0.003	0.03 ± 0.002	0.08 ± 0.009	0.12 ± 0.007	0.09 ± 0.010
Iso17	0.13 ± 0.012	0.13 ± 0.005	0.09 ± 0.006	0.07 ± 0.004	0.09 ± 0.008
16:2n-4	0.34 ± 0.016	0.53 ± 0.016	0.36 ± 0.036	0.44 ± 0.043	0.43 ± 0.029
16:3n-6	0.17 ± 0.013	0.06 ± 0.004	0.21 ± 0.035	0.31 ± 0.038	0.24 ± 0.031
17:0	0.26 ± 0.091	0.46 ± 0.011	0.29 ± 0.043	0.28 ± 0.034	0.13 ± 0.018
16:3n-4	0.41 ± 0.043	0.20 ± 0.009	0.21 ± 0.021	0.34 ± 0.052	0.52 ± 0.064
17:1	0.01 ± 0.004	0.01 ± 0.003	0.15 ± 0.016	0.09 ± 0.009	0.16 ± 0.025
16:3n-1	0.09 ± 0.039	0.11 ± 0.010	0.08 ± 0.006	0.07 ± 0.006	0.12 ± 0.006
16:4n-1	0.11 ± 0.022	0.20 ± 0.010	0.32 ± 0.033	0.68 ± 0.090	0.41 ± 0.064
18:0	3.91 ± 0.187	4.55 ± 0.093	3.06 ± 0.138	2.94 ± 0.124	3.78 ± 0.130
18:1n-13	0.14 ± 0.014	0.06 ± 0.006	0.08 ± 0.010	0.08 ± 0.006	0.06 ± 0.011
18:1n-11	1.09 ± 0.157	0.17 ± 0.022	1.21 ± 0.110	1.17 ± 0.082	0.60 ± 0.065
18:1n-9	12.30 ± 0.889	5.91 ± 0.249	9.72 ± 0.510	7.89 ± 0.423	9.52 ± 0.264
18:1n-7	2.82 ± 0.215	2.08 ± 0.081	3.19 ± 0.173	3.17 ± 0.187	3.10 ± 0.211
18:1n-5	0.63 ± 0.075	0.40 ± 0.033	0.43 ± 0.015	0.53 ± 0.017	0.60 ± 0.053
18:2d5,7	0.04 ± 0.003	0.11 ± 0.019	0.03 ± 0.003	0.03 ± 0.003	0.05 ± 0.007
18:2n-7	0.06 ± 0.011	0.22 ± 0.033	0.02 ± 0.003	0.03 ± 0.003	0.04 ± 0.005
18:2n-6	1.39 ± 0.083	1.55 ± 0.112	0.75 ± 0.026	0.69 ± 0.024	0.81 ± 0.054
18:2n-4	0.11 ± 0.009	0.11 ± 0.020	0.13 ± 0.005	0.15 ± 0.006	0.13 ± 0.008
18:3n-6	0.10 ± 0.007	0.14 ± 0.014	0.08 ± 0.003	0.08 ± 0.003	0.08 ± 0.004
18:3n-4	0.09 ± 0.007	0.06 ± 0.016	0.07 ± 0.004	0.08 ± 0.004	0.08 ± 0.009
18:3n-3	0.98 ± 0.108	1.40 ± 0.082	0.64 ± 0.033	0.52 ± 0.027	0.58 ± 0.045
18:3n-1	0.08 ± 0.008	0.14 ± 0.018	0.11 ± 0.008	0.09 ± 0.004	0.12 ± 0.008
18:4n-3	1.58 ± 0.141	1.14 ± 0.060	1.55 ± 0.085	1.82 ± 0.099	1.50 ± 0.087
18:4n-1	0.15 ± 0.016	0.04 ± 0.005	0.16 ± 0.012	0.23 ± 0.021	0.11 ± 0.020
20:0	0.07 ± 0.005	0.09 ± 0.003	0.08 ± 0.004	0.10 ± 0.005	0.07 ± 0.005

Table 2. Fatty Acid Composition of PWS Prey Species

	Pinksalmon		**Pollock**		
	Adult	**Smolt**	**Large**	**Medium**	**Small**
20:1n-11	2.53 ± 0.244	0.26 ± 0.094	6.25 ± 0.603	6.65 ± 0.503	1.40 ± 0.407
20:1n-9	1.69 ± 0.137	0.49 ± 0.074	2.37 ± 0.157	2.20 ± 0.074	2.07 ± 0.328
R20:1	1.49 ± 0.034	0.57 ± 0.117	2.54 ± 0.167	2.78 ± 0.164	0.66 ± 0.146
20:1n-7	0.25 ± 0.060	0.17 ± 0.010	0.19 ± 0.006	0.21 ± 0.005	0.15 ± 0.009
20:1n-5	0.08 ± 0.010	0.40 ± 0.032	0.10 ± 0.005	0.09 ± 0.003	0.09 ± 0.005
20:2n-6	0.31 ± 0.033	0.32 ± 0.010	0.21 ± 0.011	0.18 ± 0.007	0.23 ± 0.009
20:3n-6	0.11 ± 0.007	0.14 ± 0.012	0.04 ± 0.002	0.05 ± 0.002	0.05 ± 0.002
20:4n-6	0.98 ± 0.026	1.50 ± 0.061	0.74 ± 0.064	0.74 ± 0.053	0.89 ± 0.050
20:3n-3	0.15 ± 0.016	0.16 ± 0.008	0.10 ± 0.007	0.12 ± 0.029	0.09 ± 0.004
20:4n-3	1.91 ± 0.185	1.18 ± 0.058	0.64 ± 0.021	0.69 ± 0.034	0.63 ± 0.023
20:5n-3	12.87 ± 0.126	8.30 ± 0.232	10.28 ± 0.211	12.11 ± 0.242	12.99 ± 0.313
22:1n-11	3.60 ± 0.435	0.26 ± 0.061	6.65 ± 0.689	6.46 ± 0.497	1.80 ± 0.374
22:1n-9	0.43 ± 0.036	0.06 ± 0.011	0.82 ± 0.146	0.59 ± 0.031	0.46 ± 0.043
R22:1	8.38 ± 0.429	0.00 ± 0.000	9.34 ± 0.861	10.90 ± 0.789	3.63 ± 0.658
22:1n-7	0.08 ± 0.006	0.04 ± 0.006	0.18 ± 0.018	0.15 ± 0.006	0.12 ± 0.011
22:2n-6	0.02 ± 0.010	0.11 ± 0.010	0.02 ± 0.003	0.02 ± 0.002	0.06 ± 0.016
21:5n-3	0.33 ± 0.015	0.13 ± 0.003	0.28 ± 0.012	0.36 ± 0.014	0.32 ± 0.019
22:4n-6	0.05 ± 0.004	0.11 ± 0.009	0.08 ± 0.009	0.09 ± 0.007	0.11 ± 0.013
22:5n-6	0.14 ± 0.015	0.32 ± 0.017	0.19 ± 0.017	0.18 ± 0.015	0.23 ± 0.008
22:4n-3	0.06 ± 0.004	0.07 ± 0.006	0.07 ± 0.010	0.12 ± 0.015	0.05 ± 0.009
22:5n-3	4.40 ± 0.175	2.52 ± 0.051	1.08 ± 0.029	1.15 ± 0.030	0.96 ± 0.034
22:6n-3	20.40 ± 0.430	36.17 ± 0.543	19.02 ± 1.052	18.39 ± 0.827	26.16 ± 1.158
24:1n-11	0.02 ± 0.024	0.01 ± 0.005	0.25 ± 0.020	0.26 ± 0.018	0.08 ± 0.015
24:1n-9	0.55 ± 0.038	0.63 ± 0.038	0.94 ± 0.042	0.85 ± 0.040	1.11 ± 0.053

Table 2. Fatty Acid Composition of PWS Prey Species

	RainbowSmelt	**Rockfish**	**Sandlance**	**Shrimp**	**Squid**
					Large
n	4	1	21	2*	8
12:0	0.07 ± 0.009	0.10	0.05 ± 0.014	0.10 ± 0.028	1.43 ± 0.337
13:0	0.01 ± 0.003	0.01	0.03 ± 0.002	0.03 ± 0.009	0.01 ± 0.004
Iso14	0.01 ± 0.003	0.01	0.03 ± 0.002	0.09 ± 0.006	0.03 ± 0.011
14:0	2.59 ± 0.349	3.44	4.95 ± 0.421	3.33 ± 0.435	2.23 ± 0.393
14:1n-9	0.06 ± 0.013	0.20	0.29 ± 0.028	0.05 ± 0.006	0.11 ± 0.012
14:1n-7	0.02 ± 0.000	0.03	0.03 ± 0.004	0.01 ± 0.003	0.01 ± 0.005
14:1n-5	0.19 ± 0.046	0.08	0.06 ± 0.007	0.10 ± 0.027	0.05 ± 0.017
Iso15	0.07 ± 0.010	0.12	0.21 ± 0.017	0.17 ± 0.032	0.08 ± 0.019
Anti15	0.02 ± 0.003	0.04	0.09 ± 0.009	0.05 ± 0.007	0.03 ± 0.010
15:0	0.27 ± 0.028	0.31	0.44 ± 0.029	0.60 ± 0.139	0.22 ± 0.032
15:1n-8	0.01 ± 0.000	0.01	0.01 ± 0.002	0.00 ± 0.003	0.00 ± 0.001
15:1n-6	0.00 ± 0.003	0.00	0.00 ± 0.000	0.03 ± 0.015	0.01 ± 0.005
Iso16	0.10 ± 0.034	0.19	0.17 ± 0.017	0.58 ± 0.091	0.34 ± 0.036
16:0	18.12 ± 0.387	17.22	17.32 ± 0.568	17.21 ± 1.961	14.42 ± 1.045
16:1n-11	0.22 ± 0.024	0.45	0.50 ± 0.029	0.64 ± 0.165	0.24 ± 0.026
16:1n-9	0.34 ± 0.036	0.25	0.22 ± 0.022	0.19 ± 0.015	0.17 ± 0.020
16:1n-7	10.47 ± 1.651	6.28	4.47 ± 0.336	4.96 ± 0.210	2.37 ± 0.489
7Me16:0	0.00 ± 0.000	0.26	0.20 ± 0.041	0.00 ± 0.000	0.14 ± 0.026
16:1n-5	0.15 ± 0.010	0.14	0.19 ± 0.013	0.04 ± 0.009	0.11 ± 0.016
16:2n-6	0.15 ± 0.038	0.23	0.12 ± 0.008	0.37 ± 0.093	0.03 ± 0.023
Iso17	0.02 ± 0.003	0.12	0.12 ± 0.008	0.21 ± 0.071	0.18 ± 0.076
16:2n-4	0.28 ± 0.105	0.41	0.44 ± 0.034	0.09 ± 0.009	0.12 ± 0.044
16:3n-6	0.23 ± 0.141	0.24	0.24 ± 0.032	0.50 ± 0.160	0.27 ± 0.079
17:0	0.23 ± 0.038	0.31	0.13 ± 0.029	0.39 ± 0.115	0.15 ± 0.028
16:3n-4	0.04 ± 0.007	0.21	0.32 ± 0.050	0.36 ± 0.231	0.25 ± 0.086
17:1	0.30 ± 0.043	0.38	0.23 ± 0.021	0.85 ± 0.196	0.07 ± 0.073
16:3n-1	0.08 ± 0.009	0.13	0.14 ± 0.009	0.17 ± 0.015	0.10 ± 0.009
16:4n-1	0.13 ± 0.031	0.35	0.61 ± 0.091	0.56 ± 0.067	0.14 ± 0.079
18:0	3.80 ± 0.211	4.15	2.78 ± 0.182	2.50 ± 0.214	2.18 ± 0.141
18:1n-13	0.10 ± 0.009	0.22	0.05 ± 0.017	0.09 ± 0.020	0.09 ± 0.009
18:1n-11	0.10 ± 0.021	0.43	0.33 ± 0.032	0.18 ± 0.035	0.82 ± 0.156
18:1n-9	18.42 ± 2.628	14.21	10.47 ± 1.207	10.80 ± 0.102	10.76 ± 0.921
18:1n-7	4.76 ± 0.114	3.85	2.06 ± 0.156	5.61 ± 0.057	3.61 ± 0.358
18:1n-5	0.46 ± 0.042	0.62	0.64 ± 0.053	0.42 ± 0.088	0.51 ± 0.057
18:2d5,7	0.23 ± 0.109	0.06	0.07 ± 0.008	0.03 ± 0.003	0.05 ± 0.042
18:2n-7	0.02 ± 0.002	0.02	0.04 ± 0.004	0.05 ± 0.015	0.01 ± 0.010
18:2n-6	0.54 ± 0.181	0.98	1.13 ± 0.080	0.78 ± 0.009	0.84 ± 0.095
18:2n-4	0.10 ± 0.013	0.14	0.13 ± 0.011	0.14 ± 0.003	0.10 ± 0.021
18:3n-6	0.06 ± 0.015	0.07	0.09 ± 0.008	0.05 ± 0.015	0.08 ± 0.015
18:3n-4	0.05 ± 0.006	0.06	0.06 ± 0.005	0.07 ± 0.025	0.08 ± 0.007
18:3n-3	0.30 ± 0.134	0.69	0.94 ± 0.107	0.62 ± 0.021	0.70 ± 0.122
18:3n-1	0.16 ± 0.027	0.14	0.17 ± 0.011	0.03 ± 0.015	0.11 ± 0.018
18:4n-3	0.25 ± 0.049	1.49	2.28 ± 0.304	0.76 ± 0.294	0.77 ± 0.169
18:4n-1	0.02 ± 0.003	0.11	0.12 ± 0.021	0.07 ± 0.003	0.05 ± 0.007
20:0	0.10 ± 0.007	0.11	0.14 ± 0.009	0.16 ± 0.039	0.18 ± 0.015

Table 2. Fatty Acid Composition of PWS Prey Species

	RainbowSmelt	**Rockfish**	**Sandlance**	**Shrimp**	**Squid**
					Large
20:1n-11	0.40 ± 0.078	2.07	3.46 ± 0.802	1.62 ± 0.371	5.30 ± 1.213
20:1n-9	0.62 ± 0.139	1.11	2.11 ± 0.241	1.38 ± 0.073	3.49 ± 0.402
R20:1	0.84 ± 0.330	0.33	1.76 ± 0.370	1.21 ± 0.327	1.38 ± 0.235
20:1n-7	0.25 ± 0.148	0.37	0.19 ± 0.010	0.93 ± 0.292	0.28 ± 0.028
20:1n-5	0.07 ± 0.006	0.10	0.13 ± 0.009	0.07 ± 0.023	0.06 ± 0.014
20:2n-6	0.16 ± 0.017	0.26	0.22 ± 0.018	0.41 ± 0.012	0.72 ± 0.064
20:3n-6	0.05 ± 0.014	0.06	0.04 ± 0.003	0.04 ± 0.003	0.05 ± 0.007
20:4n-6	1.74 ± 0.467	1.80	0.76 ± 0.077	1.92 ± 0.549	0.95 ± 0.093
20:3n-3	0.03 ± 0.008	0.10	0.09 ± 0.008	0.26 ± 0.091	0.72 ± 0.101
20:4n-3	0.20 ± 0.011	0.49	0.66 ± 0.052	0.30 ± 0.024	0.62 ± 0.062
20:5n-3	8.80 ± 0.535	9.38	11.45 ± 0.414	17.74 ± 0.493	13.47 ± 0.951
22:1n-11	0.15 ± 0.012	1.50	4.78 ± 0.839	1.62 ± 0.372	3.22 ± 0.778
22:1n-9	0.14 ± 0.028	0.24	0.33 ± 0.026	0.55 ± 0.110	0.57 ± 0.067
R22:1	1.19 ± 0.182	0.01	13.32 ± 2.071	2.88 ± 0.271	5.16 ± 0.831
22:1n-7	0.00 ± 0.000	0.12	0.16 ± 0.013	0.25 ± 0.048	0.12 ± 0.013
22:2n-6	0.02 ± 0.000	0.04	0.01 ± 0.003	0.04 ± 0.012	0.01 ± 0.006
21:5n-3	0.16 ± 0.017	0.22	0.29 ± 0.030	0.39 ± 0.108	0.35 ± 0.036
22:4n-6	0.13 ± 0.029	0.20	0.07 ± 0.011	0.32 ± 0.114	0.06 ± 0.024
22:5n-6	0.26 ± 0.064	0.32	0.22 ± 0.015	0.22 ± 0.020	0.21 ± 0.020
22:4n-3	0.05 ± 0.011	0.07	0.06 ± 0.005	0.02 ± 0.003	0.09 ± 0.080
22:5n-3	1.47 ± 0.208	1.33	0.94 ± 0.035	1.09 ± 0.290	0.73 ± 0.049
22:6n-3	20.22 ± 2.652	20.01	19.25 ± 1.263	15.40 ± 0.160	23.68 ± 2.150
24:1n-11	0.04 ± 0.012	0.10	0.09 ± 0.021	0.14 ± 0.035	0.12 ± 0.036
24:1n-9	0.86 ± 0.105	0.78	1.22 ± 0.075	0.50 ± 0.100	0.66 ± 0.072

Table 2. Fatty Acid Composition of PWS Prey Species

	Squid	Tomcod	
	Small	**Large**	**Small**
n	20	14	10
12:0	0.02 ± 0.003	0.02 ± 0.002	0.01 ± 0.001
13:0	0.02 ± 0.007	0.00 ± 0.001	0.01 ± 0.000
Iso14	0.04 ± 0.004	0.01 ± 0.003	0.01 ± 0.001
14:0	2.49 ± 0.249	1.43 ± 0.115	1.33 ± 0.097
14:1n-9	0.11 ± 0.008	0.08 ± 0.012	0.14 ± 0.013
14:1n-7	0.05 ± 0.012	0.03 ± 0.005	0.02 ± 0.002
14:1n-5	0.06 ± 0.003	0.02 ± 0.003	0.00 ± 0.001
Iso15	0.05 ± 0.005	0.15 ± 0.016	0.13 ± 0.005
Anti15	0.02 ± 0.003	0.04 ± 0.008	0.05 ± 0.003
15:0	0.51 ± 0.106	0.52 ± 0.038	0.40 ± 0.016
15:1n-8	0.00 ± 0.001	0.01 ± 0.003	0.00 ± 0.001
15:1n-6	0.02 ± 0.002	0.01 ± 0.003	0.00 ± 0.000
Iso16	0.67 ± 0.060	0.32 ± 0.029	0.41 ± 0.018
16:0	19.41 ± 0.427	14.98 ± 0.174	16.54 ± 0.129
16:1n-11	0.32 ± 0.034	0.54 ± 0.043	0.57 ± 0.021
16:1n-9	0.09 ± 0.003	0.47 ± 0.015	0.40 ± 0.008
16:1n-7	3.98 ± 0.636	3.83 ± 0.280	1.78 ± 0.093
7Me16:0	0.19 ± 0.014	0.26 ± 0.016	0.25 ± 0.013
16:1n-5	0.14 ± 0.004	0.34 ± 0.042	0.28 ± 0.014
16:2n-6	0.02 ± 0.004	0.16 ± 0.055	0.03 ± 0.002
Iso17	0.05 ± 0.006	0.29 ± 0.029	0.16 ± 0.009
16:2n-4	0.15 ± 0.017	0.46 ± 0.046	0.88 ± 0.055
16:3n-6	0.26 ± 0.047	0.10 ± 0.022	0.06 ± 0.005
17:0	1.11 ± 0.218	0.67 ± 0.046	0.52 ± 0.029
16:3n-4	0.06 ± 0.005	0.32 ± 0.065	0.21 ± 0.012
17:1	0.13 ± 0.040	0.27 ± 0.085	0.01 ± 0.003
16:3n-1	0.01 ± 0.003	0.04 ± 0.010	0.07 ± 0.005
16:4n-1	0.14 ± 0.021	0.30 ± 0.029	0.34 ± 0.022
18:0	2.09 ± 0.048	5.05 ± 0.184	4.95 ± 0.117
18:1n-13	0.10 ± 0.009	1.05 ± 0.177	0.25 ± 0.066
18:1n-11	0.24 ± 0.038	0.52 ± 0.265	0.13 ± 0.011
18:1n-9	8.56 ± 0.730	8.21 ± 0.622	7.56 ± 0.227
18:1n-7	4.22 ± 0.396	5.35 ± 0.308	2.43 ± 0.104
18:1n-5	0.48 ± 0.023	0.38 ± 0.025	0.41 ± 0.020
18:2d5,7	0.03 ± 0.011	0.02 ± 0.007	0.04 ± 0.006
18:2n-7	0.15 ± 0.022	0.03 ± 0.007	0.08 ± 0.015
18:2n-6	0.76 ± 0.043	0.99 ± 0.196	1.14 ± 0.073
18:2n-4	0.16 ± 0.011	0.14 ± 0.009	0.13 ± 0.015
18:3n-6	0.05 ± 0.010	0.13 ± 0.017	0.15 ± 0.007
18:3n-4	0.05 ± 0.003	0.09 ± 0.014	0.05 ± 0.006
18:3n-3	0.21 ± 0.012	0.67 ± 0.118	0.72 ± 0.045
18:3n-1	0.04 ± 0.008	0.14 ± 0.023	0.24 ± 0.025
18:4n-3	0.71 ± 0.192	0.76 ± 0.116	1.02 ± 0.095
18:4n-1	0.09 ± 0.006	0.07 ± 0.009	0.02 ± 0.012
20:0	0.25 ± 0.026	0.08 ± 0.009	0.14 ± 0.010

Table 2. Fatty Acid Composition of PWS Prey Species

	Squid	Tomcod	
	Small	**Large**	**Small**
20:1n-11	2.04 ± 0.319	0.80 ± 0.102	0.36 ± 0.086
20:1n-9	2.66 ± 0.208	0.91 ± 0.131	0.66 ± 0.043
R20:1	0.77 ± 0.109	1.02 ± 0.167	0.58 ± 0.151
20:1n-7	0.18 ± 0.015	1.16 ± 0.144	0.28 ± 0.057
20:1n-5	0.07 ± 0.004	0.06 ± 0.009	0.25 ± 0.033
20:2n-6	0.57 ± 0.052	0.65 ± 0.063	0.44 ± 0.019
20:3n-6	0.06 ± 0.014	0.17 ± 0.017	0.10 ± 0.012
20:4n-6	0.76 ± 0.052	3.21 ± 0.213	1.91 ± 0.229
20:3n-3	0.85 ± 0.081	0.29 ± 0.032	0.18 ± 0.007
20:4n-3	0.35 ± 0.021	0.53 ± 0.038	0.53 ± 0.016
20:5n-3	16.24 ± 0.301	15.27 ± 0.551	12.74 ± 0.413
22:1n-11	1.57 ± 0.285	0.20 ± 0.043	0.08 ± 0.012
22:1n-9	0.41 ± 0.021	0.10 ± 0.015	0.07 ± 0.005
R22:1	3.95 ± 0.781	2.50 ± 0.473	1.07 ± 0.122
22:1n-7	0.11 ± 0.008	0.11 ± 0.019	0.06 ± 0.005
22:2n-6	0.02 ± 0.004	0.10 ± 0.021	0.09 ± 0.010
21:5n-3	0.43 ± 0.013	0.28 ± 0.015	0.20 ± 0.011
22:4n-6	0.12 ± 0.033	0.90 ± 0.102	0.14 ± 0.020
22:5n-6	0.15 ± 0.006	0.42 ± 0.031	0.33 ± 0.005
22:4n-3	0.01 ± 0.005	0.04 ± 0.006	0.04 ± 0.004
22:5n-3	0.50 ± 0.020	4.57 ± 0.394	1.26 ± 0.159
22:6n-3	23.55 ± 2.044	19.52 ± 1.432	34.56 ± 0.920
24:1n-11	0.00 ± 0.000	0.01 ± 0.009	0.01 ± 0.005
24:1n-9	0.43 ± 0.013	0.50 ± 0.056	0.95 ± 0.045

Values are mean weight percent of total fatty acids ± SEM.
All values derived from whole prey that were ground
and analyzed individually.
See Table 1 for collection and proximate data.

Table 3. Collection Data for Harbor Seal Blubber Samples Analyzed

Year	Area	Location	Number of Individuals Sampled
1994	PWS	NE	3
		NW	4
		SC	30
		SE	3
	GOA	Kodiak	0
		SEA	0
1995	PWS	NE	0
		NW	5
		SC	33
		SE	4
	GOA	Kodiak	8
		SEA	23
1996	PWS	NE	16
		NW	0
		SC	34
		SE	20
	GOA	Kodiak	10
		Yakutat	11
		SEA	14
	TOTAL		218

Demographic Groups	Area	
	PWS	GOA
Adult Males	35	32
Adult Females	8	10
Pregnant females	20	*
Subadults	70	17
Pups	13	4
n/a	6	3
TOTAL	152	66

*Data on pregnancy status generally not available.

Table 4. Fatty Acid Composition of Harbor Seal Blubber (n = 218)

	PRINCE WILLIAM SOUND			
	NE	**NW**	**SC**	
	all groups	**Ad/Sub**	**Adult Male**	**Adult Female**
n	19	9	23	20
12:0	0.13 ± 0.011	0.16 ± 0.014	0.11 ± 0.005	0.12 ± 0.008
13:0	0.02 ± 0.002	0.01 ± 0.002	0.01 ± 0.002	0.01 ± 0.002
Iso14	0.02 ± 0.002	0.01 ± 0.004	0.02 ± 0.002	0.01 ± 0.002
14:0	5.05 ± 0.206	3.96 ± 0.192	4.80 ± 0.237	4.23 ± 0.247
14:1n-9	0.11 ± 0.009	0.09 ± 0.017	0.10 ± 0.008	0.08 ± 0.008
14:1n-7	0.08 ± 0.004	0.10 ± 0.014	0.06 ± 0.004	0.05 ± 0.003
14:1n-5	1.51 ± 0.085	2.33 ± 0.239	1.42 ± 0.122	1.12 ± 0.079
Iso15	0.13 ± 0.006	0.10 ± 0.006	0.12 ± 0.005	0.12 ± 0.003
Anti15	0.05 ± 0.004	0.04 ± 0.007	0.06 ± 0.004	0.06 ± 0.004
15:0	0.30 ± 0.013	0.22 ± 0.008	0.25 ± 0.009	0.28 ± 0.009
15:1n-8	0.00 ± 0.001	0.00 ± 0.002	0.01 ± 0.005	0.01 ± 0.005
15:1n-6	0.07 ± 0.005	0.09 ± 0.007	0.07 ± 0.005	0.07 ± 0.005
Iso16	0.07 ± 0.003	0.07 ± 0.005	0.06 ± 0.007	0.06 ± 0.006
16:0	9.38 ± 0.370	7.78 ± 0.343	8.13 ± 0.380	9.24 ± 0.379
16:1n-11	0.91 ± 0.098	0.54 ± 0.038	0.72 ± 0.030	0.60 ± 0.035
16:1n-9	0.46 ± 0.022	0.56 ± 0.021	0.40 ± 0.015	0.41 ± 0.013
16:1n-7	16.26 ± 0.784	21.87 ± 1.378	14.50 ± 0.729	14.72 ± 0.440
7Me16:0	0.26 ± 0.006	0.26 ± 0.009	0.27 ± 0.006	0.27 ± 0.007
16:1n-5	0.17 ± 0.022	0.03 ± 0.011	0.09 ± 0.016	0.08 ± 0.019
16:2n-6	0.12 ± 0.023	0.17 ± 0.023	0.14 ± 0.021	0.17 ± 0.025
Iso17	0.12 ± 0.005	0.05 ± 0.010	0.11 ± 0.014	0.11 ± 0.015
16:2n-4	0.37 ± 0.025	0.15 ± 0.033	0.29 ± 0.033	0.27 ± 0.023
16:3n-6	0.33 ± 0.022	0.41 ± 0.035	0.37 ± 0.038	0.29 ± 0.031
17:0	0.15 ± 0.018	0.11 ± 0.009	0.14 ± 0.018	0.17 ± 0.015
16:3n-4	0.37 ± 0.028	0.15 ± 0.024	0.28 ± 0.024	0.25 ± 0.034
17:1	0.09 ± 0.048	0.44 ± 0.017	0.22 ± 0.051	0.31 ± 0.062
16:3n-1	0.06 ± 0.010	0.08 ± 0.014	0.09 ± 0.011	0.10 ± 0.011
16:4n-1	0.14 ± 0.023	0.13 ± 0.040	0.20 ± 0.032	0.15 ± 0.026
18:0	1.17 ± 0.088	0.82 ± 0.063	1.01 ± 0.064	1.12 ± 0.046
18:1n-13	0.36 ± 0.019	0.14 ± 0.034	0.37 ± 0.019	0.34 ± 0.020
18:1n-11	3.56 ± 0.269	1.34 ± 0.194	3.43 ± 0.247	2.23 ± 0.140
18:1n-9	22.25 ± 0.543	26.15 ± 1.887	22.58 ± 0.750	22.00 ± 1.057
18:1n-7	3.78 ± 0.092	4.61 ± 0.234	3.65 ± 0.128	4.09 ± 0.140
18:1n-5	0.51 ± 0.011	0.43 ± 0.015	0.49 ± 0.012	0.48 ± 0.009
18:2d5,7	0.07 ± 0.013	0.11 ± 0.016	0.04 ± 0.007	0.05 ± 0.009
18:2n-7	0.08 ± 0.013	0.16 ± 0.007	0.09 ± 0.009	0.08 ± 0.009
18:2n-6	0.99 ± 0.029	1.03 ± 0.041	1.11 ± 0.031	1.12 ± 0.022
18:2n-4	0.12 ± 0.005	0.14 ± 0.018	0.12 ± 0.006	0.11 ± 0.005
18:3n-6	0.08 ± 0.005	0.06 ± 0.008	0.04 ± 0.004	0.05 ± 0.005
18:3n-4	0.13 ± 0.008	0.12 ± 0.012	0.14 ± 0.011	0.13 ± 0.008
18:3n-3	0.57 ± 0.026	0.56 ± 0.039	0.68 ± 0.034	0.73 ± 0.027
18:3n-1	0.01 ± 0.006	0.04 ± 0.008	0.04 ± 0.005	0.05 ± 0.009
18:4n-3	0.82 ± 0.048	0.74 ± 0.036	0.98 ± 0.059	1.00 ± 0.040
18:4n-1	0.12 ± 0.008	0.17 ± 0.012	0.18 ± 0.013	0.16 ± 0.009
20:0	0.08 ± 0.008	0.04 ± 0.005	0.08 ± 0.007	0.07 ± 0.004

Table 4. Fatty Acid Composition of Harbor Seal Blubber (n = 218)

	PRINCE WILLIAM SOUND			
	NE	NW	SC	
	all groups	Ad/Sub	Adult Male	Adult Female
20:1n-11	6.22 ± 0.539	2.46 ± 0.281	7.86 ± 0.505	5.14 ± 0.412
20:1n-9	2.15 ± 0.133	1.32 ± 0.061	2.17 ± 0.101	1.78 ± 0.097
R20:1	2.83 ± 0.152	1.89 ± 0.228	3.60 ± 0.135	2.84 ± 0.104
20:1n-7	0.39 ± 0.064	0.21 ± 0.034	0.28 ± 0.034	0.30 ± 0.021
20:1n-5	0.08 ± 0.012	0.06 ± 0.014	0.07 ± 0.007	0.08 ± 0.011
20:2n-6	0.26 ± 0.018	0.17 ± 0.027	0.19 ± 0.014	0.23 ± 0.017
20:3n-6	0.06 ± 0.003	0.08 ± 0.003	0.07 ± 0.004	0.09 ± 0.007
20:4n-6	0.69 ± 0.064	0.61 ± 0.052	0.50 ± 0.031	0.68 ± 0.058
20:3n-3	0.10 ± 0.012	0.09 ± 0.020	0.19 ± 0.108	0.12 ± 0.017
20:4n-3	0.56 ± 0.032	0.52 ± 0.052	0.63 ± 0.049	0.84 ± 0.062
20:5n-3	3.93 ± 0.164	4.50 ± 0.373	4.22 ± 0.235	5.43 ± 0.288
22:1n-11	1.81 ± 0.287	0.35 ± 0.060	2.28 ± 0.300	1.74 ± 0.253
22:1n-9	0.30 ± 0.052	0.13 ± 0.037	0.21 ± 0.024	0.20 ± 0.023
R22:1	6.61 ± 0.988	3.95 ± 1.022	10.56 ± 0.774	8.38 ± 0.533
22:1n-7	0.04 ± 0.020	0.04 ± 0.035	0.03 ± 0.004	0.03 ± 0.005
22:2n-6	0.00 ± 0.003	0.01 ± 0.003	0.02 ± 0.006	0.06 ± 0.015
21:5n-3	0.25 ± 0.007	0.24 ± 0.029	0.29 ± 0.013	0.29 ± 0.012
22:4n-6	0.18 ± 0.024	0.10 ± 0.011	0.11 ± 0.013	0.15 ± 0.020
22:5n-6	0.14 ± 0.013	0.11 ± 0.009	0.11 ± 0.006	0.12 ± 0.007
22:4n-3	0.09 ± 0.009	0.05 ± 0.005	0.09 ± 0.005	0.09 ± 0.007
22:5n-3	3.62 ± 0.202	3.26 ± 0.389	4.11 ± 0.304	4.79 ± 0.309
22:6n-3	7.33 ± 0.461	8.97 ± 1.018	8.09 ± 0.538	10.39 ± 0.660
24:1n-11	0.01 ± 0.009	0.02 ± 0.007	0.02 ± 0.006	0.01 ± 0.002
24:1n-9	0.11 ± 0.014	0.03 ± 0.007	0.10 ± 0.015	0.11 ± 0.015

Table 4. Fatty Acid Composition of Harbor Seal Blubber (n = 218)

	PRINCE WILLIAM SOUND			GULF OF ALASKA
	SC		SE	Kodiak
	Subadult	Pup	all groups	all groups
n	49	5	27	18
12:0	0.13 ± 0.005	0.17 ± 0.022	0.11 ± 0.008	0.09 ± 0.009
13:0	0.01 ± 0.001	0.01 ± 0.003	0.02 ± 0.001	0.01 ± 0.001
Iso14	0.02 ± 0.001	0.02 ± 0.004	0.02 ± 0.002	0.02 ± 0.002
14:0	5.46 ± 0.129	5.35 ± 0.259	4.73 ± 0.201	4.17 ± 0.113
14:1n-9	0.12 ± 0.007	0.10 ± 0.028	0.12 ± 0.008	0.13 ± 0.009
14:1n-7	0.08 ± 0.003	0.10 ± 0.007	0.07 ± 0.004	0.08 ± 0.006
14:1n-5	1.86 ± 0.080	2.27 ± 0.232	1.46 ± 0.099	1.76 ± 0.207
Iso15	0.12 ± 0.002	0.12 ± 0.006	0.13 ± 0.004	0.13 ± 0.008
Anti15	0.05 ± 0.003	0.04 ± 0.007	0.05 ± 0.003	0.06 ± 0.006
15:0	0.24 ± 0.004	0.25 ± 0.009	0.28 ± 0.014	0.26 ± 0.016
15:1n-8	0.02 ± 0.004	0.02 ± 0.013	0.01 ± 0.002	0.01 ± 0.002
15:1n-6	0.07 ± 0.004	0.07 ± 0.009	0.07 ± 0.005	0.09 ± 0.006
Iso16	0.05 ± 0.004	0.04 ± 0.011	0.08 ± 0.004	0.09 ± 0.011
16:0	8.99 ± 0.168	10.18 ± 0.398	9.40 ± 0.252	8.33 ± 0.258
16:1n-11	0.62 ± 0.024	0.64 ± 0.054	0.55 ± 0.030	0.68 ± 0.030
16:1n-9	0.43 ± 0.012	0.46 ± 0.015	0.45 ± 0.019	0.45 ± 0.016
16:1n-7	17.59 ± 0.563	21.72 ± 0.807	16.43 ± 0.688	18.13 ± 1.210
7Me16:0	0.27 ± 0.004	0.29 ± 0.010	0.25 ± 0.005	0.27 ± 0.018
16:1n-5	0.07 ± 0.008	0.10 ± 0.027	0.15 ± 0.017	0.15 ± 0.025
16:2n-6	0.13 ± 0.010	0.11 ± 0.022	0.09 ± 0.017	0.10 ± 0.015
Iso17	0.07 ± 0.006	0.06 ± 0.010	0.10 ± 0.010	0.10 ± 0.023
16:2n-4	0.24 ± 0.025	0.29 ± 0.091	0.26 ± 0.022	0.19 ± 0.028
16:3n-6	0.43 ± 0.029	0.33 ± 0.069	0.37 ± 0.027	0.50 ± 0.032
17:0	0.13 ± 0.010	0.08 ± 0.023	0.17 ± 0.014	0.14 ± 0.018
16:3n-4	0.26 ± 0.011	0.34 ± 0.024	0.40 ± 0.034	0.38 ± 0.030
17:1	0.25 ± 0.030	0.10 ± 0.073	0.14 ± 0.041	0.20 ± 0.048
16:3n-1	0.08 ± 0.007	0.07 ± 0.015	0.07 ± 0.016	0.05 ± 0.005
16:4n-1	0.24 ± 0.032	0.16 ± 0.084	0.18 ± 0.029	0.28 ± 0.025
18:0	0.95 ± 0.031	0.95 ± 0.046	1.11 ± 0.035	0.96 ± 0.050
18:1n-13	0.30 ± 0.010	0.30 ± 0.018	0.26 ± 0.024	0.26 ± 0.029
18:1n-11	2.42 ± 0.130	2.41 ± 0.352	1.99 ± 0.185	1.50 ± 0.093
18:1n-9	23.91 ± 0.767	19.18 ± 1.436	25.51 ± 1.014	23.97 ± 1.111
18:1n-7	3.91 ± 0.107	3.56 ± 0.227	4.21 ± 0.145	4.67 ± 0.220
18:1n-5	0.46 ± 0.007	0.47 ± 0.023	0.45 ± 0.010	0.41 ± 0.013
18:2d5,7	0.08 ± 0.008	0.11 ± 0.018	0.06 ± 0.011	0.06 ± 0.011
18:2n-7	0.11 ± 0.007	0.12 ± 0.023	0.09 ± 0.013	0.09 ± 0.011
18:2n-6	1.00 ± 0.020	0.90 ± 0.034	1.10 ± 0.031	1.01 ± 0.040
18:2n-4	0.11 ± 0.004	0.12 ± 0.016	0.11 ± 0.004	0.13 ± 0.011
18:3n-6	0.06 ± 0.003	0.06 ± 0.017	0.07 ± 0.005	0.05 ± 0.004
18:3n-4	0.13 ± 0.006	0.15 ± 0.018	0.14 ± 0.007	0.12 ± 0.007
18:3n-3	0.64 ± 0.024	0.59 ± 0.077	0.62 ± 0.027	0.60 ± 0.038
18:3n-1	0.04 ± 0.004	0.02 ± 0.012	0.03 ± 0.005	0.04 ± 0.004
18:4n-3	1.08 ± 0.049	1.10 ± 0.127	0.85 ± 0.048	0.85 ± 0.042
18:4n-1	0.19 ± 0.009	0.18 ± 0.027	0.14 ± 0.012	0.18 ± 0.014
20:0	0.07 ± 0.004	0.04 ± 0.010	0.06 ± 0.005	0.05 ± 0.004

Table 4. Fatty Acid Composition of Harbor Seal Blubber (n = 218)

	PRINCE WILLIAM SOUND			GULF OF ALASKA
	SC		SE	Kodiak
	Subadult	Pup	all groups	all groups
20:1n-11	6.36 ± 0.306	5.03 ± 0.460	4.20 ± 0.375	3.94 ± 0.365
20:1n-9	1.81 ± 0.061	1.57 ± 0.068	1.79 ± 0.096	1.58 ± 0.112
R20:1	3.47 ± 0.092	3.28 ± 0.429	2.28 ± 0.126	2.52 ± 0.161
20:1n-7	0.21 ± 0.011	0.20 ± 0.027	0.28 ± 0.033	0.32 ± 0.049
20:1n-5	0.08 ± 0.007	0.07 ± 0.033	0.07 ± 0.009	0.04 ± 0.004
20:2n-6	0.17 ± 0.009	0.21 ± 0.024	0.22 ± 0.014	0.19 ± 0.017
20:3n-6	0.07 ± 0.005	0.05 ± 0.009	0.06 ± 0.004	0.07 ± 0.004
20:4n-6	0.52 ± 0.038	0.69 ± 0.099	0.57 ± 0.046	0.63 ± 0.055
20:3n-3	0.09 ± 0.013	0.15 ± 0.091	0.13 ± 0.033	0.07 ± 0.005
20:4n-3	0.48 ± 0.020	0.49 ± 0.074	0.58 ± 0.049	0.54 ± 0.049
20:5n-3	4.21 ± 0.180	4.44 ± 0.444	4.47 ± 0.271	5.96 ± 0.372
22:1n-11	2.26 ± 0.231	1.35 ± 0.200	1.42 ± 0.189	0.91 ± 0.116
22:1n-9	0.18 ± 0.012	0.13 ± 0.015	0.22 ± 0.019	0.13 ± 0.019
R22:1	12.07 ± 0.738	10.81 ± 1.878	6.67 ± 0.641	7.54 ± 0.728
22:1n-7	0.02 ± 0.003	0.00 ± 0.004	0.02 ± 0.004	0.01 ± 0.003
22:2n-6	0.03 ± 0.013	0.00 ± 0.004	0.02 ± 0.005	0.02 ± 0.004
21:5n-3	0.28 ± 0.011	0.28 ± 0.025	0.26 ± 0.011	0.32 ± 0.021
22:4n-6	0.11 ± 0.013	0.13 ± 0.024	0.13 ± 0.018	0.13 ± 0.020
22:5n-6	0.11 ± 0.013	0.17 ± 0.075	0.12 ± 0.008	0.13 ± 0.010
22:4n-3	0.06 ± 0.003	0.10 ± 0.043	0.07 ± 0.006	0.06 ± 0.004
22:5n-3	2.72 ± 0.154	3.19 ± 0.279	3.72 ± 0.314	4.39 ± 0.326
22:6n-3	6.41 ± 0.299	7.65 ± 0.795	8.37 ± 0.550	8.52 ± 0.559
24:1n-11	0.02 ± 0.003	0.00 ± 0.002	0.00 ± 0.002	0.02 ± 0.005
24:1n-9	0.09 ± 0.011	0.10 ± 0.042	0.11 ± 0.014	0.06 ± 0.006

Table 4. Fatty Acid Composition of Harbor Seal Blubber (n = 218)

	GULF OF ALASKA	
	Yakutat Ad/Sub	SEA all groups
n	11	37
12:0	0.09 ± 0.009	0.10 ± 0.005
13:0	0.02 ± 0.000	0.02 ± 0.001
Iso14	0.02 ± 0.001	0.02 ± 0.001
14:0	5.67 ± 0.308	3.37 ± 0.115
14:1n-9	0.13 ± 0.005	0.12 ± 0.009
14:1n-7	0.06 ± 0.002	0.07 ± 0.004
14:1n-5	1.02 ± 0.077	1.30 ± 0.093
Iso15	0.13 ± 0.005	0.11 ± 0.005
Anti15	0.05 ± 0.003	0.05 ± 0.003
15:0	0.24 ± 0.007	0.25 ± 0.011
15:1n-8	0.00 ± 0.001	0.00 ± 0.001
15:1n-6	0.04 ± 0.004	0.07 ± 0.003
Iso16	0.05 ± 0.005	0.07 ± 0.004
16:0	8.73 ± 0.219	7.93 ± 0.320
16:1n-11	0.51 ± 0.032	0.57 ± 0.030
16:1n-9	0.46 ± 0.023	0.48 ± 0.013
16:1n-7	10.10 ± 0.499	16.28 ± 0.668
7Me16:0	0.24 ± 0.013	0.25 ± 0.009
16:1n-5	0.19 ± 0.009	0.14 ± 0.015
16:2n-6	0.04 ± 0.004	0.10 ± 0.011
Iso17	0.09 ± 0.007	0.08 ± 0.009
16:2n-4	0.31 ± 0.011	0.18 ± 0.016
16:3n-6	0.27 ± 0.017	0.47 ± 0.032
17:0	0.15 ± 0.029	0.14 ± 0.016
16:3n-4	0.44 ± 0.015	0.50 ± 0.023
17:1	0.01 ± 0.004	0.20 ± 0.041
16:3n-1	0.07 ± 0.010	0.06 ± 0.006
16:4n-1	0.11 ± 0.028	0.24 ± 0.024
18:0	1.27 ± 0.053	1.10 ± 0.060
18:1n-13	0.30 ± 0.016	0.16 ± 0.024
18:1n-11	1.80 ± 0.180	1.52 ± 0.102
18:1n-9	35.29 ± 2.223	25.83 ± 0.891
18:1n-7	3.81 ± 0.178	4.96 ± 0.157
18:1n-5	0.44 ± 0.021	0.36 ± 0.012
18:2d5,7	0.07 ± 0.017	0.04 ± 0.005
18:2n-7	0.04 ± 0.003	0.08 ± 0.006
18:2n-6	1.08 ± 0.040	1.19 ± 0.045
18:2n-4	0.07 ± 0.011	0.14 ± 0.005
18:3n-6	0.03 ± 0.006	0.05 ± 0.003
18:3n-4	0.12 ± 0.006	0.15 ± 0.006
18:3n-3	0.54 ± 0.057	0.68 ± 0.038
18:3n-1	0.04 ± 0.003	0.04 ± 0.003
18:4n-3	0.69 ± 0.127	0.93 ± 0.087
18:4n-1	0.07 ± 0.016	0.16 ± 0.009
20:0	0.08 ± 0.008	0.05 ± 0.002

Table 4. Fatty Acid Composition of Harbor Seal Blubber (n = 218)

	GULF OF ALASKA	
	Yakutat Ad/Sub	SEA all groups
20:1n-11	6.18 ± 0.632	2.61 ± 0.199
20:1n-9	2.09 ± 0.094	2.03 ± 0.123
R20:1	2.92 ± 0.218	1.29 ± 0.081
20:1n-7	0.19 ± 0.015	0.28 ± 0.016
20:1n-5	0.08 ± 0.006	0.04 ± 0.003
20:2n-6	0.16 ± 0.014	0.21 ± 0.012
20:3n-6	0.05 ± 0.005	0.08 ± 0.003
20:4n-6	0.43 ± 0.067	0.63 ± 0.029
20:3n-3	0.04 ± 0.008	0.08 ± 0.005
20:4n-3	0.38 ± 0.071	0.68 ± 0.047
20:5n-3	2.97 ± 0.610	6.33 ± 0.268
22:1n-11	2.69 ± 0.279	0.68 ± 0.082
22:1n-9	0.24 ± 0.015	0.17 ± 0.015
R22:1	10.87 ± 0.776	4.26 ± 0.423
22:1n-7	0.02 ± 0.004	0.02 ± 0.007
22:2n-6	0.01 ± 0.008	0.04 ± 0.006
21:5n-3	0.18 ± 0.028	0.37 ± 0.010
22:4n-6	0.09 ± 0.016	0.12 ± 0.010
22:5n-6	0.09 ± 0.010	0.12 ± 0.008
22:4n-3	0.05 ± 0.007	0.07 ± 0.004
22:5n-3	2.67 ± 0.474	5.16 ± 0.239
22:6n-3	6.06 ± 0.833	9.46 ± 0.454
24:1n-11	0.04 ± 0.011	0.01 ± 0.002
24:1n-9	0.14 ± 0.012	0.07 ± 0.006

Values are mean weight percent of total fatty acids ± SEM.
See Table 3 for summary of collection data.

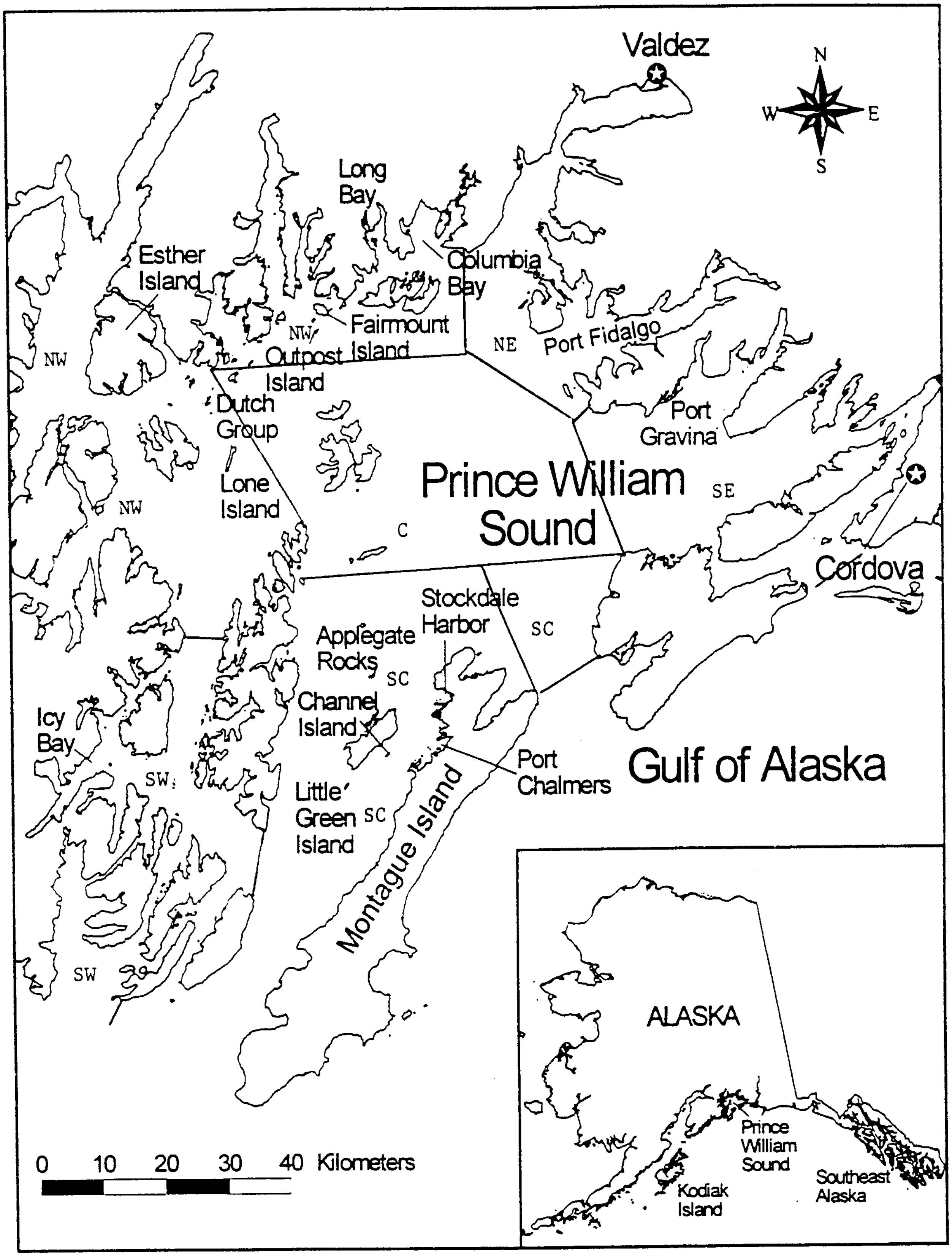
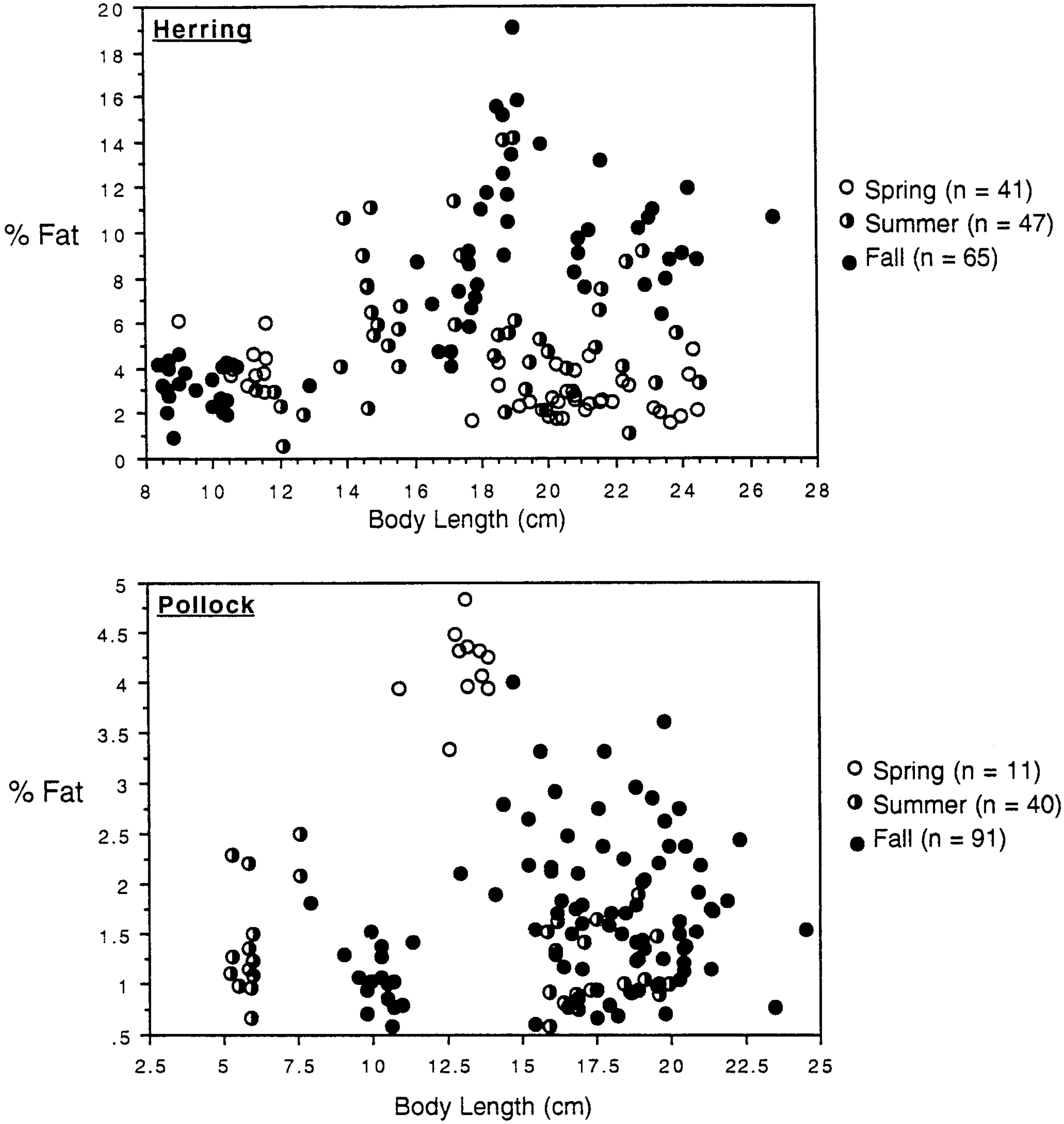


Figure 1. Prince William Sound (PWS), Alaska, showing major locations of harbor seals and prey sampled. General locations are indicated by boundary markers which coincide with fisheries zones.



Herring by season: $P < 0.0001$

Spring = 3.1 ± 0.51%

Summer = 5.6 ± 0.46%

Fall = 7.4 ± 0.51%

without NW (n = 10 NW):

Herring by season: $P < 0.0001$

Spring = 2.7 ± 0.16%

Summer = 5.6 ± 0.46%

Fall = 7.4 ± 0.51%

Pollock by season: $P < 0.0001$

Spring = 4.2 ± 0.12%

Summer = 1.4 ± 0.12%

Fall = 1.6 ± 0.08%

without NW (n = 47 NW):

Pollock by season: ns

Spring = n/a

Summer = 1.5 ± 0.18%

Fall = 1.5 ± 0.08%

Figure 2. Total fat content of PWS herring and pollock as a function of body length and season.

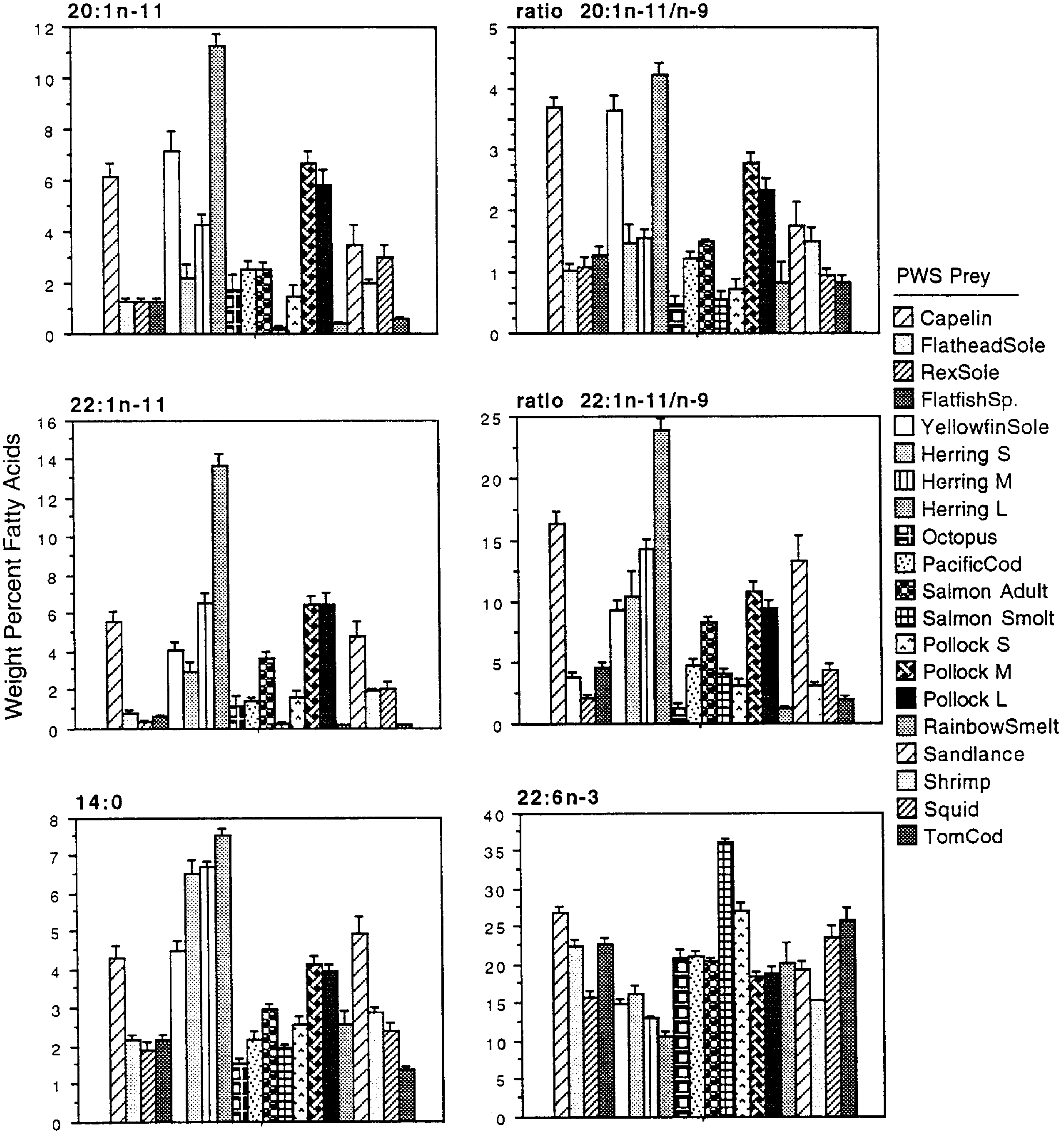


Figure 3. Selected fatty acids and isomer ratios (mean ± SEM) in prey species collected in Prince William Sound. See Table 1 for sample sizes and collection data.

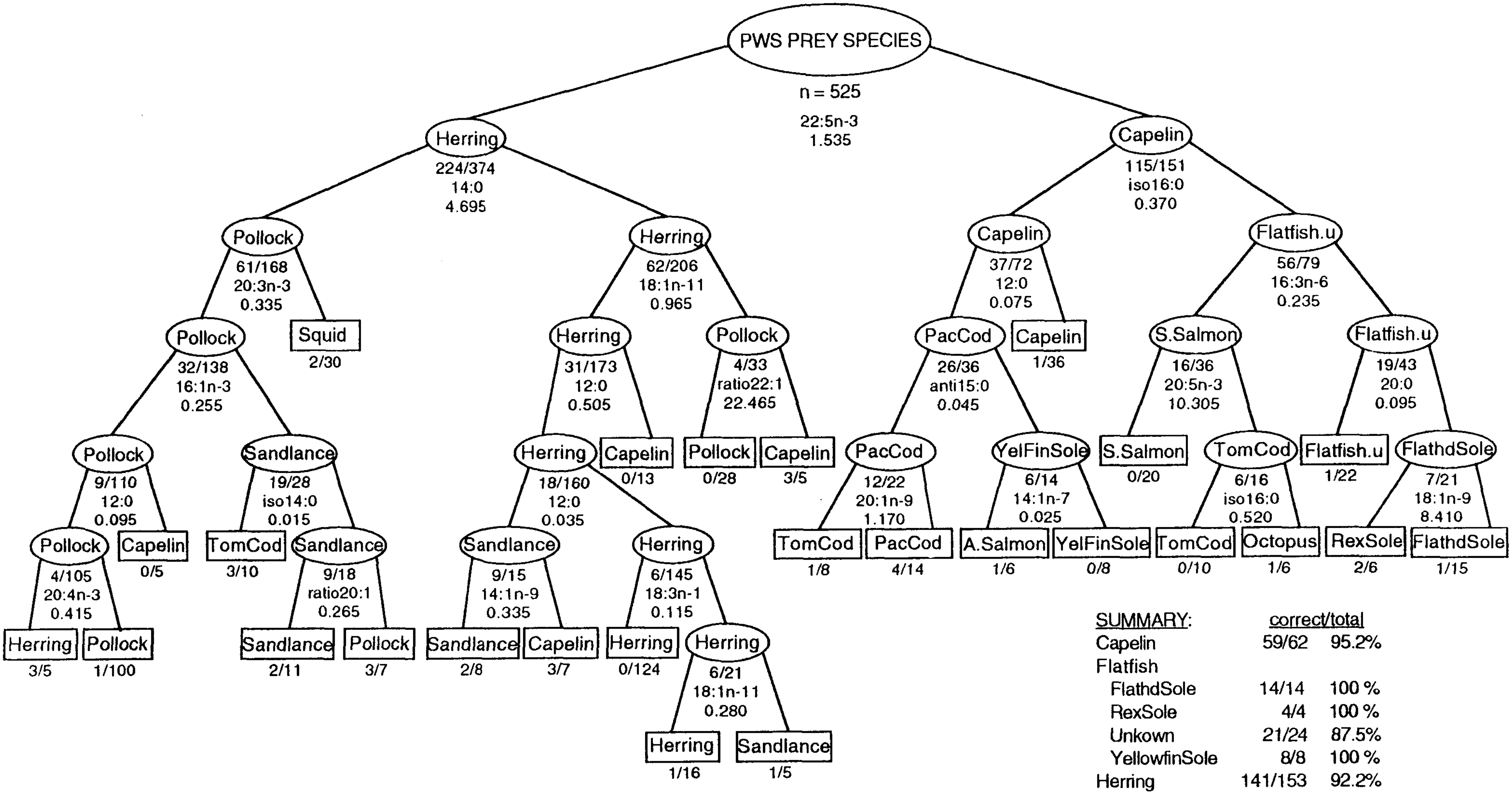
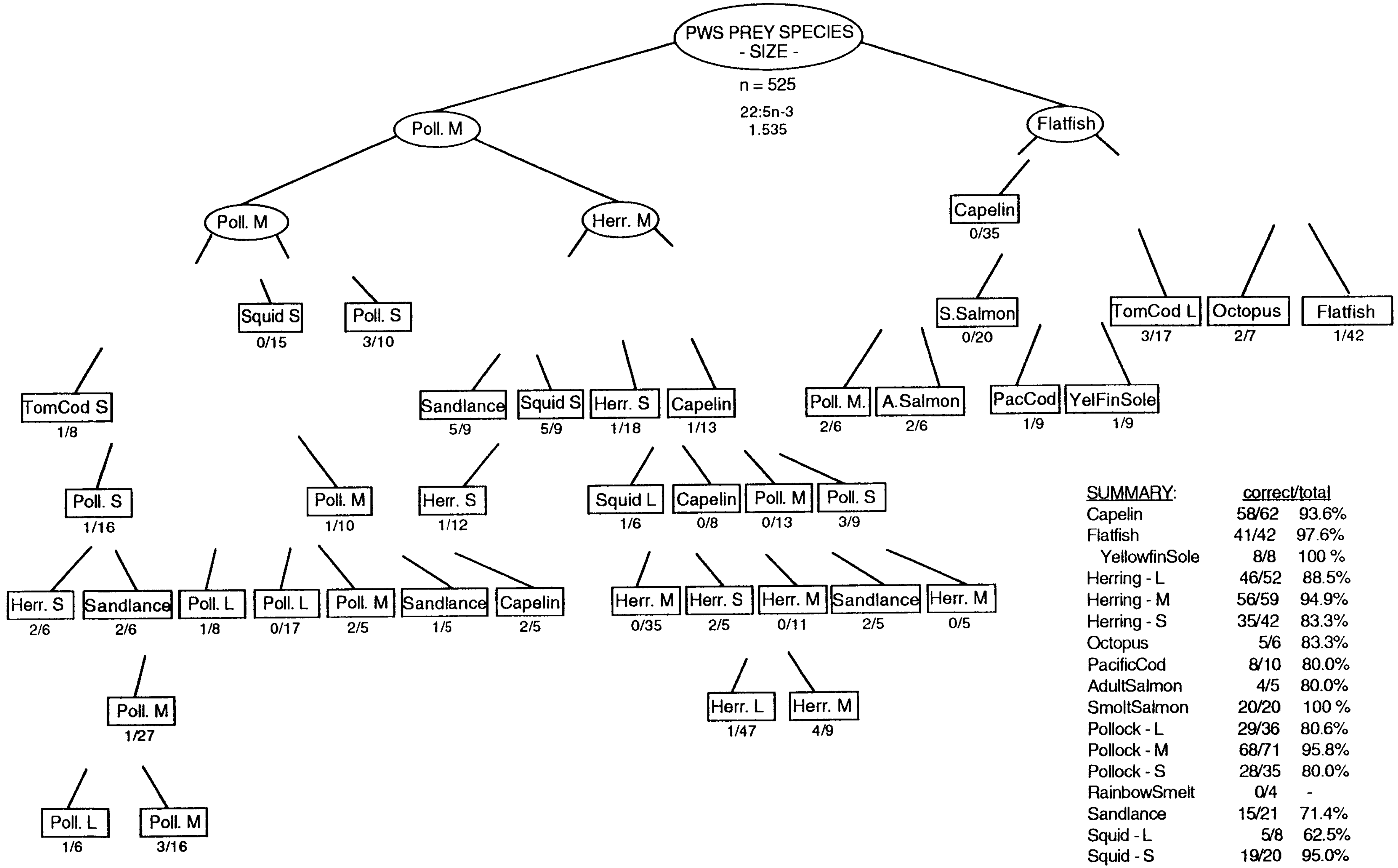


Figure 4. Classification tree of all prey sampled in PWS (sample sizes ≥ 4). Ellipses represent intermediate nodes and rectangle boxes represent terminal nodes; lables within an ellipse or rectangle indicate the classification at that node as represented by the largest number of observations in that node. The fatty acid listed at each node is the variable chosen to split; the value listed is the optimal splitting value for that fatty acid (> down right node and < down left node). Fractions under each node indicate the number of misclassifications over the total number of observations in that node.

SUMMARY:	correct/total	
Capelin	59/62	95.2%
Flatfish		
FlathdSole	14/14	100 %
RexSole	4/4	100 %
Unkown	21/24	87.5%
YellowfinSole	8/8	100 %
Herring	141/153	92.2%
Octopus	5/6	83.3%
PacificCod	10/10	100 %
AdultSalmon	5/5	100 %
SmoltSalmon	20/20	100 %
Pollock	131/142	92.3%
RainbowSmelt	0/4	-
Sandlance	19/21	90.5%
Squid	28/28	100 %
TomCod	24/24	100 %
Total:	489/525	93.1%
Misclassified:		36



SUMMARY:	correct/total	
Capelin	58/62	93.6%
Flatfish	41/42	97.6%
YellowfinSole	8/8	100 %
Herring - L	46/52	88.5%
Herring - M	56/59	94.9%
Herring - S	35/42	83.3%
Octopus	5/6	83.3%
PacificCod	8/10	80.0%
AdultSalmon	4/5	80.0%
SmoltSalmon	20/20	100 %
Pollock - L	29/36	80.6%
Pollock - M	68/71	95.8%
Pollock - S	28/35	80.0%
RainbowSmelt	0/4	-
Sandlance	15/21	71.4%
Squid - L	5/8	62.5%
Squid - S	19/20	95.0%
TomCod - L	14/14	100 %
TomCod - S	7/10	70.0%
Total:	466/525	88.8%
Misclassified:		59

Figure 5. Summary of classification tree of all prey sampled in PWS, incorporating size classes for herring, pollock, squid and tomcod. Only the final classifications and at the appropriate rank in the tree are presented for ease of viewing. See Fig. 4 legend for explanation of tree.

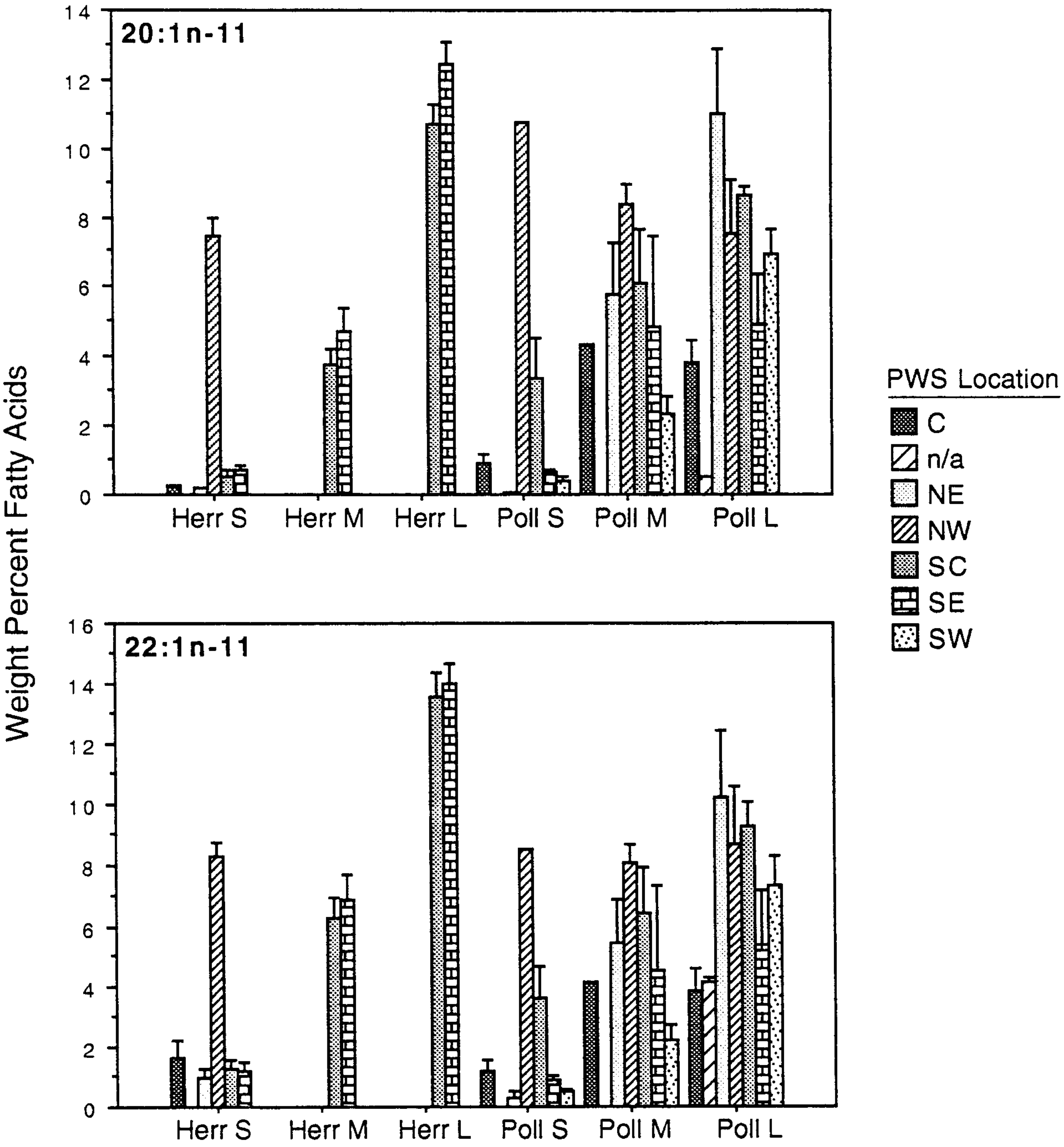


Figure 6. Two indicator fatty acids in herring and pollock across size classes (Table 1) and locations within PWS (Fig. 1).

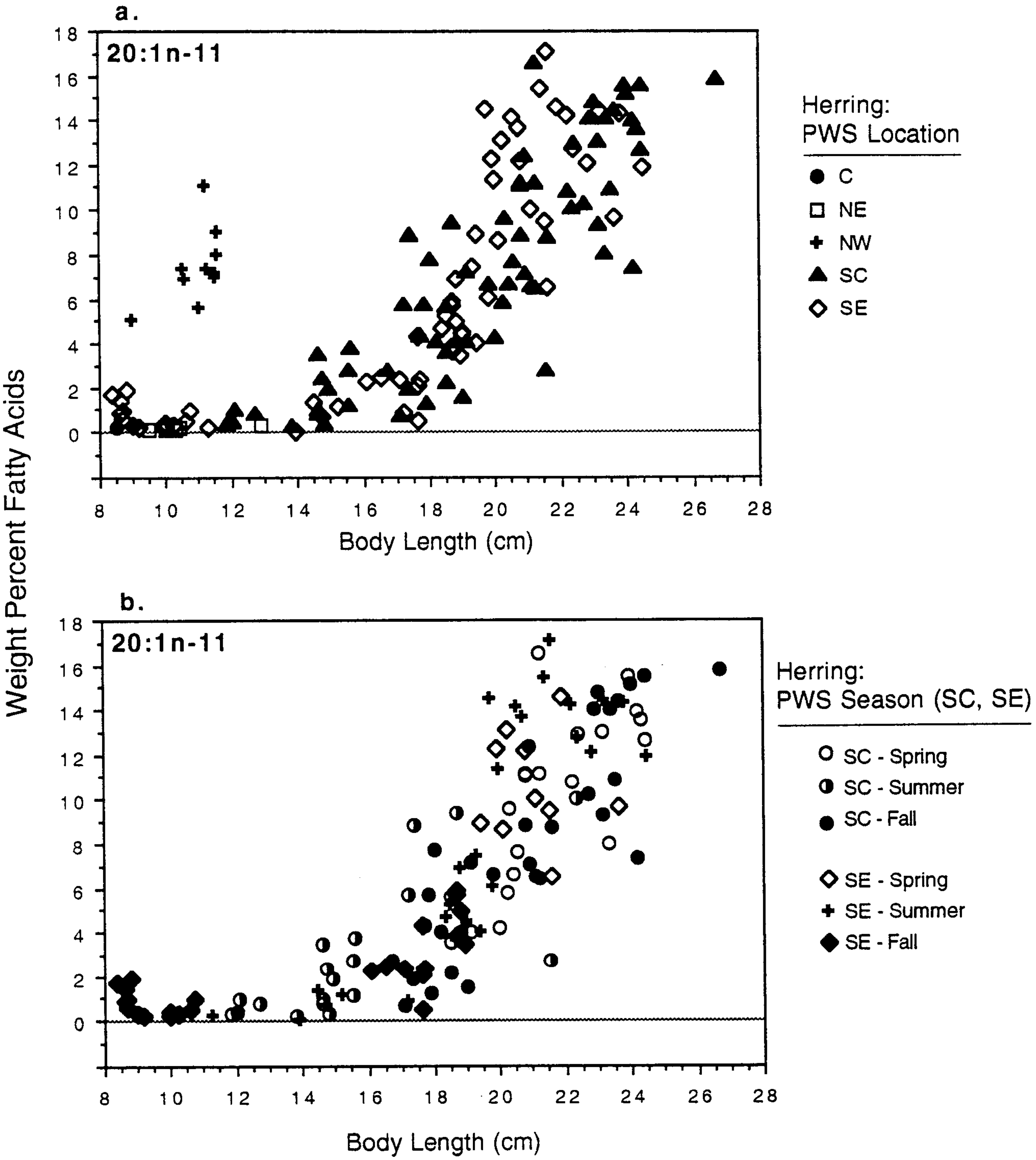
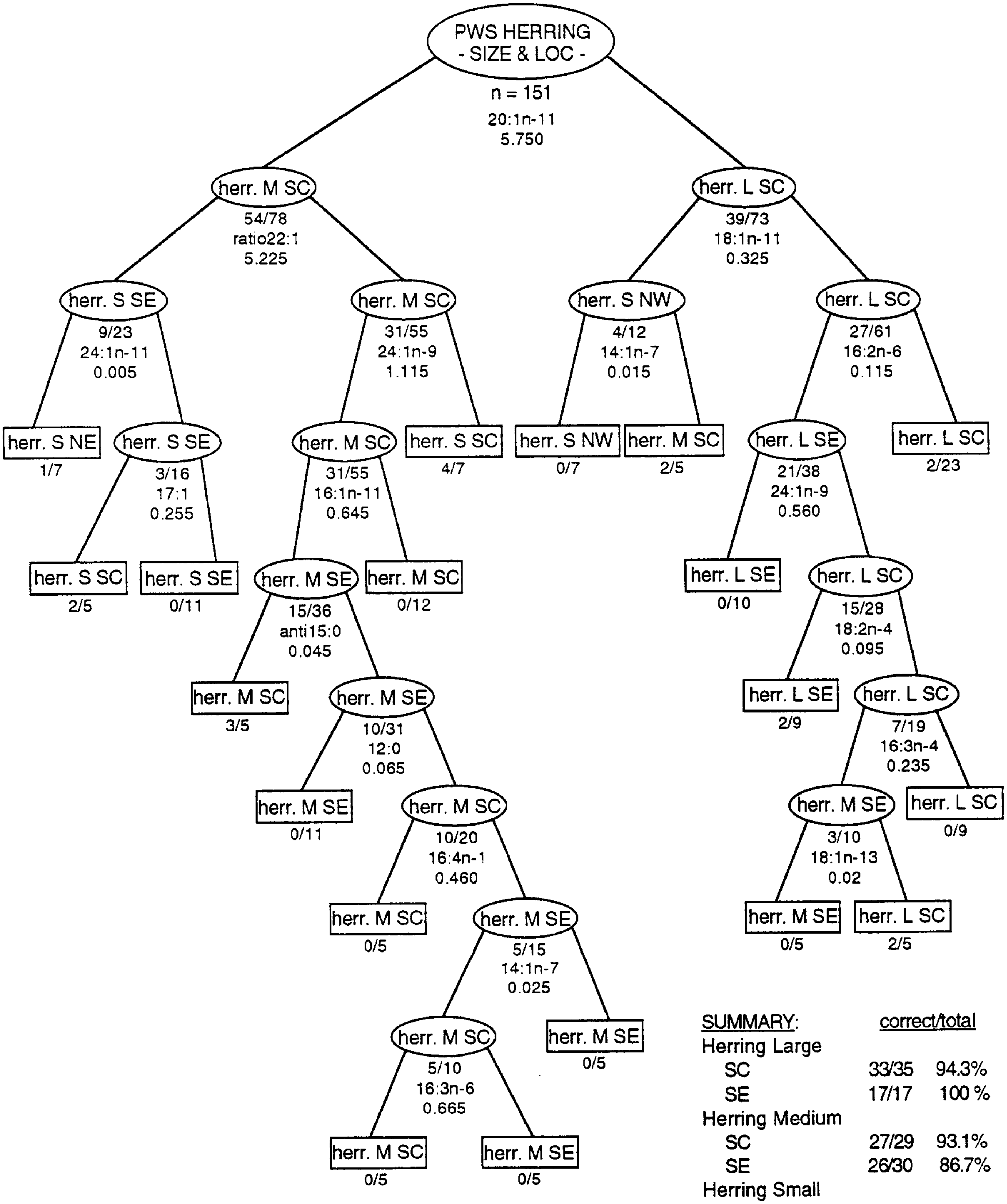
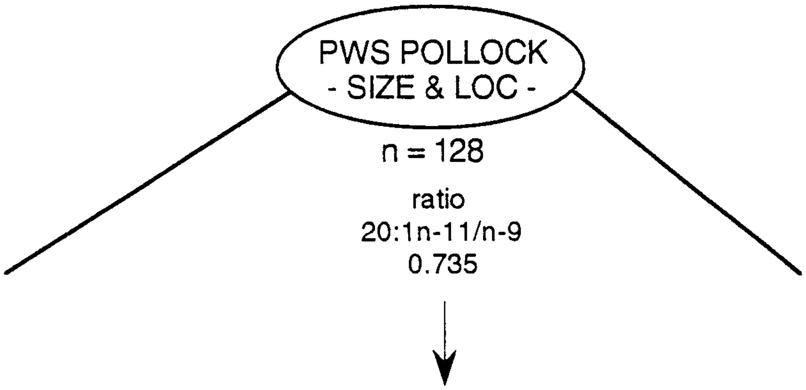


Figure. 7. Variation in fatty acid 20:1n-11 in herring as a function of body length across locations within PWS (Fig. 1) (a), and within SC and SE PWS across seasons (b).



SUMMARY:	correct/total	
Herring Large		
SC	33/35	94.3%
SE	17/17	100 %
Herring Medium		
SC	27/29	93.1%
SE	26/30	86.7%
Herring Small		
NE	6/8	75.0%
NW	7/10	70.0%
SC	6/6	100%
SE	11/16	68.8%
Total:	133/151	88.1%
Misclassified:		18

Figure 8. Classification tree of PWS herring across divisions of 3 size classes (S, M, L) and locations within PWS. See Fig. 4 legend for explanation of tree.



SUMMARY:	correct/total	
Pollock Large		
C	6/9	66.7%
NW	5/7	71.4%
SE	7/8	87.5%
SW	6/7	85.7%
Pollock Medium		
NE	11/11	100 %
NW	35/39	89.7%
SC	6/7	85.7%
SW	10/11	90.9%
Pollock Small		
C	5/5	100 %
SC	3/7	42.9%
SE	5/5	100 %
SW	12/12	100 %
Total:	111/128	86.7%
Misclassified:		17

Figure 9. Summary of classification tree of PWS pollock across divisions of 3 size classes (S, M, L) and locations within PWS. See Fig. 4 legend for explanation of trees.

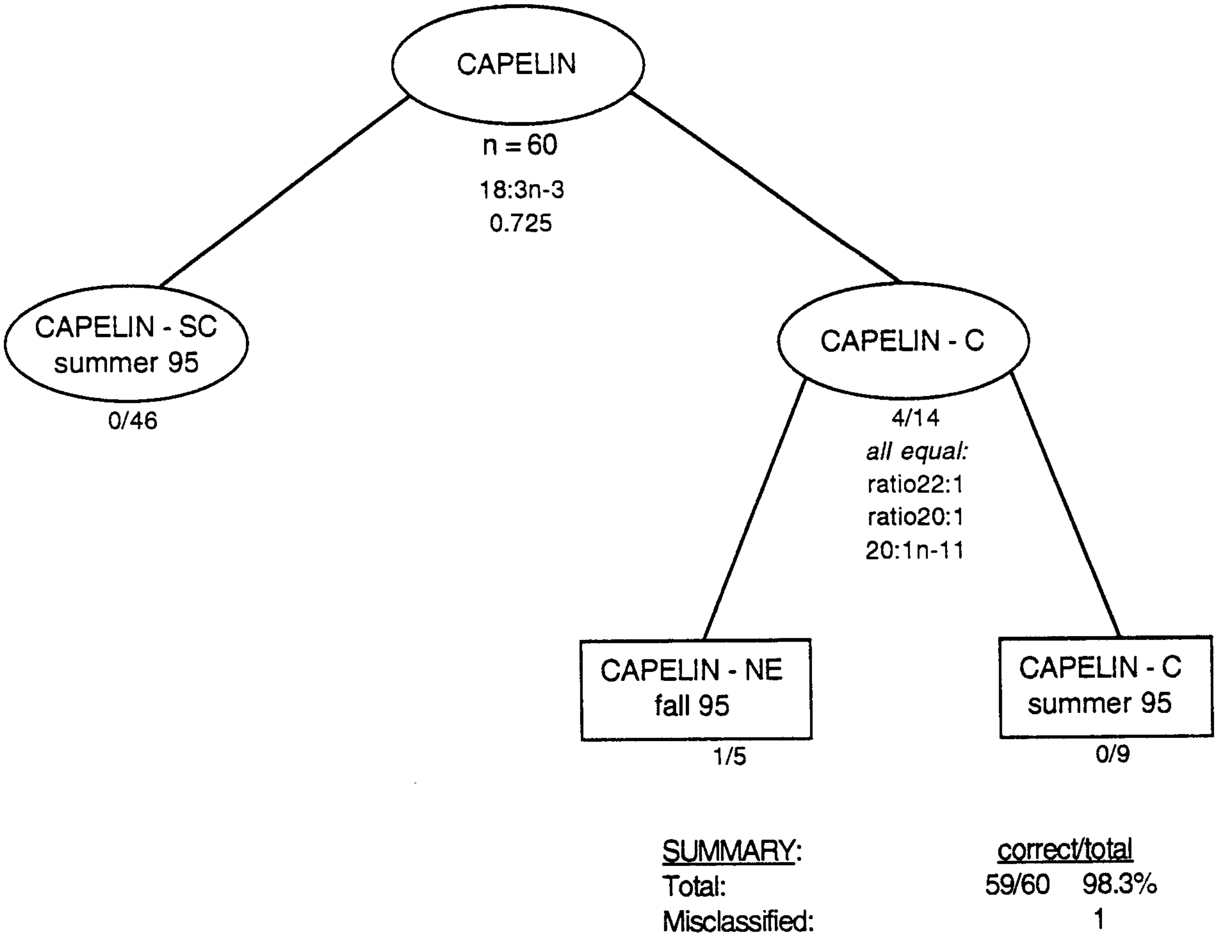
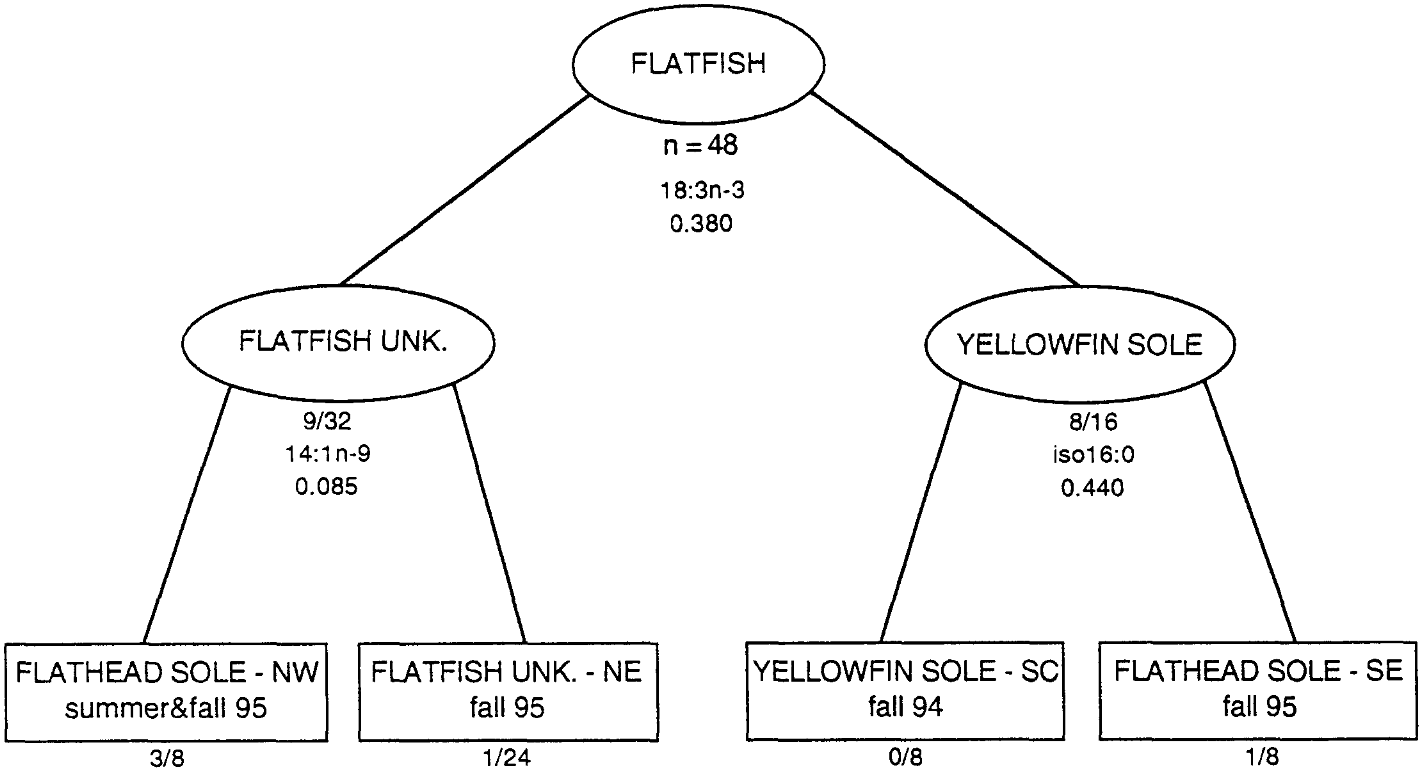
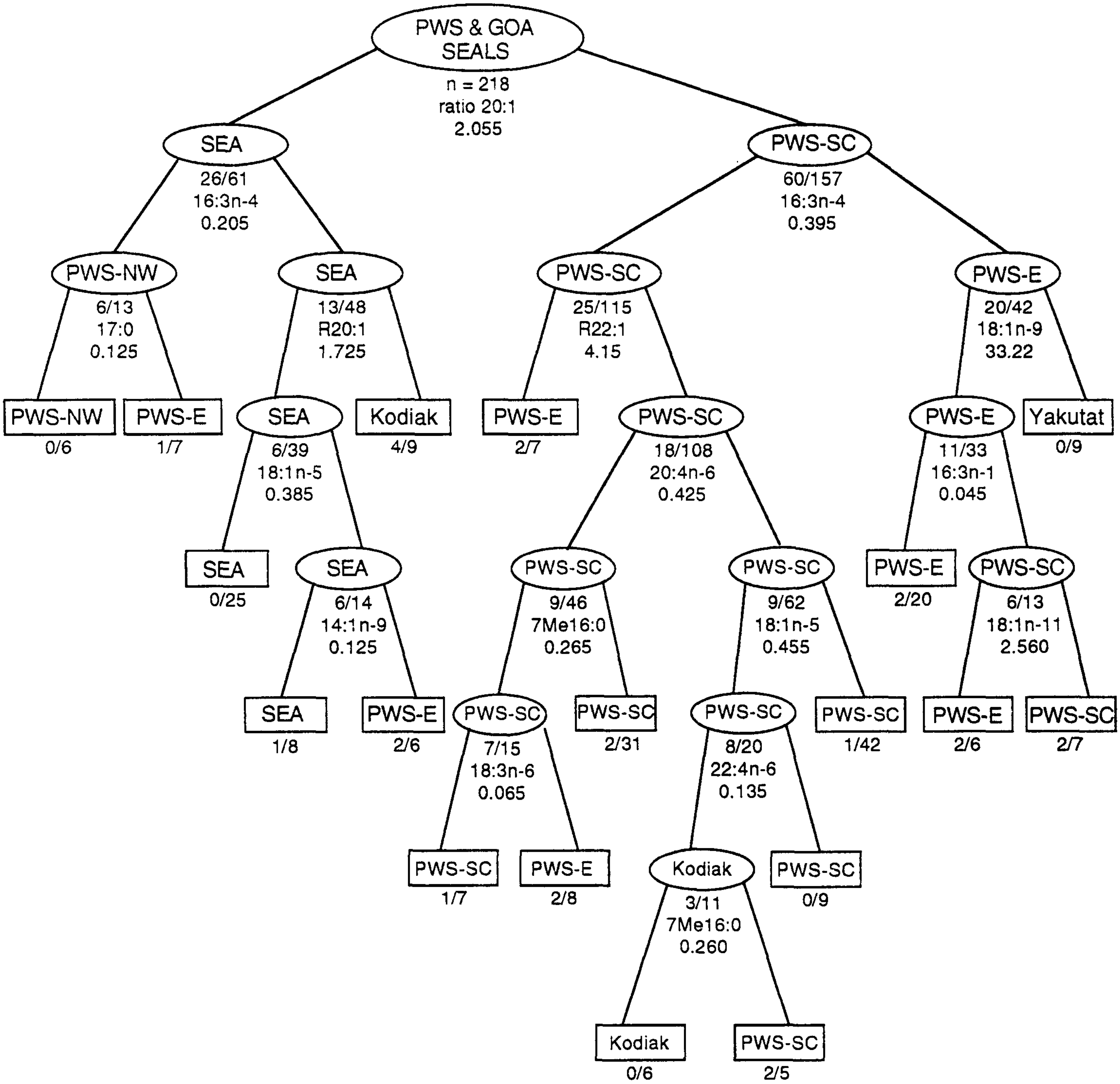


Figure 10. Classification tree of capelin across locations within PWS (Fig. 1). See Fig. 4 legend for explanation of tree.



SUMMARY:	correct/total	
Flathead Sole		
NW	5/5	100 %
SE	7/7	100 %
Flatfish unk. sp. - NE	23/24	95.8%
RexSole - SC	0/4	-
YellowfinSole - SC	8/8	100 %
Total:	43/48	89.6%
Misclassified:		5

Figure 11. Classification tree of flatfish species in PWS (all locations were represented by a single species). See Fig. 4 legend for explanation of tree.



SUMMARY:

Total: 194/218 = 89.0%
Misclassified: 24

Figure. 12. Classification tree of harbor seals, using only general sample locations within PWS and the GOA as variables. SE and NE PWS individuals are presented as PWS-E to simplify. See Table 3 for sample sizes. See Fig. 4 legend for explanation of tree.

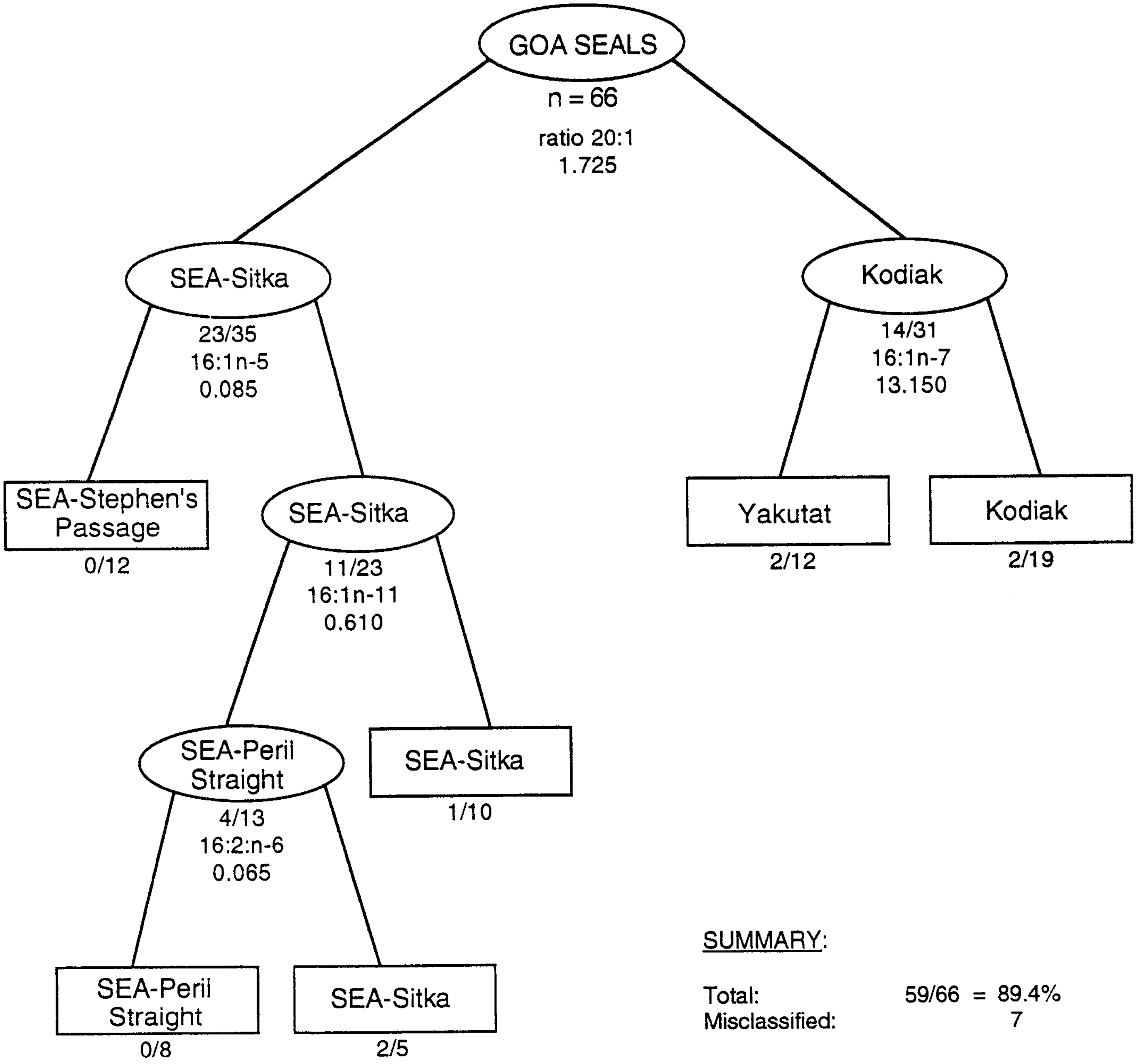
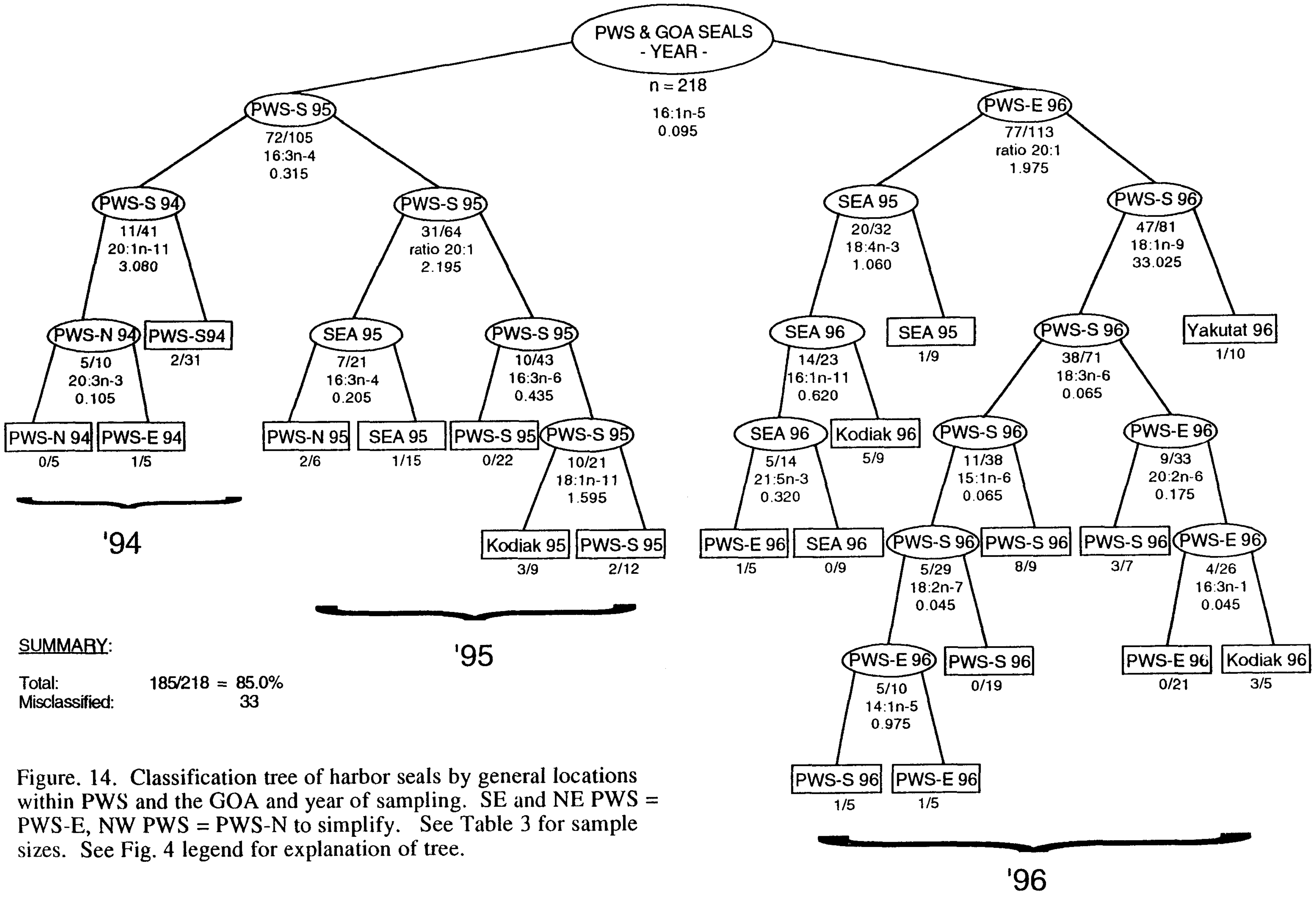


Figure. 13. Classification tree of harbor seals within smaller-scale designations in the GOA. See Fig. 4 legend for explanation of tree.



SUMMARY:

Total: 185/218 = 85.0%
Misclassified: 33

Figure. 14. Classification tree of harbor seals by general locations within PWS and the GOA and year of sampling. SE and NE PWS = PWS-E, NW PWS = PWS-N to simplify. See Table 3 for sample sizes. See Fig. 4 legend for explanation of tree.

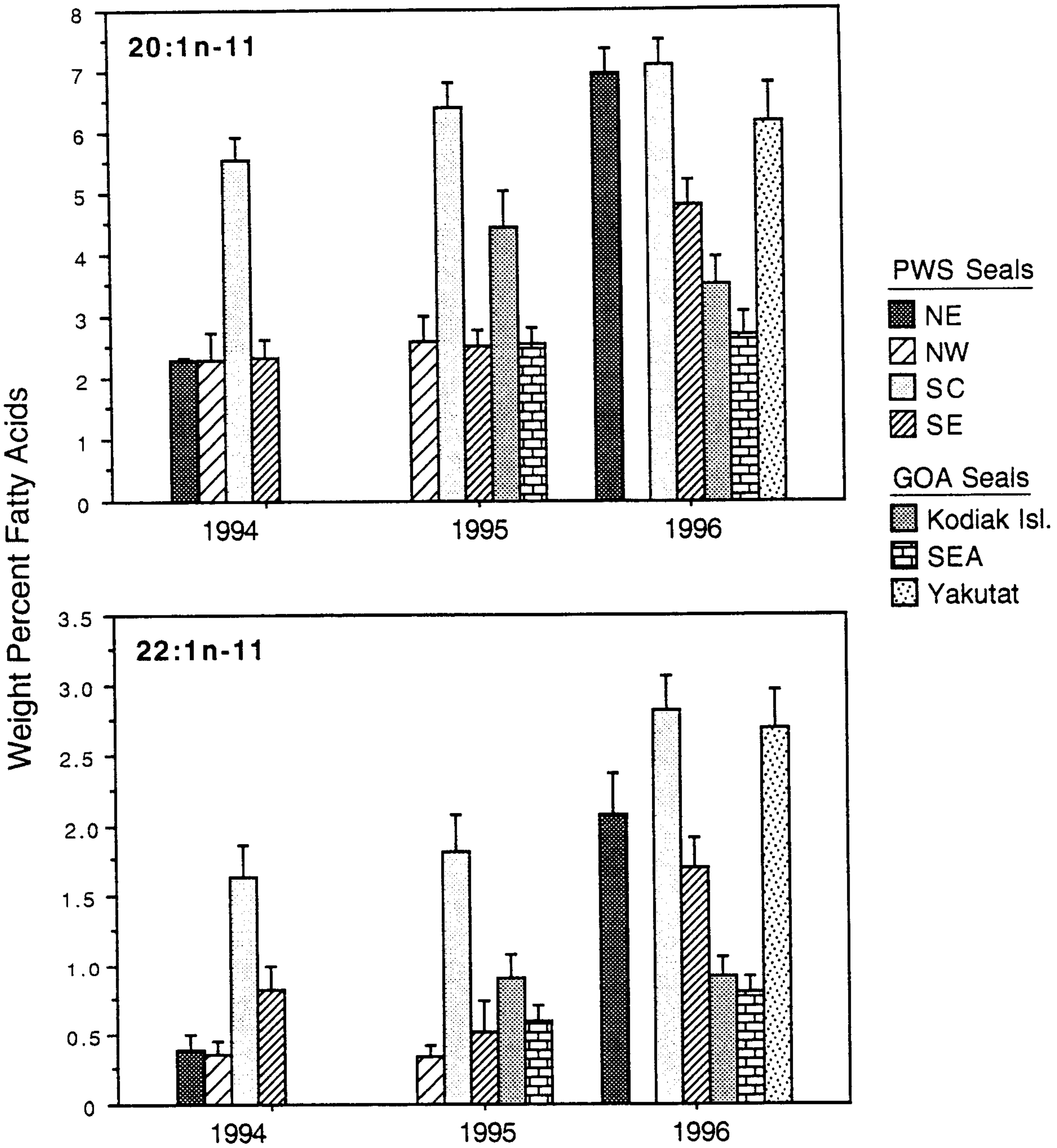
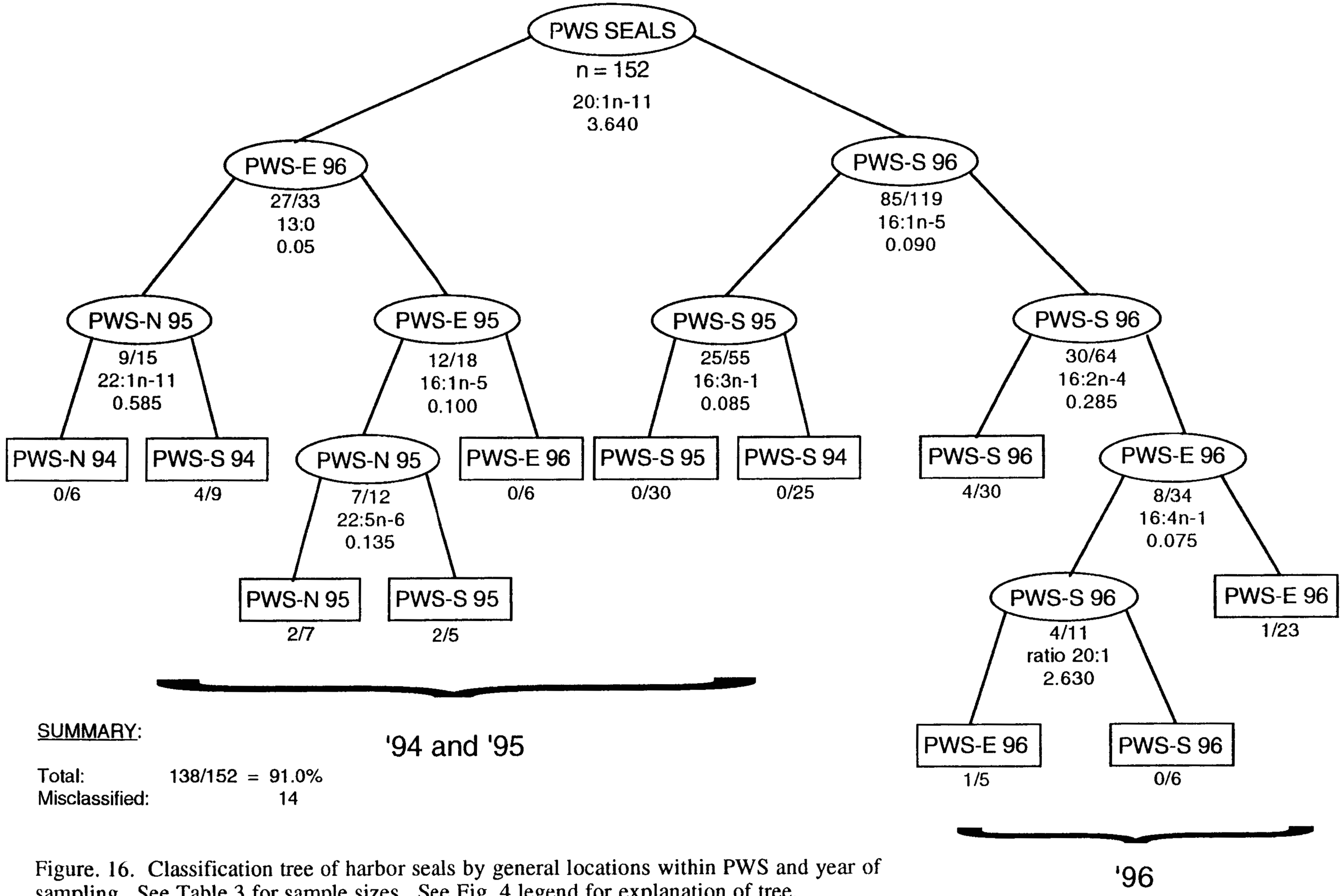


Figure 15. Two indicator fatty acids in harbor seals from locations within PWS and the GOA across three years of study. See Table 3 for sample sizes. The year 1996 differed significantly from years 1994 and 1995 ($P < 0.0001$, ANOVA).



SUMMARY:

Total: 138/152 = 91.0%
Misclassified: 14

Figure. 16. Classification tree of harbor seals by general locations within PWS and year of sampling. See Table 3 for sample sizes. See Fig. 4 legend for explanation of tree.

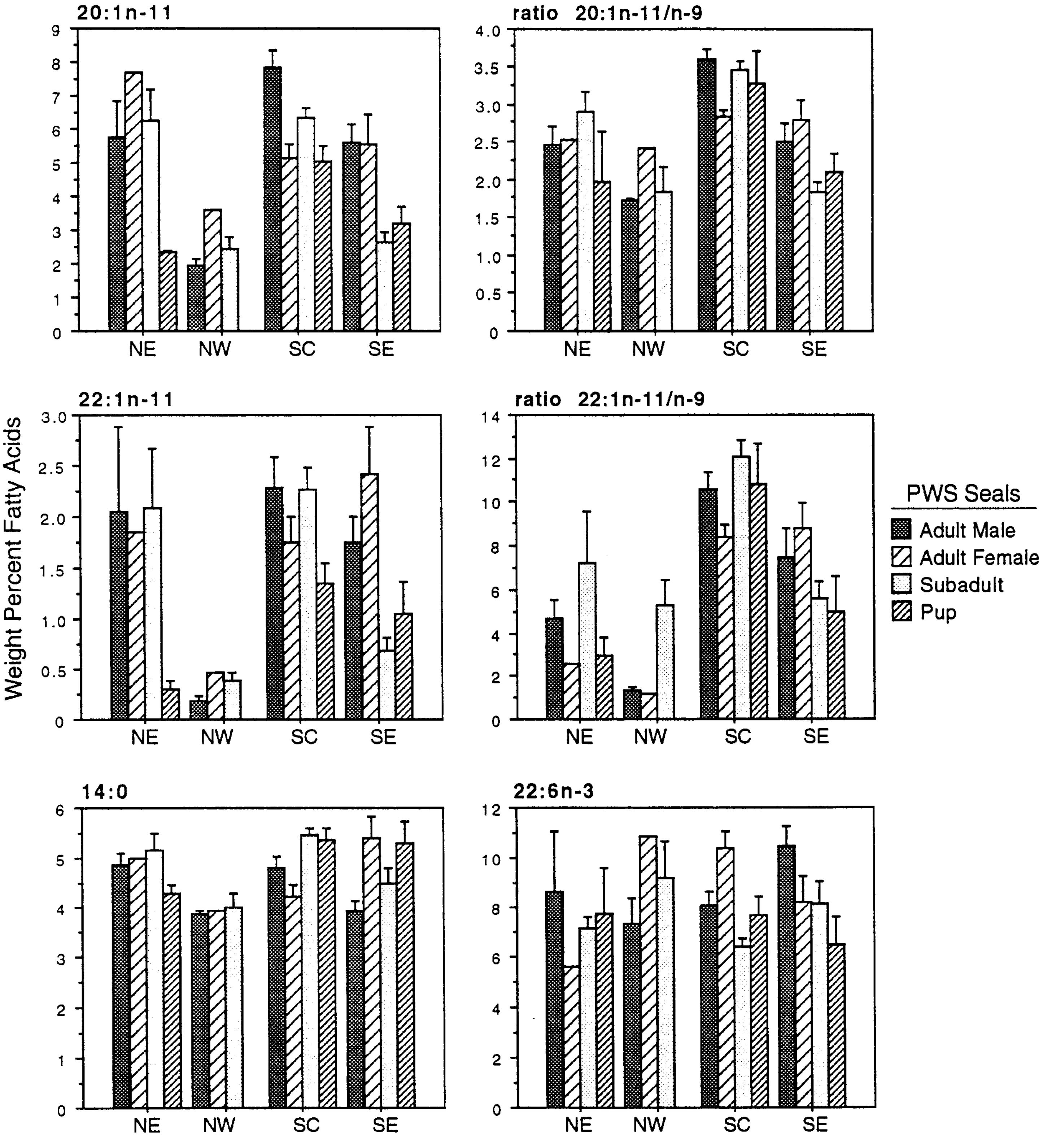


Figure 17. Selected fatty acids and isomer ratios (mean ± SEM) in harbor seals within PWS as a function of age-class or demographic group. Overall sample sizes are listed in Table 3. Adult males almost always differed from adult females, and subadults differed from either adult males or adult females depending upon the fatty acid and the location in PWS (see results).

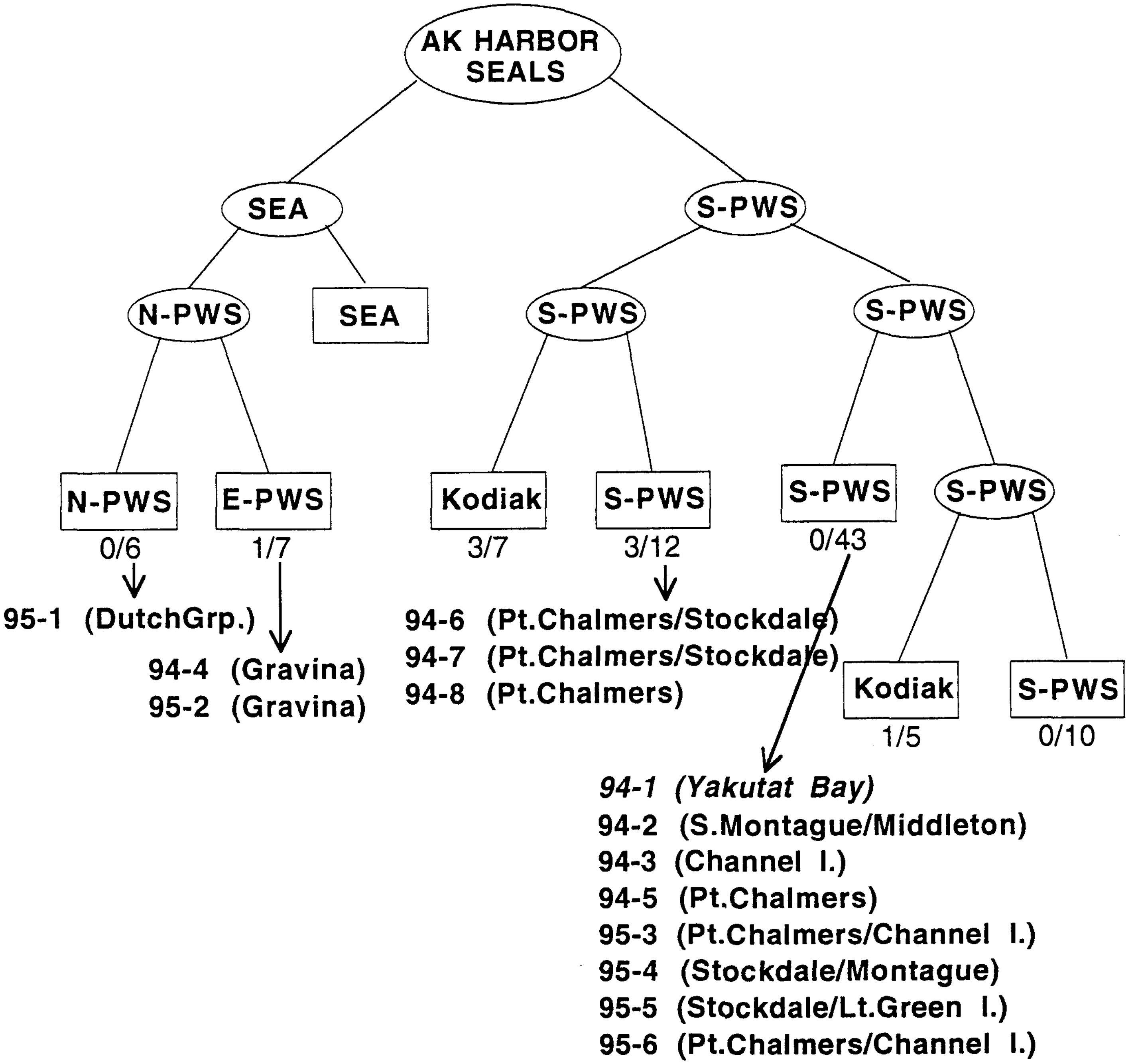


Figure 18. Location of satellite-tagged seals within 1994/1995 classification tree on a large scale of both PWS and the GOA. Almost all animals tagged remained at or near their original location of capture; only one left PWS for any period (to Yakutat) although may not have done so prior to fatty acid sampling. No tagged individual was misclassified.

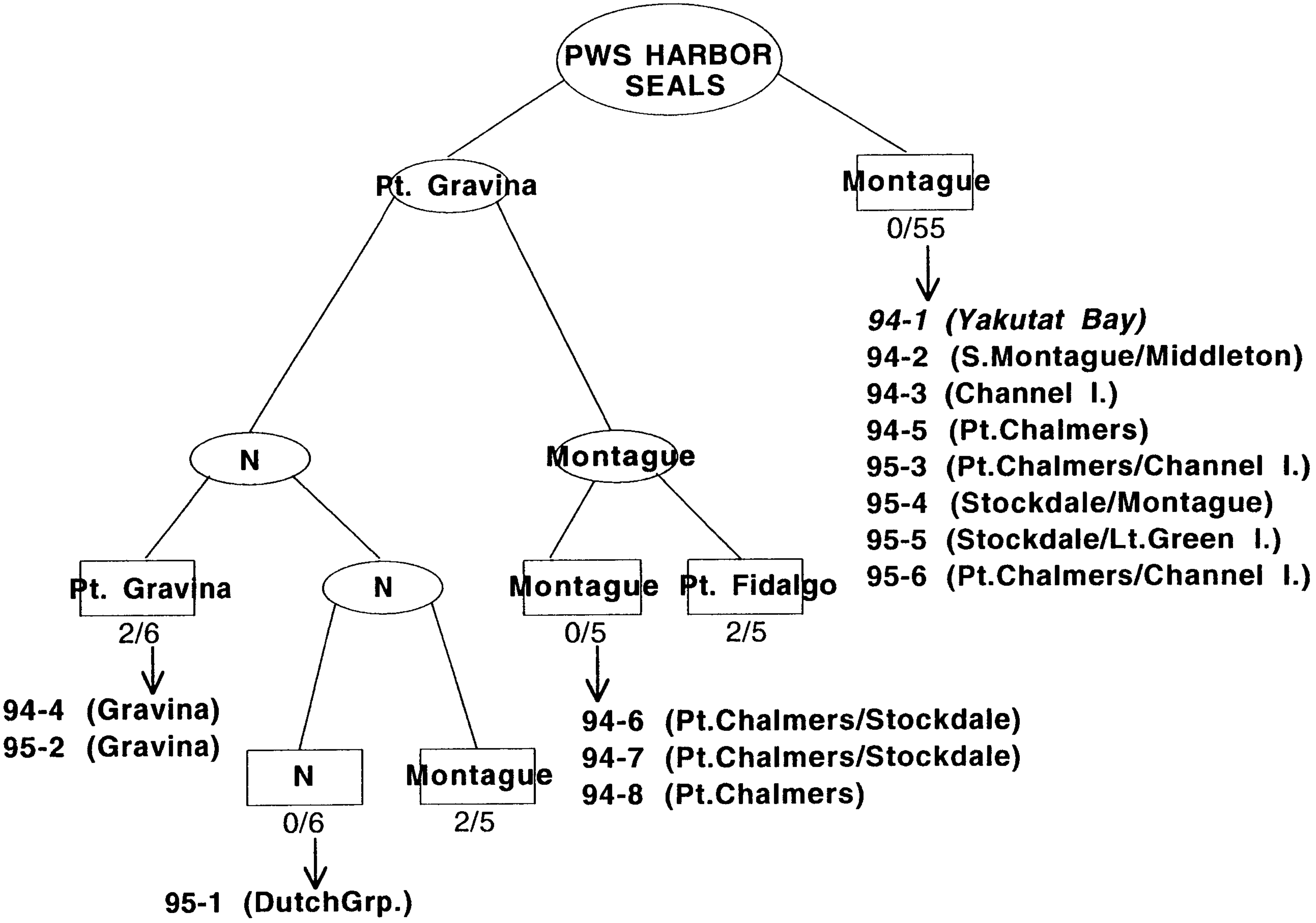


Figure 19. Location of satellite-tagged seals within 1994/1995 classification tree on a finer scale resolution within PWS. No tagged individual was misclassified.

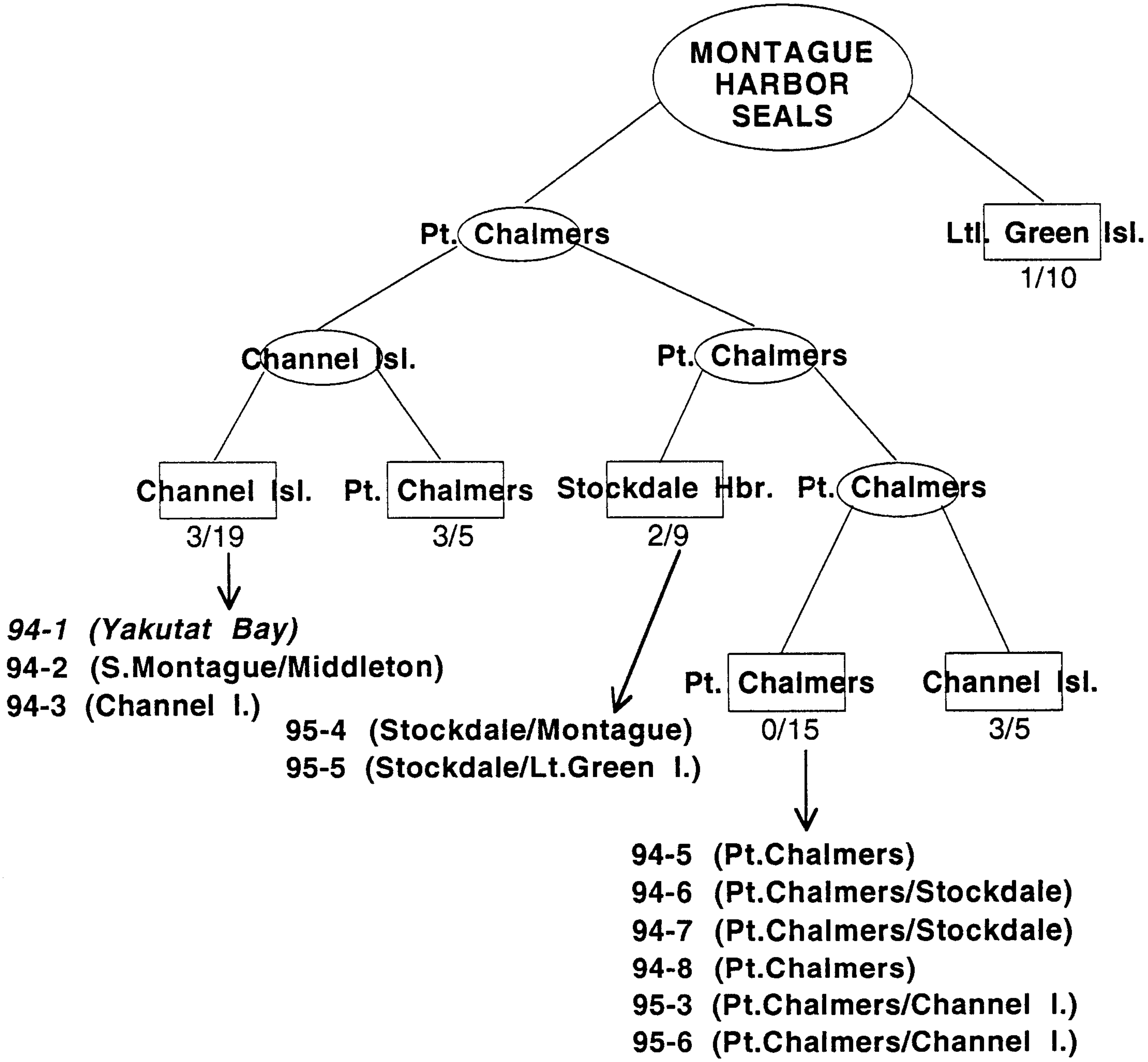


Figure 20. Location of satellite-tagged seals within 1994/1995 classification tree on a fine scale resolution within PWS at Montague Island. Almost all animals tagged remained at or near the specific haul-out site at which they were tagged throughout the study; only one left PWS for any period (to Yakutat) although may not have done so prior to fatty acid sampling. No tagged individual was misclassified.

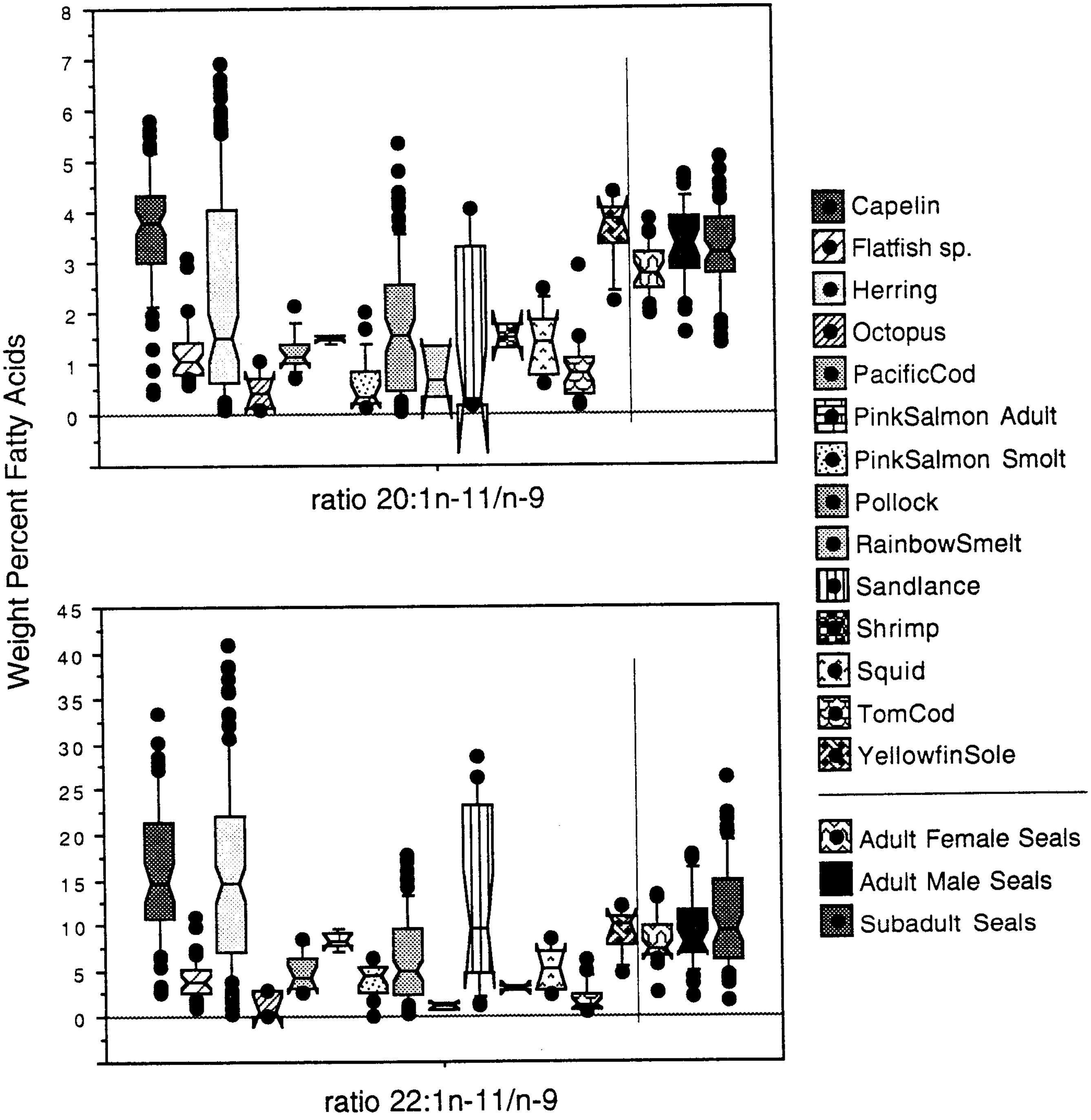


Figure 21. Box plots of selected isomer ratios in prey collected in PWS in comparison to that found in blubber of harbor seals from all areas of PWS (excluding NW PWS). The notched areas of each box is the 95% confidence interval on the mean; dots represent outliers. See Tables 1 and 3 for sample sizes.