Exxon Valdez Oil Spill
Restoration Project Annual Report

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

Restoration Project 98064
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 98064 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, 1996 Annual Report, and 1997 Annual Report. Fatty acid studies funded under Restoration Project 94320-F (Tropic Interactions of Harbor Seals in Prince William Sound) were included in the 1994 annual report for 94064. Fatty acid studies were continued under 95064, 96064, 97064 and 98064.

Abstract: The 1998 trend counts of harbor seals in PWS were 10%-13% higher than 1996-1997 counts Overall, counts were 18% lower in 1998 than 1990. We tested Bayesian model was more flexible. We caught and sampled 107 seals in 1997-1998 and attached satellite tags to 20 pups. Movements of pups were similar to non-pups, with most relocations near the tagging site. Fatty acid analysis has been conducted on 1,056 individual prey and 667 seal blubber samples, including 286 from the 1970s. Fatty acid signatures indicated that dietary differences between 1994-1995 and 1996-1997 were minor compared to differences between the 1970s, when PWS seals ate more pink salmon and smelt and less flatfish. Young PWS seals were in very good condition: in 1997 and 1998, pups were 43% and 39% body fat and yearlings were 23% and 27% fat. Diving behavior of non-pup seals showed a steady decrease in diving effort from February to July, and a preference for deeper dives in winter than in summer. Seals dove more actively in the middle of the night. Adults were more focused in their diving than subadults, and females were more focused than males.

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 1989-1998, morphometric measurements of all seals that have been caught and handled, location and dive data for 71 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, 1300 College Road, Fairbanks, AK 99701-6009. E-mail: kathy_frost@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 B3H4J1. E-mail: siverson@is.dal.ca. Phone (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.

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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. 98064 from October 1997 through September 1998, and some preliminary results from October 1998 through March 1999 under 99064. The report has been prepared as five chapters presenting: a) analysis of trend count surveys during 1990-1998 using Poisson regression, b) movements of satellite tagged harbor seal pups, c) foraging ecology as indicated by fatty acid analysis, d) Bayesian hierarchical models for estimating harbor seal trends, and 5) diving behavior of non-pup harbor seals.

The objectives for 98064 were modified somewhat from the objectives originally presented in the 3-year proposal submitted to the EVOS Trustee Council in 1995. It became clear from sensitivity analyses and simulations developed as part of the harbor seal population model that survival of age classes 0-4 has a large impact on the dynamics of the harbor seal population. The population would be far more sensitive to changes in survival of these age classes than to changes in adult survival. We also thought it likely that younger seals would be more sensitive to changes in food availability.

Initially, it was not possible to instrument small, subadult seals with satellite-linked depth recorders (SDRs) because the tags were too large. However, developments in satellite tag design meant that reliable 0.25-watt tags, small enough to be carried by pups, were available by summer 1997. With the newly acquired capability to monitor the movements and diving behavior of small seals, we changed the focus of this study to emphasize pups and juveniles. In lieu of instrumenting more adults during 1997 and 1998, we attached small satellite tags to newly-weaned pups (12 in 1997 and 8 in 1998). We also caught and sampled more yearlings and other subadults than in previous years.

These proposed modifications will provide us with a more well-rounded picture of what harbor seals in PWS are doing. It is clear from the tagging studies conducted to date that movement patterns of subadults and adults are different, and that subadults are more likely to range over a wider area. Since pups are thought to be an especially vulnerable age class, and also less flexible in the range of prey they can consume, it will be extremely valuable to obtain information on their movements and diving behavior.

Chapter 1 – Monitoring

In 1998, aerial surveys were flown during the molting period at 25 trend count haulout sites that have been monitored since 1984. The unadjusted mean count (830) was higher than counts in either 1996 or 1997. 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. When Poisson regression was used to adjust counts to a standardized set of survey conditions, results showed a highly significant decline of 2.4% per year. Adjusted molting period counts for 1998 were 18% lower than counts in 1990 (p=0.001). Overall, molt period counts have declined by 58% since the first trend count surveys were conducted in the early 1980s. These results show that the long-term decline has not ended.

Time of day was the most significant factor affecting the counts of seals during aerial surveys, followed by date, and time of count relative to low tide. Tide height was not significant. The model predicted that counts would have been highest in the period 2-4 hrs before midday, 1.5 hr before to 1.5 hr after low tide, and on the earliest survey dates in mid-August.

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. In response to these problems, we conducted a reanalysis this past year of trend count data using hierarchical Bayes models that relate observed seal count to covariates.

Chapter 2 – Tagging

In this report we summarize behavior and movements of twelve harbor seal pups tagged with SDRs in summer 1997. Seven of the seals were always located near the haulout where they were captured or near adjacent haulouts. One pup moved from Little Green Island where it was captured to Danger Island in mid-August and remained there until tracking stopped in early October. Two seals moved to northeastern PWS and visited tidewater glaciers in Unakwik Inlet and/or College Fiord. Three seals moved to Hinchinbrook Entrance and in some cases into the Gulf of Alaska.

Prior to the 1997 field season we had used only two 0.25 watt SDRs. A prototype that we attached to a subadult seal in fall 1995 performed erratically and was considered a failure (Frost et al. 1997). One that we attached in fall 1996 worked much better, giving regular locations over a period of 89 days. Tags deployed in 1997 lasted much longer, lasting from 21-313 days (average 152 days). Four of them transmitted for more than 200 days and one for 313 days. Locations were generally received on about 50% of the days the tags were attached. We cannot say for sure why some of the tags stopped sending signals after relatively short periods. Weaned harbor seal pups have a relatively high natural mortality rate, and it is likely that some of the seals died within a few months after tagging. Some may have experienced electronic failure. We think it unlikely that any of the tags were shed prematurely.

Fifty-seven seals were captured, sampled, and tagged in 1998, including 14 pups and 16 yearlings. Each seal was weighed, measured, and samples collected as follows: blood, blubber for fatty acids analysis, skin for genetics studies, and whiskers for stable isotope studies. Eight newly-weaned pups were instrumented with small 0.25-watt SDRs.

Chapter 3 – Foraging Ecology

Fat content has been determined for 1,052 individual prey in 15 taxa. Eulachon had the highest fat content of any species analyzed, averaging 19% fat, but reaching as high as 25% fat. Herring had the next highest average fat content (5-10% fat), but this ranged widely from 0.5 - 19.1%. The lowest fat contents (1%) tended to be found among some flatfish, shrimp and octopus. As illustrated most clearly in herring, the highest fat contents are found in the fall and lower contents in the spring and summer.

Fatty acid signatures were determined for 1,052 individual prey from PWS, representing more than 20 taxa (capelin, chum salmon, eulachon smelt, flathead sole, rex sole, rock sole, yellowfin sole, unidentified flatfish, herring, octopus, Pacific cod, pink salmon, pollock, rainbow smelt, rockfish, sandlance, sculpin, shrimp, squid (several species), and tomcod). Species were clearly distinguishable by their fatty acid signatures with an average of 93% accuracy. Groups of species, such as flatfish and salmon, were also predictable. Fatty acid signatures of prey such as pollock, capelin and herring also differed by size class and location, with season having little effect. For the first time in 1998, samples of herring were available from outside of PWS near Kodiak. Kodiak herring were comparable to general PWS and composition was well predicted by size class.

Blubber from 667 Alaska harbor seals has now been analyzed for fatty acids. Approximately two thirds of these were collected during this project. The rest were archived samples collected mostly in the 1970s by ADF&G. The estimation of actual diets from fatty acid signature analysis requires the development of an elaborate statistical model which uses prey species signatures to compute the most likely mixture of signatures which would "match" the signature of the seal. During 1998, our modeling to use fatty acids for estimating diet composition made considerable progress. However, the model still requires further developmental work in several areas, which we plan to address in the final year of this project. Alternative competing diets using changes in the model parameters need to be thoroughly investigated in order to provide an error estimate for diets. An ability to truly add in a prey variance component is still underway. At the moment, for instance, the model is having some difficulty in reliably distinguishing pollock and sandlance from herring in PWS, and this is almost certainly because we are using composite prey averages.

Realizing that the model is still in the developmental stage, we present some preliminary findings based on analyses of subsets of data collected from the 1970s and 1990s. Analysis of present day seals indicates that for both adults and subadults, diets in 1994 and 1995 were quite different than diets in 1996 and 1997. Diets in 1998 were quite similar to 1994-1995. The pronounced difference in diet among years is consistent with results from satellite tagged seals, which indicated that more seals fed outside of PWS, particularly in the Copper River delta, in 1996 and 1997 than in the previous two years.

The differences in estimated diets based on samples collected in the 1970s and samples from the 1990s were substantial. Differences for adults were much greater than for subadults. Based on these preliminary analyses, flatfish (and perhaps especially yellowfin sole) appear to be a large consistent proportion of the diet of most seals, both earlier and at present. Although previous analyses of harbor seal stomach contents from the 1970s do not suggest flatfish as such an important dietary component, discrepancies could result from methods used. Flatfish, especially yellowfin sole, represents one of the largest biomasses of finfish in the Bering Sea and GOA, hence they should be amply available to harbor seals. Furthermore, recent data from underwater cameras attached to harbor seals on the Scotian Shelf, suggest that flatfish are quite easy for harbor seals to catch and consume. This would argue for flatfish appearing consistently in the diets of less experienced juveniles as well.

While flatfish may be a consistent item in the diet of harbor seals, it may not be nearly as important - per gram fish - as consuming a species such as eulachon. Flatfish are low in fat and may be easy for juveniles to catch. However, if juveniles consume just 5%-7% of high-fat eulachon in their diet, they can fatten more readily. Certainly, juveniles studied in the past two years (1997-1998) have been found to be very high in body fat content and eulachon was prominent in all of these signatures. While diet composition tells us about the biomass eaten by seals, the contribution to the fatty acid signature may tell us what is most important to survival.

It appears that diets of PWS harbor seals in the 1970s were generally lower in flatfish and higher in pink salmon than present day. Diets of harbor seals at Kodiak Island in the 1970s were higher in sandlance and were more diverse than present day, containing substantial amounts of octopus, pink shrimp and squid in the 1970's. Evidence also suggests that adult diets are more diverse than diets of yearlings or half-year olds and contain prey such as octopus, pink salmon and squid. In contrast it would appear that juveniles do not catch these later items (and/or that these prey may be more difficult to catch) and instead depend on a more simple diet.

The current results of fatty acid signature analysis are very promising. Results suggest that determining diets or changes in diets over time is possible using fatty acid signatures and may provide clues not only to changes in foraging patterns, but also to differences in local prey availability or preferences by individuals. It may also provide information about predominant species size classes at the spatial and temporal scales that are essential to the nutrition of individual animals. However, as stated previously, the current estimates should be considered indeed as estimates, and future focus must be on further development and refinement of the model we have begun in order to have full confidence in our estimations.

Body composition was determined for 34 seals captured in June-July 1998. Newly weaned pups averaged 28 kg body mass and were 39% body fat. Although body mass of these pups was slightly but significantly lighter than pups in 1997, there was no significant difference in body fat content. In contrast, 1998 yearlings were significantly lighter than yearlings in 1997 but were also significantly fatter. Older subadults in 1998 averaged a remarkably high 23-26% body fat, which again, appeared to be higher than those measured in 1997, however this could not be tested due to small sample sizes. When compared to harbor seal pups at Sable Island, Nova Scotia, fat content was similar but body mass averaged 3-7 kg greater. PWS yearlings were almost double the fat content of Sable Island yearlings.

Chapter 4 – Bayesian analysis

As a pilot project in 1998, we used Bayesian hierarchical models to assess trends of harbor seals in PWS. In our previous trend analyses, Poisson regression was used to adjust counts to a standardized date, time of day, and time relative to low tide. Then linear regression was used to assess trend for the adjusted counts. The whole procedure was bootstrapped to assess significance of trends. We found several problems with this method. First, the number of estimated parameters was very large. Second, we wished to develop models for each site, but it was difficult to combine trend estimates from each site into an overall assessment of trend. The Bayesian hierarchical model helped solve these problems by using a Poisson regression model for each of the 25 sites, where the mean of the Poisson distribution depended on the factors: 1) year, 2) time of year, 3) time of day, and 4) time relative to low tide. Then, the 25 site parameters for each factor in the Poisson mean were given a normal distribution. Results showed that at most sites, 1) counts decreased yearly, 2) counts decreased throughout August and September, 3) counts decreased throughout the day, and 4) counts were at a maximum just a few minutes before low tide; however, there was considerable variation among sites. To get overall trend we used a weighted average of the trend at each site, where the weights depended on the overall abundance of a site. The overall trend, like the Poisson regression analysis, indicated a continued significant decrease in the harbor seal population. Comparison of methods showed similar parameter estimates, but the Bayesian hierarchical model allowed more flexible use of trend indices in a single statistical framework.

Chapter 5 – Diving Behavior

We have been deploying satellite depth recorders (SDRs) on harbor seals in PWS since 1993. Valuable data have been obtained from these tagged seals, particularly the details of when and where they move. To date other data provided by the SDRs have not been thoroughly analyzed, in large part because individual variability and summing of SDR dive data into bins have made analyses using standard statistical techniques difficult. For this reason, we have been working to develop a statistically robust analytical method that accounts for individual variability, temporal autocorrelation, and the binned nature of data. We used this method to analyze the diving behavior of 37 harbor seals tagged with SDRs in PWS during 1993-1996. Repeated measures mixed models for effort, focus, and preferred depth bin were created using the MIXED procedure in SAS.

Models indicated that diving effort remained steady throughout winter, then declined from February to July. Preferred depth was deepest during winter and shallowest during May-July. Diving was shallow and focused in Copper River Delta and Cook Inlet and deeper and less focused near Yakutat and southwest of Montague Island, reflecting regional bathymetry. Collinearity between month and region in the preferred depth model suggests that seals migrate to regions of deeper preferred depth in winter, perhaps indicating a seasonal cycle in type or depth of prey. The steady decrease in diving effort during spring and summer indicates that seals gradually increase the proportion of time they spend hauled out as the molt period approaches. However, diving effort increased abruptly in September, making it clear that surveys to estimate population size must be carefully timed.

Diurnal and demographic changes in diving behavior were minor but significant. Diving effort was greatest at night (2100-0300 hrs), and most focused during the day (0900-1500 hrs). Diving was more focused for females than males, and for adults than subadults. These insights into foraging and hauling out behavior have practical management applications for improving surveys and evaluating habitat use by season, region, and depth.

CHAPTER ONE

MONITORING THE TREND OF HARBOR SEALS IN PRINCE WILLIAM SOUND, ALASKA, AFTER THE *EXXON VALDEZ* OIL SPILL

OBJECTIVE 1

Monitor the abundance and trends of harbor seals at trend count sites in oiled and unoiled areas of PWS to determine whether the PWS harbor seal population has declined, stabilized, or increased since the EVOS.

OBJECTIVE 2

Recommend a schedule for continued aerial survey monitoring based on observed trend and statistical characteristics of survey data.

OBJECTIVE 9

Provide information to subsistence hunters so they can make informed decisions about the appropriate level of harvest for harbor seals.

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MONITORING THE TREND OF HARBOR SEALS IN PRINCE WILLIAM SOUND, ALASKA, AFTER THE *EXXON VALDEZ* OIL SPILL

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ABSTRACT

We used aerial counts to monitor the trend in numbers of harbor seals, *Phoca vitulina richardsi*, in Prince William Sound, Alaska, following the 1989 *Exxon Valdez* oil spill. Repetitive counts were made at 25 haulout sites during the annual molt period each year from 1990 through 1998. Unadjusted counts indicated no consistent trend in the number of seals. However, a generalized linear model indicated that time of day, date, and time relative to low tide significantly affected seal counts and should be taken into account during data analysis. When Poisson regression was used to adjust counts to a standardized set of survey conditions, results showed a highly significant decline of 2.4% per year. The number of harbor seals on the trend count route in eastern and central PWS has been declining since at least 1984 with an overall population reduction of 57% through 1998. Adjusted 1998 counts were higher than either of the two previous years, but it is too soon to know whether this is the beginning of an increase in numbers or simply due to annual variability in counts.

Programs to monitor long-term changes in animal population sizes should account for factors that can cause short-term variations in indices of abundance. The inclusion of such factors as covariates in models can improve the accuracy of monitoring programs.

Key words: aerial surveys, *Exxon Valdez* oil spill, generalized linear model, harbor seal, *Phoca vitulina richardsi*, Poisson regression, population monitoring, Prince William Sound, trend analysis

NOTE: An earlier version of this chapter, including data through 1997, was published in the April 1999 issue of the journal Marine Mammal Science.

INTRODUCTION

Monitoring programs to track long-term changes in population size are increasingly important in applied ecological studies. While indices of abundance have long been used in classical wildlife management, they have assumed additional importance in recent years as a means of measuring anthropogenic impacts on the natural world, and the recovery, or lack thereof, from such impacts. Along with the realization of the importance of monitoring and environmental assessment programs has come increased attention to the design of such programs (Eberhardt and Thomas 1991, Taylor and Gerrodette 1993, Link et al. 1994) and their analysis (Mapstone 1995, Thomas and Martin 1996, Craig *et al.* 1997).

Harbor seals are one of the most common marine mammal species in Prince William Sound (PWS), Alaska, and adjacent parts of the Gulf of Alaska. PWS has over 4,800 km of coastline, consisting of many fiords, bays, islands, and offshore rocks. The exact number of harbor seals inhabiting the region is unknown, but is at least several thousand (T. R. Loughlin, unpublished report, National Marine Mammal Laboratory, NMFS, Seattle, WA.). Between 1984 and 1988 the number of seals counted at haulout sites in eastern and central PWS declined by about 40% (Frost et al. 1994a).

On 24 March 1989, the *T/V Exxon Valdez* ran aground on Bligh Reef in northeastern PWS, spilling approximately 40 million liters of crude oil (Morris and Loughlin 1994). Studies conducted as part of a "Natural Resources Damage Assessment" program documented a substantial impact of the spill on harbor seals (Frost *et al.* 1994a & b, Lowry *et al.* 1994, Spraker *et al.* 1994). Approximately 300 seals were estimated to have died due to the spill, and pup production in 1989 was about 26% lower than normal (Frost *et al.* 1994a). Subsequent to the oil spill as part of damage assessment and restoration science studies programs, monitoring of the harbor seal population was continued by flying aerial surveys during 1990-1998.

Many studies have demonstrated effects of time of day, date, and tide on the hauling out behavior of harbor seals (Schneider and Payne 1983, Stewart 1984, Harvey 1987, Pauli and Terhune 1987, Yochem *et al.* 1987, Thompson and Harwood 1990, Moss 1992). The data to describe those behavioral patterns have usually come from continuous or repetitive visual observations of seal haulouts, or from telemetry studies. Information derived from those studies has been used in the design of harbor seal surveys, to the extent that survey programs are generally designed to occur on dates and at times when the greatest number of seals are expected to be out of the water and available for counting (Pitcher 1990, Harvey *et al.* 1990, Olesiuk *et al.* 1990, Huber 1995). However, once a "survey window" has been established counts have usually been treated as replicates during analyses, and the possible effects of other factors on annual abundance estimates have been ignored.

This paper presents an analysis of aerial survey counts of harbor seals in PWS. The objectives are to: 1) describe how covariates affected counts of harbor seals during surveys; 2) use the covariates to adjust haulout counts; and 3) determine whether or not significant population trends have occurred.

METHODS

Aerial Surveys

We conducted aerial surveys along a trend count route that covered 25 harbor seal haulout sites in eastern and central PWS (Figure 1). The route included 7 sites that were substantially affected by the *Exxon Valdez* oil spill and 18 unoiled sites that were outside of the primary affected area (Frost *et al.* 1994a). In addition, during 1998, we added several sites that include substantial numbers of seals but were not part of previous trend count routes. These included the Dutch Group in northwestern PWS, Hanks Island near the Sheep Point haulout, and Double Bay to the west of Canoe Pass. Surveys were flown during the molting period (August-September) in 1984 and 1988-1998.

Visual counts of seals were conducted from a single-engine fixed-wing aircraft (Cessna 185) at altitudes of 200-300 m, usually with the aid of 7-power binoculars. Counts were usually conducted from two hours before low tide to two hours after low tide. A survey normally included counts at all 25 sites, but occasionally some sites could not be counted because of poor weather or a rapidly rising tide. For each survey the date, time and height of low tide, and time of sunrise and sunset were recorded. Each site was circled until the observer was confident that an accurate count had been made, and the time of the count was recorded. For larger groups of seals (generally those of 40 or more) color photographs were taken using a hand-held 35-mm camera, and seals were counted from images projected on a white surface. Each year several survey flights, usually 7-10, were made.

Factors Affecting when Seals are Hauled Out

We used a generalized linear model (McCullagh and Nelder 1989) with a log link function and a Poisson distribution to analyze the factors that may affect the number of seals hauled out and available to be counted during surveys. The model may be written as: $\Pr(Z_{tij} = z) = \exp(-\lambda_{tij})\lambda_{tij}^{z} / z!$ with $ln(\lambda_{tij}) = \beta'\mathbf{x}_{tij}$ where β is a parameter vector and $\mathbf{x}_{tij}$ is a vector containing information on the state of covariates: year, site, time of tide, height of tide, time of day, date for the j^{th} flight at site i in year t.

To estimate the average count at each site in any given year, we first used a model that contained site, year, and the interaction of site by year. These factors were used in all models. Then, effects for time of day, time of low tide, date, and tide height were entered into the model one at a time. If a factor with m parameters increased 2*log-likelihood by more than a χ^2-distribution with m degrees of freedom at α=0.05, we considered the factor to affect significantly the number of seals counted at haulouts. The factor with the largest 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 not significant. Time of day and time relative to low tide were analyzed as categorical data. Time increments before and after midday were placed in six separate categories and increments before and after low tide in eight categories. We combined some categories within a factor when preliminary analysis indicated that it could be done without changing the fit (again, if combining two categories decreased 2*log-likelihood by more than a χ^2-distribution with one degree of freedom, we considered that the fit was essentially unchanged). Date was a continuous variable entered into the model as a polynomial up to a quadratic power. Dates were numbered beginning 15 August and scaled so that each day was equal to 0.1 to keep parameter estimates from becoming too small (causing problems with significant digits in software packages). To construct the initial model, we used data from all surveys conducted during 1984-1997.

After obtaining a parsimonious model and fitting the parameters as described above, the count data were adjusted to a standardized set of covariates. The adjustment amounts to estimating counts at each site for each year as the expected count under optimal conditions.

Trend Analysis

A linear regression model was fitted to the adjusted yearly count estimates for 1990-1998. This model assumes constant amount of change per year. We also considered a model on the log-scale, where the rate of change is constant. Again, we used a generalized linear model (McCullagh and Nelder 1989) with a log link function and a Poisson distribution to model trend through time. This is also called Poisson regression. Linear and Poisson regressions were also fitted to the unadjusted counts.

This analysis was complicated because we first adjusted yearly counts for each site to a standardized date, time of day, and time relative to low tide, then summed over sites to get a yearly index, and then used the index in a trend regression analysis. Under these circumstances, it is difficult to pass the uncertainty associated with adjusting the counts to the trend analysis. Therefore, we used bootstrap methods (Efron and Tibshirani 1993, Manly 1997) for the whole procedure. We resampled with replacement from the daily flights for each year, with the number of resamples equal to the actual number of flights for that year. After obtaining the bootstrap sample, we used the generalized linear model to re-estimate parameters, adjusted the counts based on the bootstrap parameter estimates, and then did both linear and Poisson regression trend estimation on the bootstrap samples. The trend parameters from the bootstrap appeared symmetrically distributed and centered on the original parameter estimate. Bootstrapping the whole procedure was quite computer intensive and only 200 resampled estimates were obtained, so we used the standard bootstrap method by taking,

$$\text{estimate} \pm z_{\alpha/2}(\text{Bootstrap Standard Deviation})$$

(Manly 1997) and if 0 was contained in the interval, there was little evidence of trend for the stated α-level.

Bootstrapping was used to estimate variance of the unadjusted counts by resampling from the actual count values for each site in each year.

RESULTS

Survey Effort

Most sites were surveyed six or seven times during 17-25 August (Table 1). A few sites which have had zero counts for the past several years (such as Storey Island and Payday) were surveyed fewer times to speed up the surveys and allow us to narrow our survey window relative to time of low tide. Three new sites were added to the survey route in 1998: Double Bay, Hanks Island, and the Dutch Group. Double Bay is directly en route between Canoe Pass and Schooner Rocks, and thus easily added to the route. Double Bay had an average of 31 seals in 1998. The Dutch Group is the largest rocky haulout site in northern PWS, and was one of the four largest sites we counted on our survey route. We thought it was important to add such a significant site since most other haulouts in the northern sound have declined to just a small number of seals that are intermittently present. Hanks Island is very near to Sheep Point, which now appears to be abandoned, and may have replaced Sheep Point as the haulout in that area.

Factors Affecting when Seals are Hauled Out

Three primary factors significantly affected the counts of seals during aerial surveys (Table 2). Time of day was the most significant factor, followed by date, and time of count relative to low tide ($P < 0.001$ for all three). Tide height was not significant.

The model predicted that counts would have been highest in the period 2-4 hrs before midday with 24% more seals expected than 2-4 hrs after midday (Figure 2a). (These calculations are obtained from Table 2 by taking the exponent of the parameter estimates; e.g., exp (-0.2767) = 0.758, or 24.2% lower counts in the period 2-4 hours after midday). Relative to low tide, the model predicted the highest counts from 1.5 hr before to 1.5 hr after low tide, with substantially lower counts (about 29% lower) more than 1.5 hrs after low tide (Figure 2b).

With regard to date, the model predicted that the highest counts would have occurred on the earliest survey dates, and that there would be an approximately linear decrease in counts throughout the survey period (Figure 2c). Relative to 15 August, counts would have been 21% lower on 31 August and 44% lower on 16 September. The effects of these three factors were combined in a model for all survey years that reflected "optimum" conditions for time of day, tide and date. The "adjusted counts" derived from this model are shown in Table 3.

Trends in Seal Counts

Annual changes in both unadjusted and modeled adjusted counts were substantial (Table 4). Unadjusted counts ranged from 23% below to 17% above the previous year's counts, and regression analysis indicated no significant trend (Table 4; Figure 3a).

Annual adjusted counts were 19%-77% higher than unadjusted counts, depending on time, tides and dates the surveys were flown (Table 4). The adjusted counts showed a significant decline in the number of seals in the trend area with linear ($P = 0.01$) and loglinear ($P = 0.002$) regression analysis (Figure 3a). A examination of post-spill adjusted counts for sites that were and were not oiled in 1989 indicated no obvious difference in trend between the two groups of sites (Figure 3b)..

DISCUSSION

Factors Affecting Harbor Seal Counts

We were concerned about the effects that date, time of day, and tide might have had on our aerial survey counts. There are several ways to deal with covariate effects in study design. The best approach that results in the least variability is to design the study so that the potential covariates are constant. For example, for harbor seals we would like to sample on consecutive days from 15-21 August, at 10:00 am, and at slack low tide. However, the fact that weather conditions and the time and height of low tide on a particular date vary from year to year precludes such an approach. Another approach is to randomize sampling relative to the covariate. For example, if survey dates are chosen randomly from within the general molt period the effect of that covariate across years would "cancel out." This would result in more variability than keeping the covariates constant, but it is still design-unbiased, so simple linear or nonlinear trend models could be used to examine trend. However, it would only be possible to use this approach for one covariate such as date, and that would be logistically impractical. The third approach, the one we adopted, is to sample over a one to two week period as weather allows, and then use a model to adjust the counts to a standard set of conditions.

Aerial surveys are commonly used for assessing abundance of harbor seals. Most survey programs try to use a relatively narrow and standard "survey window" (i.e., they attempt to hold covariates constant). Some investigators have used correction factors to adjust counts to account for certain measurable covariate effects. Olesiuk et al. (1990) used a correction factor to adjust for differences in dates of surveys relative to the pupping season. Thompson and Harwood (1990) used time-lapse photography to measure changes in the number of seals hauled out relative to time of day, then used that relationship to standardize aerial counts. Frequently, however, the assumption has been made that some or all potential covariate effects are unimportant and that ignoring them will have little effect on interpretation of results.

Our analysis showed that time of day, date, and time relative to low tide all significantly influenced harbor seal counts in PWS, and an assumption that covariate effects were negligible would have been erroneous. The model predicted counts to be highest before midday, and within 1.5 hours of low tide. The model also predicted that peak counts would occur earlier in August than our surveys historically have begun, and that counts would decrease from the earliest survey date throughout the survey period. Our purpose in developing this model was to understand the factors affecting our counts, not to describe the behavior of harbor seals. Nonetheless, the results are consistent with those of investigators who have conducted behavioral studies of harbor seals in that the proportion of seals hauled out is related to date, time of day, and tide.

Many studies have shown that there are site-specific variations in harbor seal behavior patterns depending on habitat type, effects of disturbance, and other factors (*e.g.*, Harvey 1987, Olesiuk et al. 1990, Moss 1992, Thompson *et al.* 1997), and therefore parameter values for covariate effects could vary greatly in different situations. If annual counts are to be used to monitor harbor seal trend in an area, studies should be done to assess factors that could influence seal behavior at that locale (Thompson *et al.* 1997). Results from those studies can be used for designing an initial survey protocol, as well as to select variables that should be recorded during surveys and used in subsequent data analyses.

Trend in Harbor Seal Numbers in PWS

Our analysis of PWS harbor seal counts showed that adjusting counts to consider variation in survey conditions greatly improved our ability to detect a trend. If we ignored the possible effects of covariates and looked only at unadjusted counts we would have concluded that, although there was a negative slope to the regression line, the trend in seal numbers during 1990-1998 was not significant. When we considered covariates and counts from each year were "normalized" to standard conditions, the decline in seal numbers became highly significant. Because the model corrects each individual count for three covariates it is difficult to determine which aspects of survey design biased the interpretation of results from unadjusted counts. A partial explanation can be seen in the effect of date. During 1990-1994, the median dates for our surveys ranged from 27 August to 4 September, while the median dates during 1995-1998 were 21-23 August. Because a lower proportion of seals would be hauled out on later survey dates, counts made in earlier years were biased low therefore masking the declining trend in abundance.

The adjusted count of seals on the trend route in 1998 was 18% lower than in 1990, indicating that the population has been declining at an average rate of 2.4% per year. This is lower than the estimated rate of decline for 1990-1997 (-4.6%) suggesting that the population may be starting to stabilize.

The number of harbor seals on the trend count route in eastern and central PWS has been declining since at least 1984 (Frost *et al.* 1994a). Using the parameter estimates derived in this study to correct the 1984 count data we estimate an adjusted trend route count of 2,488 seals for that year. This indicates an overall population reduction of 58% during the period 1984-1998.

One objective of studies done in PWS subsequent to the *Exxon Valdez* oil spill has been to monitor recovery of injured species. In the case of harbor seals, the *Exxon Valdez* Oil Spill Trustee Council has determined that recovery will have occurred when the population trend is stable or increasing. Based on this study, we conclude that as of 1998 harbor seals in PWS have not yet recovered from the oil spill.

Significance to Monitoring Studies

Measurement of the trend in abundance of a population is an important tool for wildlife conservation. For example, as noted above, the decision of whether or not harbor seals in PWS have "recovered" from the *Exxon Valdez* oil spill depends entirely on whether or not the population is still declining.

In some cases it may be possible to use survey data to assess population trends without concern for covariate effects, for example where changes are relatively large, data are collected over long periods of time, and study design holds covariates relatively constant. The conclusion that harbor seal numbers on Tugidak Island in the Gulf of Alaska underwent a major decline appears reliable, as counts were made under strict conditions, the decline was large (about 85%), and data were collected over a 12 year period (Pitcher 1990). Confidence in the Tugidak situation is increased by the fact that similar trends were seen in both pupping and molting period counts. Conclusions that harbor seal numbers have increased in southern California (Stewart *et al.* 1988), Oregon (Harvey *et al.* 1990), and Washington (Huber 1995) also are likely to be correct, although in those studies counts were made in a relatively wide range of conditions and consideration of covariates in data analyses would likely improve the assessment of trends.

Where covariates have strong effects that cannot be avoided in study design they must be accounted for in the analysis. For example, Beaufort state and cloud cover have strong effects on counts of harbor porpoise (*Phocoena phocoena*), and therefore Forney *et al.* (1991) used those factors as covariates in their trend analysis. In an analysis of Florida manatee (*Trichechus manatus latirostris*) aerial survey data, Garrott et al. (1995) modeled the effects of survey conditions and air and water temperature on counts. About 50% of the variation in counts was explained by those variables, and when counts were adjusted for covariate effects a significant increase was seen in the number of manatees counted on the east coast of Florida during 1982-1991.

In many situations, analyses of the kind we performed are not possible because data have been collected intermittently, inconsistently, or for only a few years. In the case of PWS harbor seals these analyses were possible, and useful, because there was a consistent, relatively long-term data set from which to develop models for use in adjusting data. The PWS example demonstrates the importance of long-term, cost-effective monitoring programs that allow the evaluation of population trends, and can also provide a way to measure the impacts of human activities or accidents such as the *Exxon Valdez* oil spill.

ACKNOWLEDGMENTS

This study was conducted as part of the *Exxon Valdez* Oil Spill Restoration Program, funded by the *Exxon Valdez* Oil Spill Trustee Council. Funding for harbor seal surveys in PWS in 1992 was provided by the National Marine Fisheries Service, National Marine Mammal Laboratory. Ken Pitcher conceived the idea of harbor seal trend counts in PWS, and Dennis McAllister and Jon Lewis flew some of the earlier surveys. We thank Steve Ranney, the pilot for all of the aerial surveys, for his careful and conscientious support. Rob DeLong assisted with data analyses and presentation. Dean Hughes, Joe Sullivan, Sheila Westfall, Melanie Bosch, Melissa Johnson, and Diana Ground provided administrative support for this project. Grey Pendleton, Tim Gerrodette, Jeff Laake, and an anonymous reviewer provided helpful comments.

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Table 1. Unadjusted daily counts of harbor seals at selected haulouts in Prince William Sound, 17-25 August 1998.

	17-Aug	18-Aug	19-Aug	20-Aug	22-Aug	23-Aug	25-Aug	Site Mean	N
Hanks Island	3	5	0	-	2	3	6	3	6
Sheep Pt	2	0	0	-	0	4	0	1	6
Gravina Island	0	0	4	-	0	31	20	9	6
Gravina Rocks	35	25	29	-	37	50	44	37	6
Olsen Bay	87	91	79	-	40	71	79	75	6
Porcupine	0	0	0	-	0	0	-	0	5
Fairmount	0	9	10	-	0	8	17	7	6
Payday	0	0	0	-	-	-	0	0	4
Olsen Island	0	0	0	-	-	0	0	0	5
Point Pellew	2	2	1	-	-	-	5	3	4
Little Axel Lind	0	0	0	-	-	0	0	0	5
Dutch Group	165	111	136	-	130	151	129	137	6
Storey Island	0	0	0	-	-	-	-	0	3
Agnes Island	36	34	45	-	57	56	59	48	6
Little Smith Island	1	6	3	1	4	5	12	5	7
Big Smith Island	12	16	28	-	56	46	29	31	6
Seal Island	42	28	28	33	39	37	40	36	7
Applegate Rocks	165	171	142	80	128	102	127	139	7
Green Island	4	0	6	1	20	31	17	13	7
Little Green Island	13	12	21	13	52	41	24	27	7
Channel Island	113	137	-	63	87	106	99	108	6
Port Chalmers	121	115	135	86	134	118	147	128	7
Stockdale Harbor	21	15	20	2	31	30	35	25	7
Montague Point	0	0	1	0	3	0	0	1	7
Rocky Bay	60	51	48	5	45	52	57	52	7
Schooner Rocks	36	27	22	15	36	42	32	33	7
Canoe Pass	41	9	37	19	79	78	67	52	7
Double Bay	-	4	12	4	49	50	39	31	6

Table 2. Parameter estimates for factors affecting counts of hauled out harbor seals in Prince William Sound. Estimates are based on data collected 1984-1998.

Factor	Category	Parameter estimate
Time of day	before (midday - 4 hr)	-0.0415
	(midday - 4 hr) to (midday - 2 hr)	-0.0000
	(midday - 2 hr) to (midday)	-0.1096
	(midday) to (midday + 2 hr)	-0.1717
	(midday + 2 hr) to (midday + 4 hr)	-0.2767
	after (midday + 4 hr)	-0.1717
Date	day/10 since August 15	-0.1063
	$(\text{day}/10)^2$ since August 15	-0.0236
Time relative to low tide	before (lowtide - 1.5 hours)	-0.1667
	(lowtide - 1.5 hrs) to (lowtide - 1 hr)	-0.0436
	(lowtide - 1 hr) to (lowtide - 0.5 hr)	0.0000
	(lowtide - 0.5 hr) to (lowtide)	-0.0608
	(lowtide) to (lowtide + 0.5 hr)	0.0000
	(lowtide + 0.5 hr) to (lowtide + 1 hr)	-0.0608
	(lowtide + 1 hr) to (lowtide + 1.5 hrs)	0.0000
	after (lowtide + 1.5 hrs)	-0.3373

Table 3. Adjusted mean counts of harbor seals at selected haulout sites in Prince William Sound, August-September 1990-1998.

	1984	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**
Sheep Point	60.8	23.2	0.0	0.4	0.9	0.6	6.4	0.0	0.5	0.0	0.0	1.5
Gravina Island	35.4	22.6	34.6	8.7	17.8	35.5	22.4	14.3	22.0	29.9	18.5	12.7
Gravina Rocks	60.0	76.8	59.7	36.0	35.5	46.1	59.4	82.3	73.0	49.4	70.5	47.8
Olsen Bay	202.6	136.3	75.3	121.1	107.1	61.2	105.2	68.6	141.7	139.7	128.4	97.1
Porcupine	41.0	6.0	12.0	1.1	19.3	10.5	3.8	1.1	0.0	0.0	0.0	0.0
Fairmount	132.8	70.9	59.0	36.9	22.9	16.9	26.6	3.1	22.1	0.0	10.2	9.8
Payday	15.9	2.8	2.7	6.2	6.3	0.3	0.4	0.2	0.0	0.0	0.0	0.0
Olsen Island	53.9	20.6	12.8	16.7	13.1	6.0	3.2	6.6	0.0	0.0	3.5	0.0
Point Pellew	31.3	33.5	42.6	37.1	29.9	17.9	14.0	0.2	4.4	8.5	5.4	3.3
Little Axel Lind	37.8	31.4	41.0	24.4	13.3	9.7	3.6	0.0	0.0	0.0	0.0	0.0
Storey Island	15.6	8.0	5.2	4.1	0.6	0.2	0.4	0.0	0.4	0.0	0.0	0.0
Agnes Island	111.1	62.9	60.6	59.2	50.7	63.9	31.8	54.5	69.6	47.0	55.9	61.6
Little Smith Island	106.7	52.2	37.7	47.9	32.2	46.6	35.4	40.7	50.5	27.8	23.4	6.5
Big Smith Island	133.1	132.9	68.9	47.0	44.2	62.2	51.6	62.5	33.3	36.7	56.4	39.1
Seal Island	152.2	123.8	62.7	63.1	83.4	72.6	58.5	61.4	38.6	47.8	18.4	44.8
Applegate Rocks	303.2	266.4	157.2	191.9	138.3	89.7	78.7	89.9	176.7	177.5	101.6	173.9
Green Island	83.0	77.0	31.1	40.1	32.2	54.5	40.6	36.7	14.3	15.2	23.9	16.2
Channel Island	406.7	153.8	167.5	61.6	135.1	119.6	171.1	92.4	123.4	59.2	101.9	123.7
Little Green Island	81.0	91.6	55.9	49.0	20.0	81.5	68.4	40.2	48.2	33.7	55.5	32.2
Port Chalmers	103.5	130.0	117.6	159.3	139.9	94.8	164.4	106.1	107.7	98.0	89.3	172.9
Stockdale Harbor	52.8	84.0	79.6	78.2	59.8	64.4	20.4	48.5	44.1	48.3	27.9	33.1
Montague Point	74.0	58.4	62.7	59.9	35.3	14.6	1.7	9.3	0.9	0.2	1.2	0.9
Rocky Bay	58.5	20.1	33.6	17.9	26.4	36.2	31.3	58.1	76.2	62.0	48.1	67.4
Schooner Rocks	113.0	119.1	106.4	75.2	70.9	87.8	93.6	49.5	36.3	36.1	46.0	41.5
Canoe Passage	22.0	70.4	36.8	39.4	64.5	39.4	32.7	54.9	42.5	44.9	43.0	66.7
Totals	**2487.8**	**1874.6**	**1423.4**	**1282.5**	**1199.6**	**1132.7**	**1125.5**	**981.3**	**1126.4**	**961.8**	**928.9**	**1052.7**

CHAPTER TWO

TAGGING OF HARBOR SEAL PUPS IN PRINCE WILLIAM SOUND WITH SATELLITE-LINKED DEPTH RECORDERS, 1997-1998

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OBJECTIVE 8

Determine foraging range and diving behavior of harbor seal pups and juveniles and compare to similar information for other age groups.

Table 4. Unadjusted and adjusted mean counts, and regression analyses, for harbor seal trend counts in Prince William Sound, 1990-1998. Adjusted counts were derived using parameter estimates in Table 1. Standard deviations of slope estimates were calculated by bootstrapping.

Year	Unadjusted Count	Adjusted Count	% Difference Unadj. & Adjusted
1984	1796	2488	+39
1988	1057	1875	+77
1989	815	1423	+75
1990	779	1282	+65
1991	920	1200	+30
1992	769	1133	+47
1993	774	1126	+45
1994	740	981	+33
1995	869	1126	+30
1996	808	962	+19
1997	751	929	+24
1998	830	1053	+27
linear regression			
slope estimate	-3.929	-38.479	
standard deviation	4.770	16.540	
Pr (H_0: slope=0)	0.2050	0.0100	
loglinear regression			
slope estimate	-0.0049	-0.0338	
standard deviation	0.0060	0.0120	
Pr (H_0: slope=0)	0.2054	0.0025	

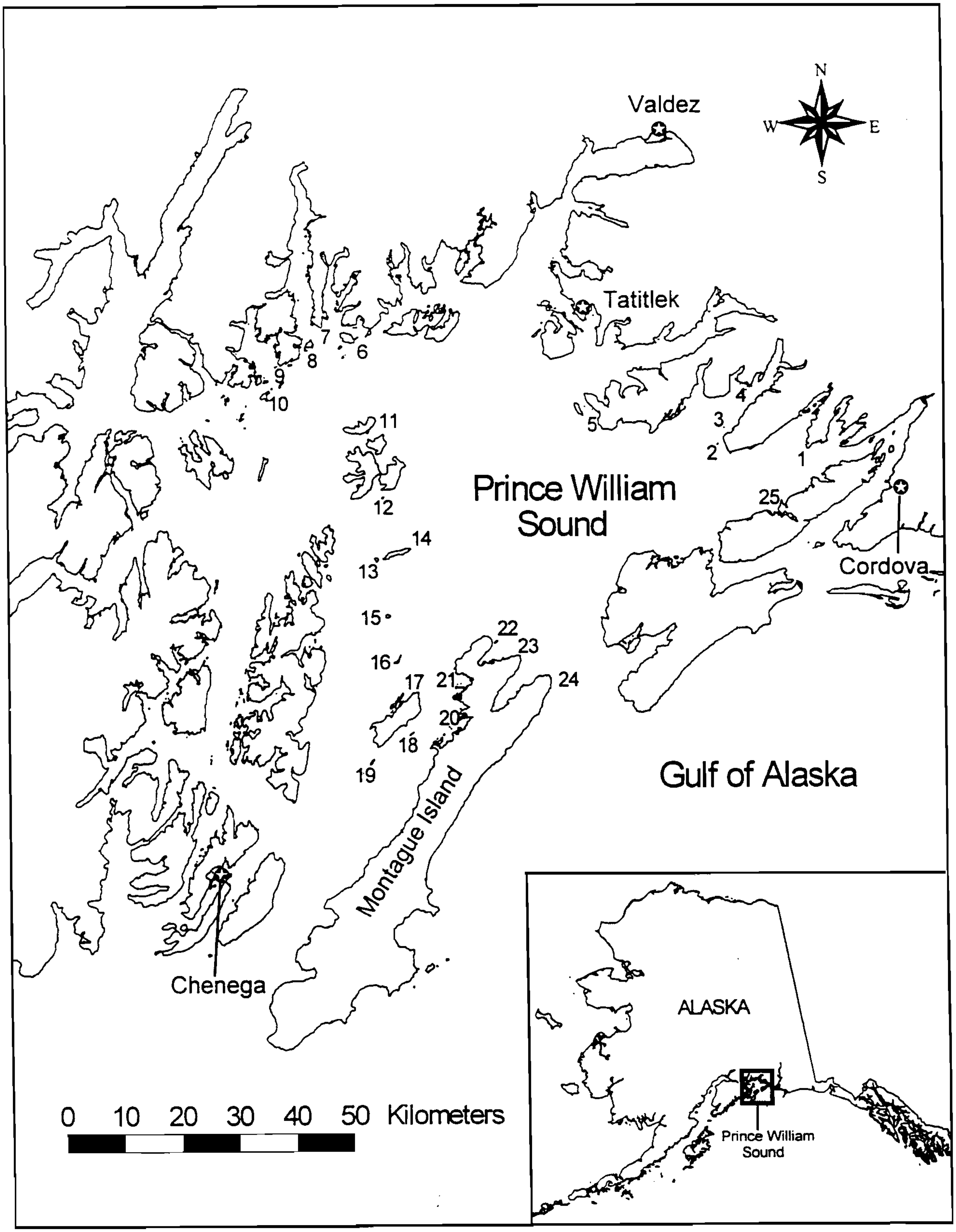


Figure 1. Map showing trend count sites for aerial surveys of harbor seals in Prince William Sound, Alaska, 1984-1998. Sites 11-17 were oiled by the *Exxon Valdez* oil spill.

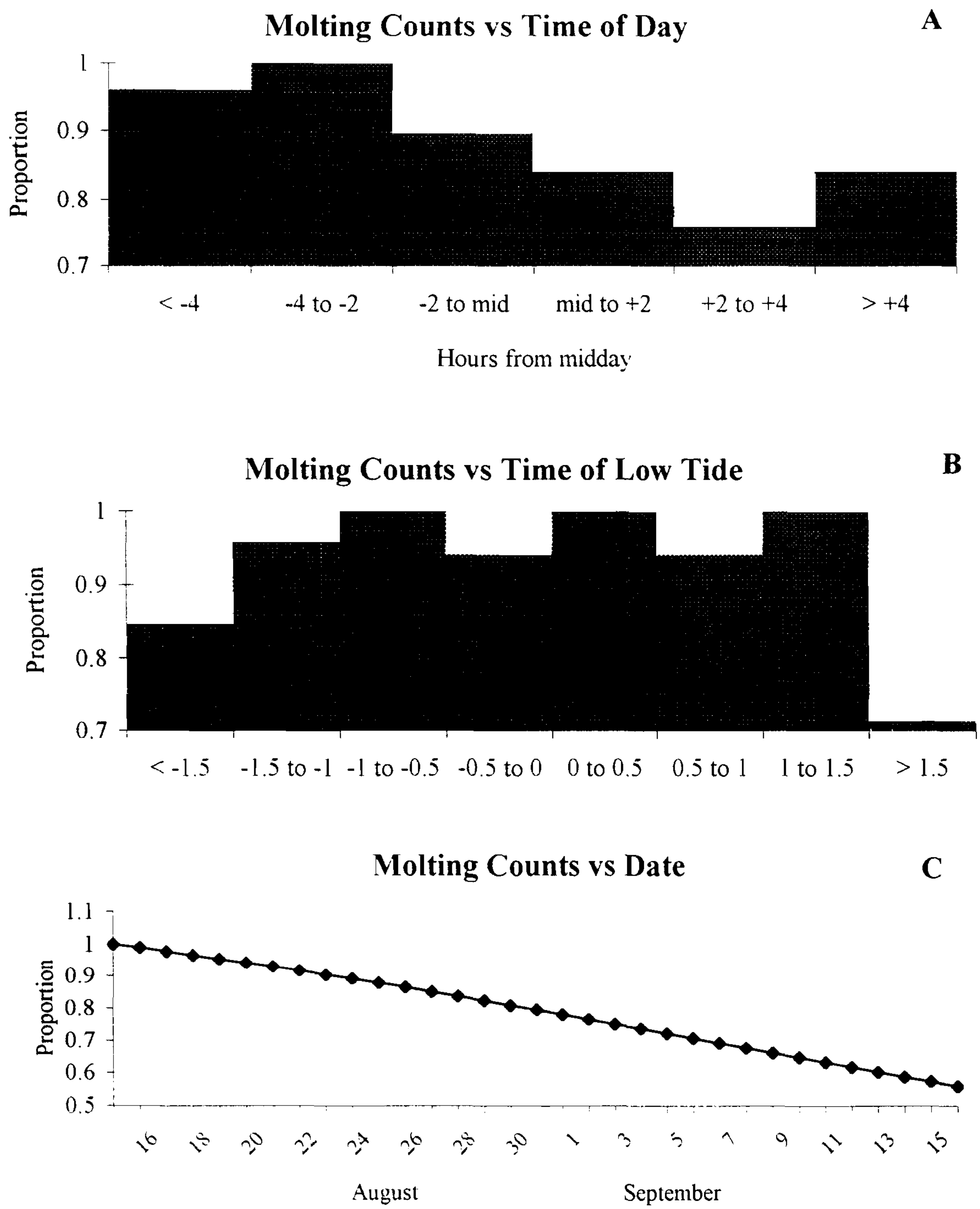
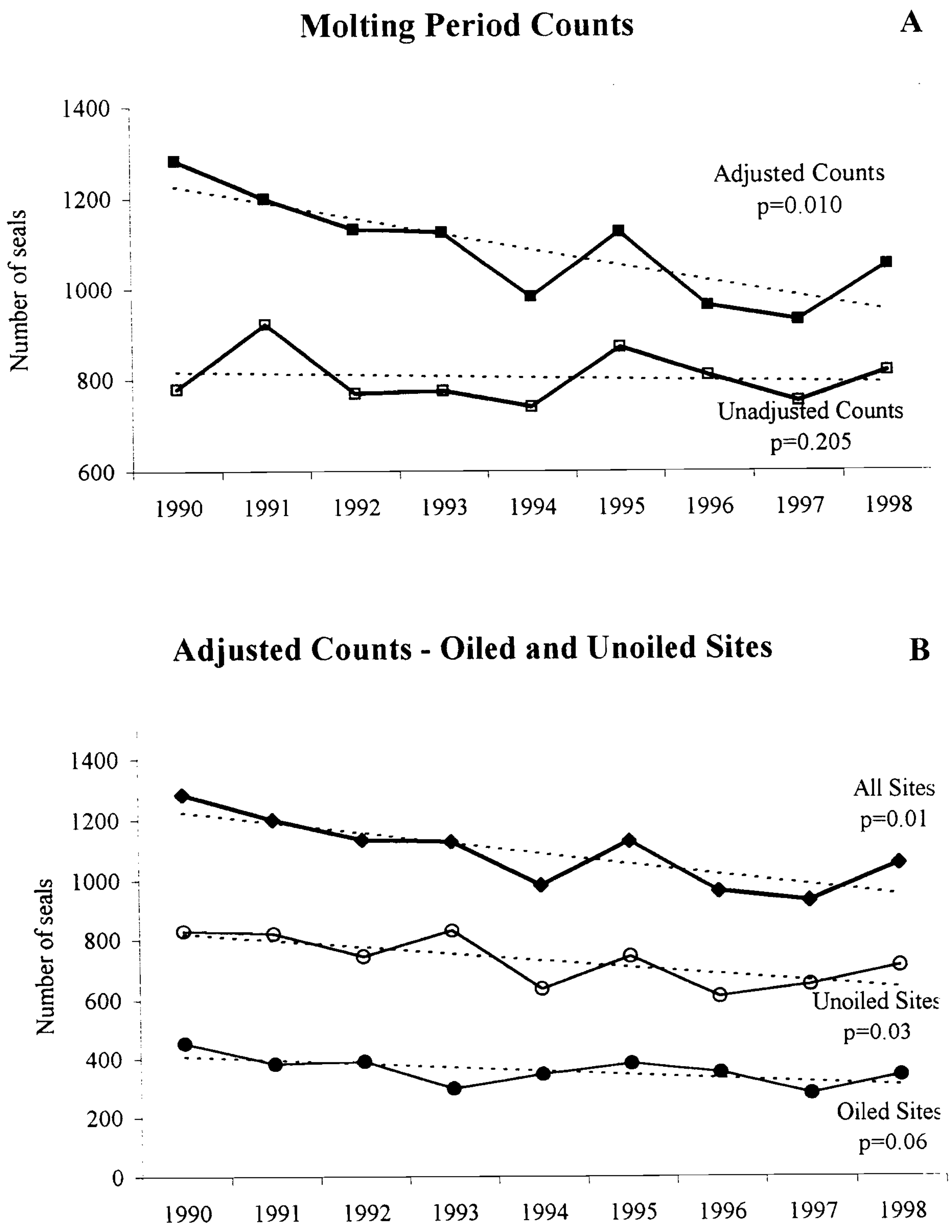


Figure 2. Effects of time of day (A), time relative to low tide (B), and date (C) on counts of harbor seals in Prince William Sound, Alaska.


Molting Period Counts A

Adjusted Counts - Oiled and Unoiled Sites B

Figure 3. Trend in abundance of harbor seals in Prince William Sound, 1990-1998: a) unadjusted and adjusted counts, and b) adjusted counts for oiled and unoiled sites. Dashed line shows the overall trends based on linear regression.

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TAGGING OF HARBOR SEALS IN PRINCE WILLIAM SOUND WITH SATELLITE-LINKED DEPTH RECORDERS, 1997-1998

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INTRODUCTION

A major component of the EVOS harbor seal Restoration Science Study has been the use of satellite-linked depth recorders (SDRs) to investigate seal movements and behavior. Pilot studies done in 1991 were not very successful (Frost and Lowry 1994), but beginning in 1992 seals were regularly captured and tagged at several locations in Prince William Sound (PWS) (Frost et al. 1995, 1996, 1997; Lowry and Frost 1998). The geographic emphasis of the tagging work has been southcentral PWS, at haulouts in the region between Seal Island and Port Chalmers.

Initially the SDRs available were relatively large, and they were applied to larger, generally adult, seals. As smaller tags became available, emphasis shifted to tagging juveniles. During the period from May 1992 through September 1996, successful tag deployments were made on 51 seals (15 adult females, 12 adult males, 11 juvenile females, 11 juvenile males, 2 pups).

An even smaller SDR became available in 1996, and we attached one to a pup in September. In June-July 1997, the small SDRs were attached to 12 pups (Lowry and Frost 1998). Eight additional SDRs were attached to pups in 1998. In this report we summarize behavior and movements of seal pups tagged with SDRs in 1997, and present preliminary results of seal captures and pup tagging done in summer 1998.

METHODS

Capture and Tagging of Seals

Field work was conducted in southcentral PWS during 23-30 June 1998. 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, 1997). 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 older than pups were sedated with a mixture of ketamine and diazepam administered intramuscularly at standard doses (Geraci et al. 1981), or by intravenous injection of diazepam. Pups were manually restrained. 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, flipper-punch skin samples for genetic analysis (G. O'Corry-Crowe and R.

Westlake, Southwest Fisheries Science Center, La Jolla, CA), and blubber biopsies for analyses of fatty acids (S. Iverson, Dalhousie University) and energy content (M. Castellini, University of Alaska Fairbanks). Deuterium oxide was administered orally to some seals.

SDRs were glued to the mid-dorsal surface of seals using Devcon quick-setting epoxy (Fedak et al. 1984, Stewart et al. 1989). The SDRs were manufactured by Wildlife Computers (Redmond, WA). All units attached in 1998 were type ST-10 (0.25-watt) transmitters measuring 10 cm x 5 cm x 3 cm and weighing 170 g. They were powered by 2 lithium 2/3 A cells and were rated for about 15,000 transmissions.

SDRs stored dive depths, dive durations, and the amount of time spent at depth in six hour blocks (0300-0900 hrs, 0900-1500 hrs, 1500-2100 hrs, and 2100-0300 hrs local time) that were transmitted to the satellite once the six hour period was complete. Dive data for pups tagged in 1998 were accumulated in 10 bins as follows: depths of 4-10m, 11-20m, 21-35m, 36-50m, 51-75m, 76-100m, 101-150m, 151-200 m, 201-250m, and over 250 m; and durations of 0-1 minutes, >1-2 minutes, >2-3 minutes, >3-4 minutes, >4-5 minutes, >5-6 minutes, >6-8 minutes, >8-10 minutes, >10-12 minutes, and greater than 12 minutes. In addition the tags included timeline software (version 3.14), which recorded for each 20 minute segment of the day whether the conductivity switch had been mostly wet or mostly dry.

To conserve battery power, all tags were programmed to transmit only during hours of good satellite coverage (0400-1900 hours local time). Tags were set for a transmission cycle of one day on and one day off. In addition, the number of transmissions sent per day was limited to 100. With such a programming protocol, the tags should have operated over a period of about 300 days if the batteries provided 15,000 transmissions.

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 screening 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 daily position for each seal based on all records obtained for a 24 hour period, local time. An additional database was created from the all-location database that included only on-land records with location quality greater than zero, and all at-sea records. Average positions were calculated from that database for each haulout bout (i.e., one or more consecutive on-land locations).

RESULTS

Capture and Tagging of Seals

In 1998 we captured and processed 57 seals; 14 were pups, 16 were yearlings, and 27 were older than yearlings (Table 1). We attached eight SDRs to pups captured at Little Green Island (2), Applegate Rocks (2), Seal Island (2), and Port Chalmers (2).

Performance of Tags Attached to Pups in Summer 1997

The performance of SDRs attached to harbor seal in PWS in 1997 is summarized in Table 2. The SDRs operated for 21-313 days (average=152 days). Half of the tags continued to operate until at least November 1997, and one lasted until May 1998. Locations were received on 24%-62% of the days transmitters were operational, with an average of 0.5-1.2 locations received per day.

Movements of Seals Tagged in Summer 1997

The locations and movements of seals tagged in June-July 1997 are shown in Figure 1 and are summarized in Table 3. Seven seals (97-2,3,4,5,6,8,12) were always located near the haulout where they were captured or near adjacent haulouts. Included in this group were the four animals that were tracked for the shortest periods (28-86 days), and three that were tracked for longer periods (118-210 days). One pup (97-7) moved from Little Green Island where it was captured to Danger Island on about 13 August and remained there until tracking stopped on 4 October. Two seals (97-1 and 11) moved to northeastern PWS and visited tidewater glaciers in Unakwik Inlet and/or College Fiord. Three seals (97-9,10,11) moved to Hinchinbrook Entrance and in some cases into the Gulf of Alaska.

Seal 97-1 moved extensively within PWS (Figure 2). For the first three months it remained in the area between Seal Island where it was tagged and the north end of Montague Island. In late September it moved to the west side of Knight Island, to Unakwik Inlet, then to College Fiord. From there it went to the Dutch Group, then back to College Fiord. It spent the latter half of November near the mainland west of Knight Island then moved to the north end of Culross Island where it stayed until mid-February. It then moved to the Dutch Group where it remained until tracking ended in March.

Seal 97-9 made two relatively long trips (Figure 3). In late September it moved from Port Chalmers where it was tagged to Sheep Bay in eastern PWS then back to the north end of Montague Island. It remained in that area until mid-February when it made a trip southeastward into the Gulf of Alaska, to a point about 90 km offshore. After about eight days in the Gulf it returned to Montague Island and was at Port Chalmers when the last location was received in April.

Seal 97-10 stayed near Port Chalmers where it was tagged for about two months then moved to the vicinity of Seal Rocks in the Gulf of Alaska (Figure 4). It remained near Seal Rocks until late October then moved to the Wooded Islands area. When the last location was received in late November it was back at Seal Rocks.

Seal 97-11 moved to Rocky Bay about two weeks after it was tagged at Applegate Rocks and spent the next month in the Hinchinbrook Entrance area (Figure 5). It then moved back into PWS and stayed in the region between Applegate Rocks and the north end of Montague Island until March. It then moved to College Fiord where it spent much of March, before returning to the Applegate region where it remained until tracking ended in May.

DISCUSSION

Capture and Tagging of Seals

Seal capture operations in PWS during June 1998 went very well. Our primary objective was to catch and tag weaned pups. Sizes of pups we handled ranged from 24.3-32.2 kg. Based on the data in Pitcher and Calkins (1979) we expected weaned pups to weigh 20-25 kg, therefore we are confident that the great majority of our sample of pups had been weaned or were ready to be weaned.

Satellite-linked Depth Recorder Performance

Prior to the 1997 field season we had used only two 0.25 watt SDRs. A prototype that we attached to a subadult seal in fall 1995 performed erratically and was considered a failure (Frost et al. 1997). One that we attached in fall 1996 worked much better, giving regular locations over a period of 89 days. Based on the success of the 0.25 watt tag tested in fall 1996 we decided to use those units on pups tagged in summer 1997.

For the tags attached in 1997 we made several modifications to the programming to ensure that the batteries would last at least 300 days (see methods). It appears that this approach was successful, as four tags transmitted for more than 200 days and one for 313 days. Because the tags were duty-cycled and were limited in their daily transmissions, we generally received locations on only about 50% of the days the tags were attached. We obtained relatively few good locations per day compared to the results from 0.5 watt SDRs attached to adult and juvenile seals (Frost et al. 1996, 1997; Lowry and Frost 1998). As a result, some short duration movements may have been missed, and tracks of longer seal movements are not very detailed. Nonetheless, we think that the data received provide a good indication of the general movements and areas used by the weaned pups.

We cannot say for sure why some of the tags stopped sending signals after relatively short periods. Weaned harbor seal pups have a relatively high natural mortality rate, and it is likely that some of the seals died within a few months after tagging. Some may have experienced electronic failure. We think it unlikely that any of the tags were shed prematurely. On June 27, 1998 we captured a yearling seal at Applegate Rocks that had been tagged with an SDR the year before at Seal Island (seal 97-1). The seal was beginning to molt and the mesh fabric was loose but still attached under the SDR itself. The antenna was broken at the base.

Movements of Harbor Seal Pups

During the period that they were tracked, most of the 12 pups equipped with SDRs in summer 1997 did not make extensive movements. Most relocations were near the locations where seals were captured, but some were in eastern and western PWS, and the Gulf of Alaska east of Montague Island (Figure 1). The earliest that any of the pups tagged in 1997 made a long distance movement was August 20 when 97-10 was located at Seal Rocks in the Gulf of Alaska. Most long distance movements were after late September (Table 3). Therefore, it is not surprising that we did not document much movement in the seals that were only tracked for 1-3 months.

The two harbor seal pups that we tagged in previous years each made several long trips, one between eastern PWS and College Fiord and the other between the Copper River Delta and the Gulf of Alaska west of Middleton Island (Lowry and Frost 1998). The datasets from those seals begin in September when the pups were about four months old. Two of the seals tagged in 1997 showed a roughly similar pattern. Pup 97-1 made several trips to tidewater glaciers in Unakwik Inlet and College Fiord (Figure 2), and 97-10 used the Gulf of Alaska between Seal Rocks and Wooded Islands (Figure 3).

As would be expected, the pups that were tracked for relatively short periods of time were at or near the haulout where they were captured when the last locations were received (Table 3). The same was true for seal 97-9 that was tracked until April and 97-11 that was tracked until May. Seal 97-1 was at the Dutch Group, about 50 km distant from Seal Island when it's last location was received in March. However, in late June 97-1 was recaptured at Applegate Rocks, the closest haulout to Seal Island. Overall, these results suggest a tendency for harbor seal pups in PWS to either stay near, or return to, the vicinity of their birth site.

In 1997 and 1998 combined, 20 SDRs have been attached to pups captured at Little Green Island (5), Applegate Rocks (6), Seal Island (4), and Port Chalmers (5). An additional seven SDRs will be attached to pups at these locations in 1999. A full analysis of movements and behavior of weaned harbor seal pups in PWS will be done when the data are available for all 27 tagged seals.

ACKNOWLEDGEMENTS

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Table 1. Harbor seals captured, sampled, and tagged during field operations in Prince William Sound, June-July 1998.

Specimen	Location	Date	PTTID	Age	Sex	Wt (kg)	SL (cm)	CL (cm)	AxG (cm)
PWS-01-98	Seal Island	6/24/98		YRL	F	37.0	104.0	116.0	91.0
PWS-02-98	Seal Island	6/24/98	2280	PUP	F	29.6	86.0	93.0	85.0
PWS-03-98	Seal Island	6/24/98		YRL	F	36.1	109.0	118.0	92.0
PWS-04-98	Seal Island	6/24/98		AD	F	65.0	130.0	135.5	103.0
PWS-05-98	Seal Island	6/24/98		AD	F	49.9	125.0	134.0	93.0
PWS-06-98	Seal Island	6/24/98		AD	M	60.5	132.0	139.0	100.0
PWS-07-98	Applegate Rocks	6/24/98		YRL	M	33.3	99.0	109.0	85.0
PWS-08-98	Applegate Rocks	6/24/98		AD	M	67.6	141.0	147.0	96.5
PWS-09-98	Applegate Rocks	6/24/98		PUP	F	23.5	90.0	96.0	77.0
PWS-10-98	Applegate Rocks	6/24/98		YRL	F	33.1	-	-	-
PWS-11-98	Applegate Rocks	6/24/98		SUB	M	61.4	130.0	135.0	103.5
PWS-12-98	Applegate Rocks	6/24/98		AD	F	59.9	138.0	149.0	94.0
PWS-13-98	Applegate Rocks	6/24/98		AD	F	64.5	143.0	150.0	98.0
PWS-14-98	Applegate Rocks	6/24/98		SUB	M	50.2	113.0	122.0	96.0
PWS-15-98	Applegate Rocks	6/24/98	2281	PUP	M	30.5	92.0	100.0	87.0
PWS-16-98	Little Green Island	6/25/98		YRL	M	36.2	107.0	114.0	86.0
PWS-17-98	Little Green Island	6/25/98		YRL	M	38.8	109.0	118.0	88.0
PWS-18-98	Little Green Island	6/25/98	2283	PUP	F	28.3	91.0	101.0	82.0
PWS-19-98	Little Green Island	6/25/98		AD	F	72.0	138.0	153.0	99.0
PWS-20-98	Applegate Rocks	6/25/98		PUP	M	28.6	94.0	101.0	85.0
PWS-21-98	Applegate Rocks	6/25/98		YRL	M	31.6	101.0	112.0	83.0
PWS-22-98	Applegate Rocks	6/25/98		AD	F	65.7	134.0	138.0	102.0
PWS-23-98	Applegate Rocks	6/25/98		AD	F	58.2	129.0	140.5	96.0
PWS-24-98	Little Green Island	6/26/98		YRL	M	38.0	107.0	115.0	89.0

Table 1. Continued

Specimen	Location	Date	PTTID	Age	Sex	Wt (kg)	SL (cm)	CL (cm)	AxG (cm)
PWS-25-98	Little Green Island	6/26/98		YRL	F	30.1	100.0	108.0	76.0
PWS-26-98	Little Green Island	6/26/98		SUB	F	52.9	128.0	135.0	100.0
PWS-27-98	Channel Island	6/26/98		AD	F	53.6	131.0	145.0	90.0
PWS-28-98	Channel Island	6/26/98		PUP	F	24.3	94.0	97.0	81.0
PWS-29-98	Channel Island	6/26/98		SUB	M	41.3	112.0	119.0	93.0
PWS-30-98	Channel Island	6/26/98		SUB	M	41.1	115.0	124.0	91.0
PWS-31-98	Channel Island	6/26/98		AD	F	55.0	138.0	147.5	92.0
PWS-32-98	Port Chalmers	6/26/98		SUB	M	40.9	112.0	122.0	89.0
PWS-33-98	Port Chalmers	6/26/98	2286	PUP	F	29.0	93.0	95.0	85.0
PWS-34-98	Port Chalmers	6/26/98		AD	F	60.6	148.0	152.0	96.0
PWS-35-98	Port Chalmers	6/26/98	2287	PUP	F	26.2	93.0	103.0	81.0
PWS-36-98	Port Chalmers	6/26/98		YRL	F	30.3	103.0	113.0	82.0
PWS-37-98	Little Green Island	6/27/98		YRL	F	35.1	112.0	115.0	86.0
PWS-38-98	Little Green Island	6/27/98	11038	PUP	F	29.9	95.0	104.0	85.0
PWS-39-98	Applegate Rocks	6/27/98		YRL	F	31.1	101.0	107.0	84.0
PWS-40-98	Applegate Rocks	6/27/98		YRL	F	32.7	110.0	126.0	89.0
PWS-41-98	Applegate Rocks	6/27/98		YRL	M	31.8	104.0	115.0	80.0
PWS-42-98	Applegate Rocks	6/27/98		SUB	F	44.0	112.0	113.0	104.0
PWS-43-98	Applegate Rocks	6/27/98		SUB	F	35.8	109.0	123.0	87.0
PWS-44-98	Applegate Rocks	6/27/98	11039	PUP	M	28.4	91.0	103.0	83.0
PWS-45-98	Seal Island	6/28/98		YRL	F	31.8	105.0	115.0	81.0
PWS-46-98	Seal Island	6/28/98		PUP	M	30.1	93.0	106.0	81.0
PWS-47-98	Seal Island	6/28/98		PUP	F	25.1	89.0	97.0	84.0
PWS-48-98	Seal Island	6/28/98	11040	PUP	M	32.2	91.0	101.0	86.0

Table 1. Continued

Specimen	Location	Date	PTTID	Age	Sex	Wt (kg)	SL (cm)	CL (cm)	AxG (cm)
PWS-49-98	Seal Island	6/28/98		AD	F	54.5	132.0	142.0	96.0
PWS-50-98	Channel Island	6/29/98		AD	M	84.6	144.0	155.0	112.0
PWS-51-98	Applegate Rocks	6/27/98		AD	F	-	-	-	-
PWS-52-98	Applegate Rocks	6/27/98		AD	F	-	-	-	-
PWS-53-98	Applegate Rocks	6/27/98		AD	M	-	-	-	-
PWS-54-98	Channel Island	6/29/98		PUP	M	31.6	99.0	104.0	85.0
PWS-55-98	Channel Island	6/29/98		YRL	M	32.9	107.0	112.0	85.0
PWS-56-98	Channel Island	6/29/98		AD	M	71.1	141.0	150.0	107.0
PWS-57-98	Channel Island	6/29/98		SUB	M	56.1	137.0	142.0	98.0

Table 2. Performance of satellite-linked depth recorders attached to harbor seal pups in Prince William Sound, June-July 1997.

SDR	ID Number	Sex	Date Attached	Date of Last Transmission	Total Days Operational	No. Days w/ Locations	Total No. Locations
11038	97-1	F	6/27/97	3/9/98	256	119	219
11039	97-2	F	6/27/97	10/22/97	118	28	38
11040	97-3	F	6/27/97	8/15/97	46	22	42
11041	97-4	M	6/27/97	8/25/97	60	26	33
11042	97-5	M	6/28/97	1/23/98	210	112	214
11043	97-6	F	6/28/97	12/16/97	172	106	198
11044	97-7	F	6/28/97	10/4/97	99	46	74
2093	97-8	F	6/28/97	9/21/97	86	50	90
2094	97-9	M	6/28/97	4/18/98	295	168	313
2095	97-10	M	6/29/97	11/20/97	145	57	78
2096	97-11	F	7/1/97	5/10/98	314	151	247
2097	97-12	F	7/1/97	7/28/97	28	16	21

Table 3. Summary of movements of harbor seal pups satellite tagged in Prince William Sound, June-July 1997.

ID	Start Date	Tag Location	Other Major Locations Used	Last Haulout	End date
97-1	6/27/97	Seal I.	N. end Montague I. 7/27-9/24; Knight I. Psg. 9/26-10/25; Unakwik Inlet 10/30-11/1; College Fiord 11/3, 11/14-15; Dutch Group 11/5, 2/18-3/9; Main Bay 11/17-12/3 Culross Passage/N. Culross I. 12/7-2/13	Dutch Group	3/9/98
97-2	6/27/97	Seal I.	Big Smith I. 8/3-10/22	Big Smith I.	10/22/97
97-3	6/27/97	Applegate Rks.	Rocky Bay 7/28-31	Applegate Rks.	8/15/97
97-4	6/27/97	Applegate Rks.		Applegate Rks.	8/25/97
97-5	6/28/97	Little Green I.	Channel I. 7/17-9/16	Little Green I.	1/23/98
97-6	6/28/97	Little Green I.	SW Montague I. 7/3-8/5; Pt. Chalmers/Stockdale Hbr. 8/19-12/14;	Stockdale Hbr.	12/16/97
97-7	6/28/97	Little Green I.	Channel I. 7/25-8/11; Danger I. 8/13-10/4	Danger I.	10/4/97
97-8	6/28/97	Port Chalmers		Pt. Chalmers	9/21/97
97-9	6/28/97	Port Chalmers	Channel I. 7/25-9/18; Sheep Bay/SE PWS 9/20-22 Little Green I. 10/6-15, 1/12-16; Hinchinbrook Ent/GOA 2/15-25;	Pt. Chalmers	4/18/98
97-10	6/29/97	Port Chalmers	Channel I. 7/4-24; Seal Rocks/GOA 8/20-10/24 SE Montague I./Wooded Is. 10/28-11/20	Seal Rocks	11/20/97
97-11	7/1/97	Applegate Rks.	Hinchinbrook Ent./Rocky Bay 7/16-8/13; Pt. Chalmers/Channel I. 8/27-9/17; College Fiord 3/5-22	Applegate Rks.	5/10/98
97-12	7/1/97	Applegate Rks.	Rocky Bay 7/6, 7/18	Applegate Rks.	7/28/97

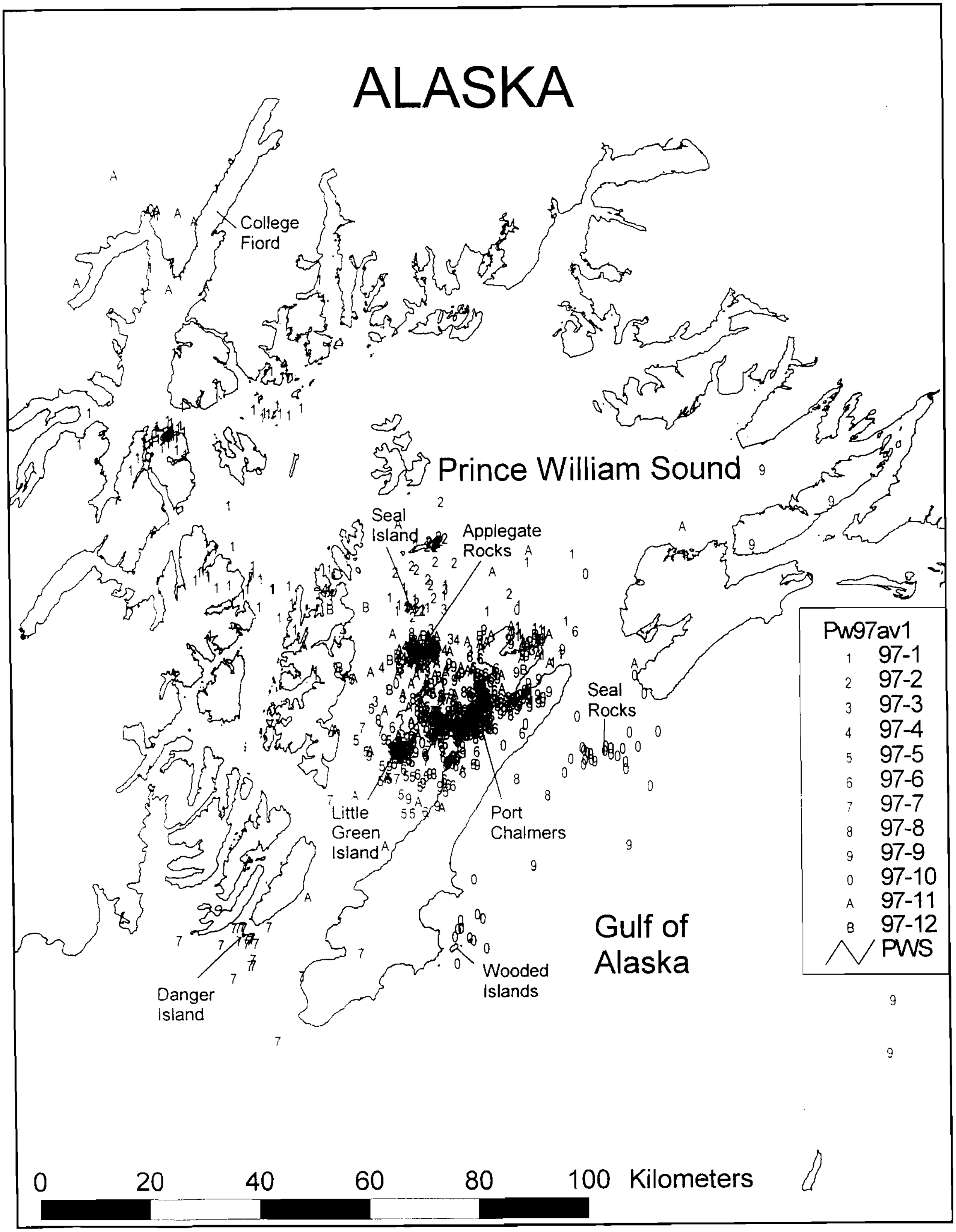

Figure 1. Average daily locations of 12 harbor seal pups satellite tagged in Prince William Sound, 27 June 1997-10 May 1998.

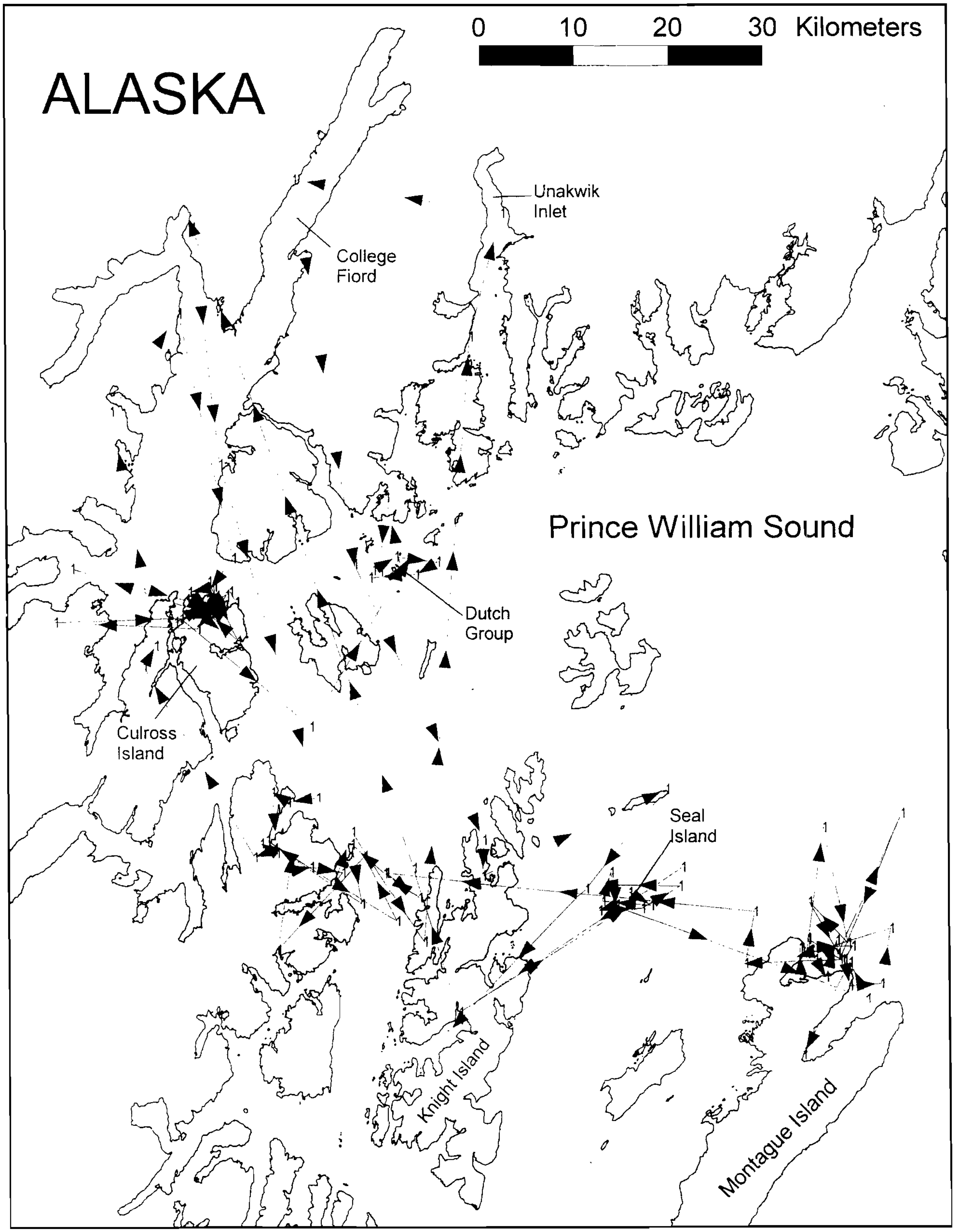

Figure 2. Average daily locations and movements of harbor seal pup 97-1, 27 June 1997-9 March 1998.

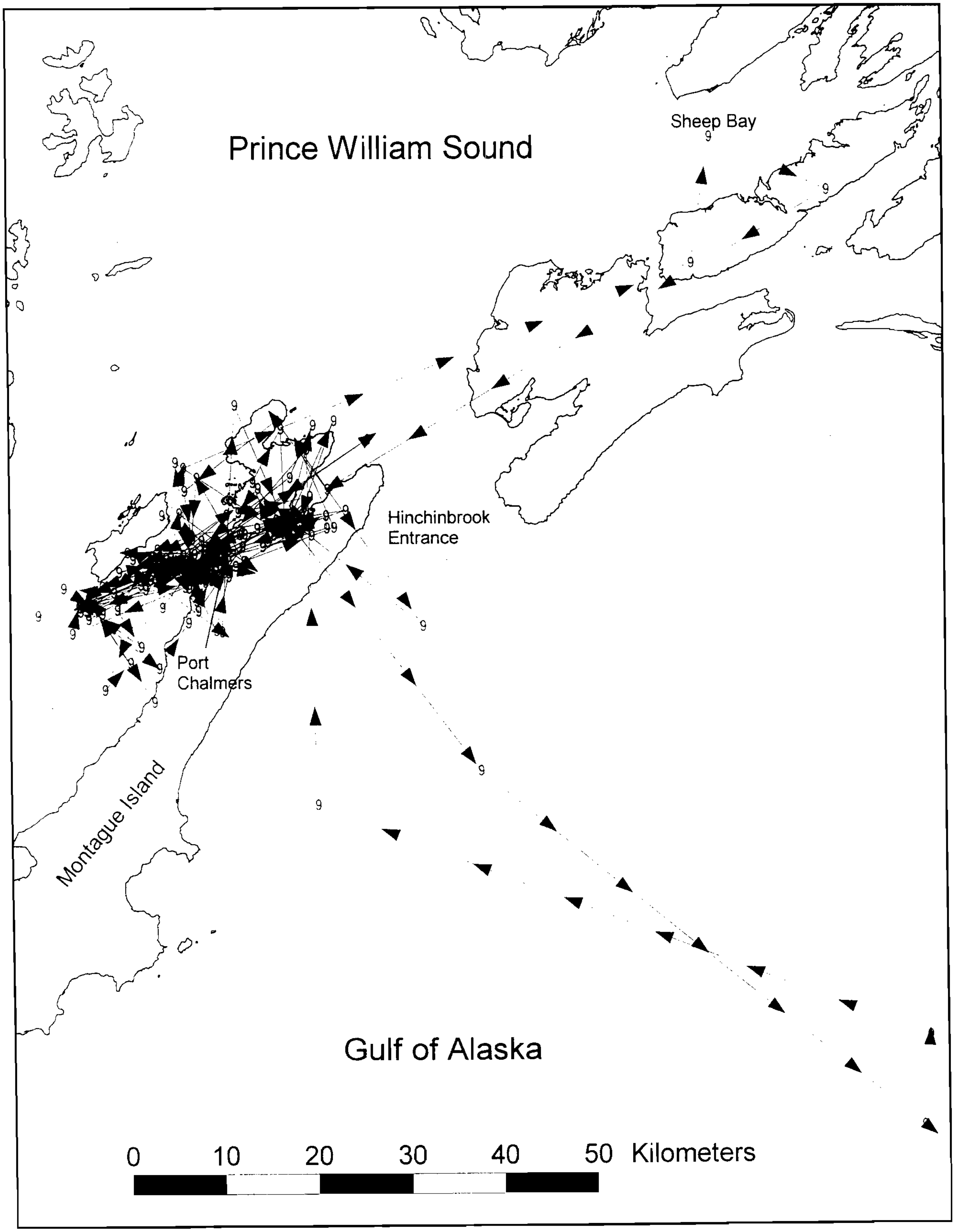

Figure 3. Average daily locations and movements harbor seal pup 97-9, 28 June-18 April 1998.

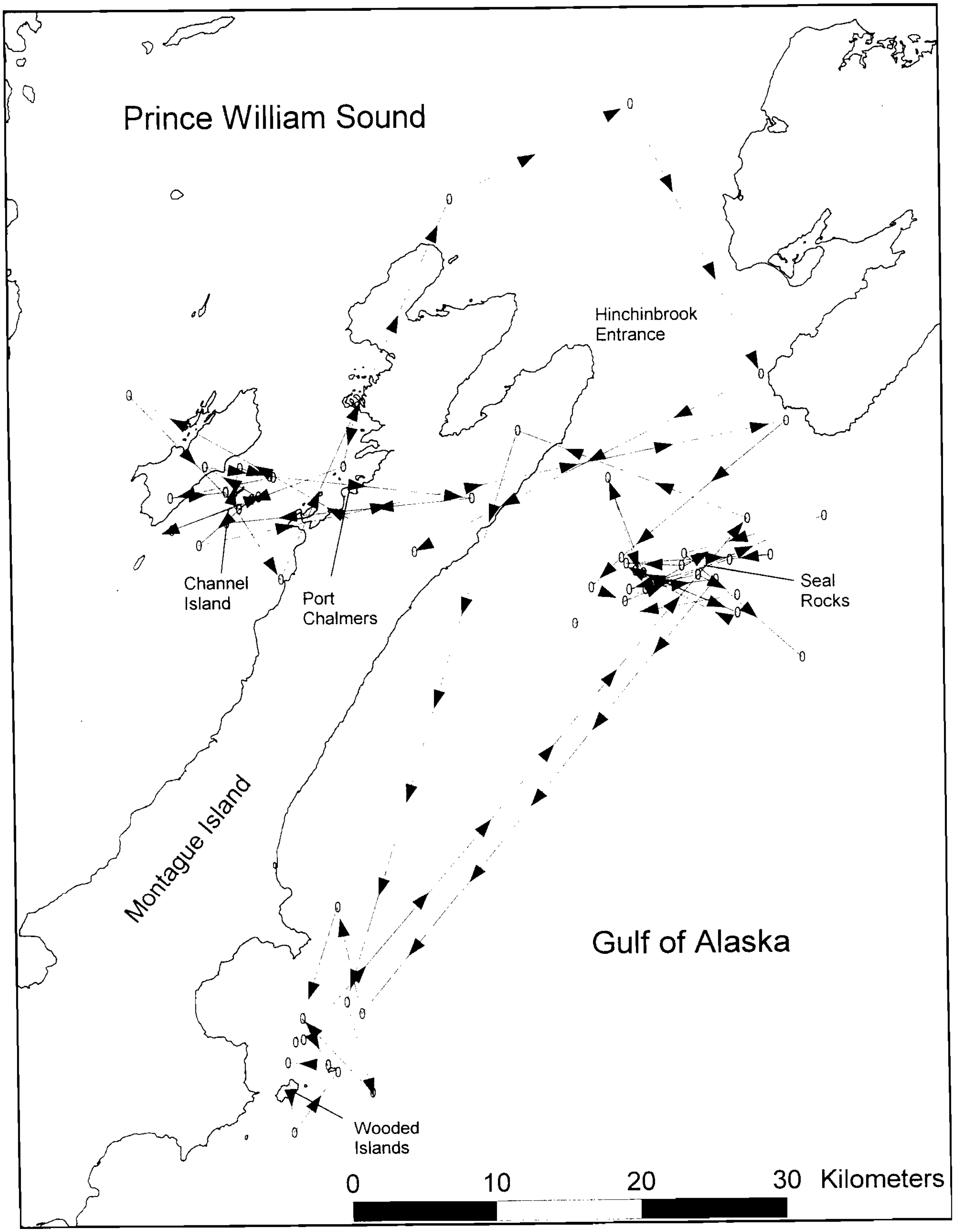

Figure 4. Average daily locations and movements harbor seal pup 97-10, 29 June-20 November 1997.

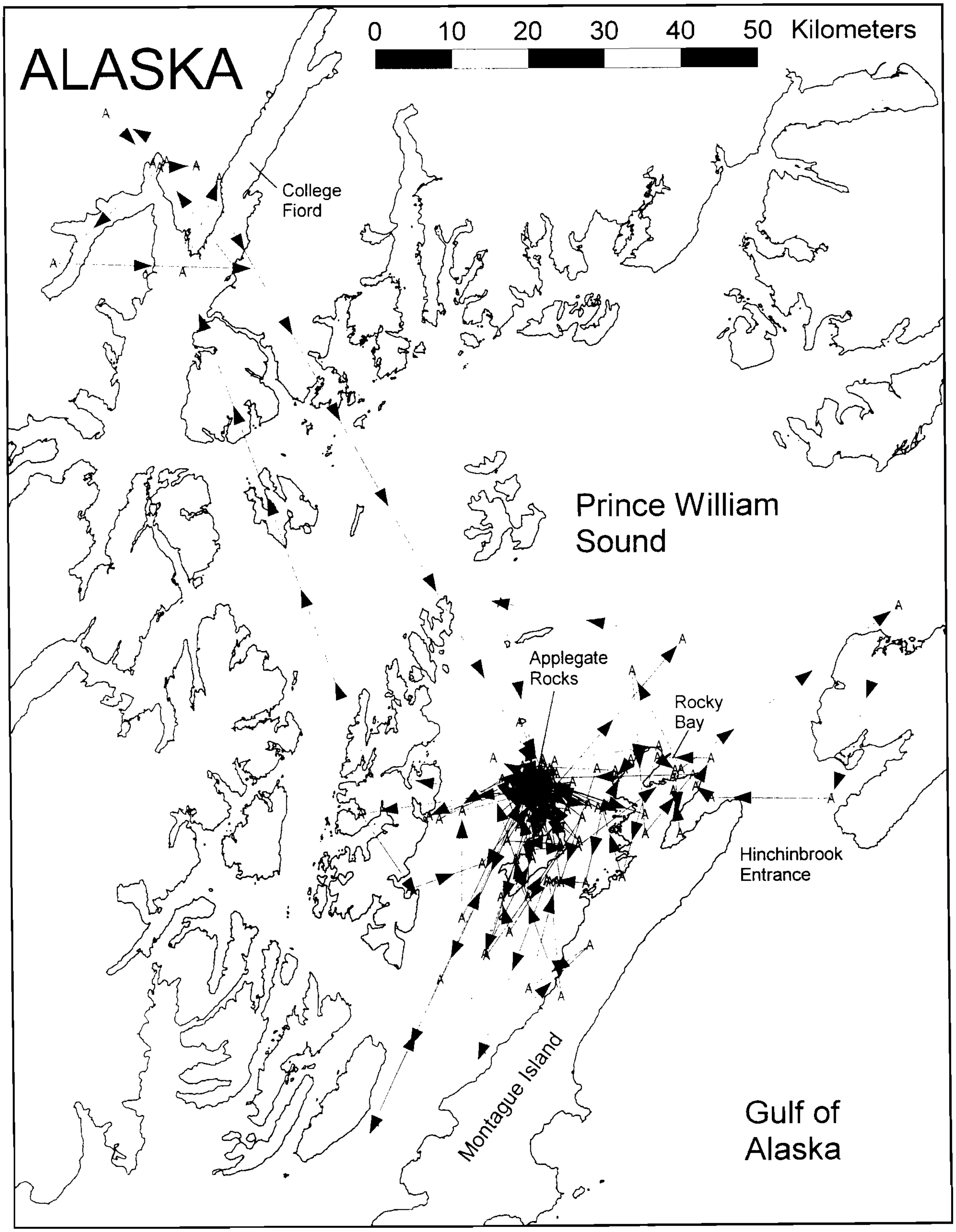

Figure 5. Average daily locations and movements of harbor seal pup 97-11, 1 July 1997-10 May 1998.

CHAPTER THREE

THE USE OF FATTY ACID SIGNATURES TO INVESTIGATE FORAGING ECOLOGY AND FOOD WEBS IN PRINCE WILLIAM SOUND, ALASKA: HARBOR SEALS AND THEIR PREY

OBJECTIVE 3

Identify important prey species in the diets of harbor seals in PWS, with a particular emphasis on pups and yearlings, and determine whether there are dietary differences among different components of the population.

OBJECTIVE 4

In conjunction with research efforts being done on the Scotian Shelf, develop mathematical models and associated software programs to quantitatively estimate species composition of individual harbor seal diets.

OBJECTIVE 5

Determine whether there are differences in diets and important prey species among populations of harbor seals in areas of the Gulf of Alaska where they are continuing to decline (e.g., PWS and northern Gulf of Alaska) and areas where the population is stable or increasing (Southeast Alaska).

OBJECTIVE 6

Determine whether changes in harbor seal diets and important prey species have occurred over the past two decades.

OBJECTIVE 7

Compare estimates of abundance and importance of harbor seal prey to trawl survey data and data obtained from seabird diet studies being conducted concurrently under the APEX program.

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THE USE OF FATTY ACID SIGNATURES TO INVESTIGATE FORAGING ECOLOGY AND FOOD WEBS IN PRINCE WILLIAM SOUND, ALASKA: HARBOR SEALS AND THEIR PREY

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INTRODUCTION

Marine mammals and seabirds are apex predators in ecosystems in which fishes and cephalopods are important prey. Hence, marine mammals may have significant effects on or be affected by prey populations. The diets of pinnipeds may also serve as an indicator of relative abundance and distribution of prey species (e.g., Sinclair et al. 1994). Thus, there has been considerable interest in understanding the diets of free-ranging pinnipeds and the possible effects of variation in prey abundance and prey quality on pinniped populations (e.g., Anonymous 1993; NRC 1996). 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 (*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 et al. 1992). 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 have furthered the idea of using predators as samplers of forage fish abundances (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).

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. Although documentation from the 1970s or before is scarce, since 1984 harbor seal numbers in PWS have declined by about 63%, with only part of this decline attributable to the 1989 Exxon Valdez oil spill (Frost et al. 1999). 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 the decline of other apex predators. Thus, understanding the diet of harbor seals, particularly over time and in areas of stable versus decreasing populations, 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 and Brieby 1986; Olesiuk 1993; Bowen and Harrison 1996). Due to the rapid passage of food from the gut, stomachs collected from killed seals are often empty (Harwood and Croxall 1988; Bowen et al. 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 and 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. Finally, and perhaps most importantly, only the last meal consumed, and usually only that consumed near haul-out locations and breeding sites, can be studied using these methods and thus diets from a large part of the species foraging habits or range may be missed. Past studies of harbor seal diets in PWS and the Gulf of Alaska (GOA) have been conducted using these types of methods (Pitcher 1980a and 1980b), however, this is not currently possible in PWS: tidal washout at most haulouts precludes collection of fecal material and killing individuals in a declining population for stomach contents analyses is untenable.

Thus the use of fatty acid signature analysis (Iverson 1993) has been advanced to study marine food webs and pinniped diets. 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 and 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 even when not fattening (Kirsch et al. submitted). 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. 1998). To date, the methods of fatty acid signature analysis have been used both to identify general trophic level of diets and to detect major and minor shifts in diet within populations (Iverson 1993; Iverson et al. 1997a; Iverson et al. 1997b; Smith et al. 1997).

The current study, funded by the EVOS Trustee Council, represents one of the two largest ecosystem studies to date employing fatty acid signature analysis. In results from the first several years of the current Restoration Project (1995-1997), 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 groups and habitat within PWS (Iverson et al. 1997b). Evidence also suggested changes in the diets of harbor seals over several years of study (Iverson et al. 1998). Results from this study, as well as studies on the Scotian Shelf of eastern Canada (S. Iverson and W. D. Bowen, pers. comm.), have indicated the continued ability to accurately identify prey species by their fatty acid signatures, regardless of potential seasonal or habitat changes. Thus, the information provided to date from fatty acids has already furthered our knowledge of the spatial scales of foraging utilized and perhaps required by harbor seals. The ultimate goal of this work, in addition to sampling seals and to building the requisite prey library for analysis, has been to advance the use of fatty acids to the point of being able to use them in a quantitative manner to actually estimate species composition of the diets of individual seals. This would allow the first clear evaluation of the possible effects of patterns of and changes in diets on the declining harbor seal population, especially in combination with information on prey abundance patterns obtained through the APEX program.

Here we report on the work undertaken during the last year towards achieving these goals. At the close of last year's report (Iverson et al. 1998), a total of 792 prey representing 18 taxa had been analyzed and blubber samples from a total of 296 harbor seals in PWS and the GOA had been analyzed. The first modeling project had just begun to actually try to reconstruct the diets of free-ranging seals. During the last year, we have focused more heavily on the modeling effort, although we have continued to build the prey base (upon which the accurate use of the model depends) as well as to analyze more seals, with the aim that when the model is fully completed all samples previously analyzed can be modeled. Because of the time and financial support required, the modeling project has been undertaken as a joint venture, funded by both the Exxon Valdez Oil Spill Trustee Council and by a research grant to S.J.I. from the Natural Sciences and Engineering Research Council (NSERC), Canada. In the present report, we focus primarily on the state of the model development and its preliminary application to selected seals in both PWS and the Kodiak Island area. We also have the opportunity to compare these current seals (sampled in 1994-1998) with a number of seals sampled from both PWS and Kodiak in the late 1970s. Results of diet estimates must be considered preliminary at this stage. However, we expect the model to be largely refined and close to completion by next year's report. We also report on a continued study examining the nutritional condition of PWS seals at young ages post-weaning by measuring total body composition.

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 1994-1997 and stored frozen until analysis. An additional sampling of herring from the Kodiak Island region of GOA was also collected and analyzed. A total of 1,052 individual prey representing 25 taxa [capelin, chum, eulachon smelt, flathead sole, rex sole, unidentified flatfish sp., yellowfin sole, greenling, Pacific herring, octopus, Pacific cod, pink salmon (adults and smolts), walleye pollock, rainbow smelt, rex sole, rock sole, copper rockfish, sandlance, sculpin, pink shrimp, shrimp unidentified sp., squid (3 species), and tomcod] have now been analyzed (792 previously, 260 in the past year) for total fat content and fatty acid composition for the present report and included in the current prey library used in the model (Table 1). The most detailed sampling, by region within PWS and over size classes, has been for herring (n = 332) and pollock (n = 186), however reasonably large samples sizes are becoming available for other species such as capelin (n = 79), eulachon smelt (n = 20), flatfish (n = 88), pink salmon (n = 40 smolts), rex sole (n = 23), sandlance (n = 80), squid (n = 117) and tomcod (n = 38). Most species were not sampled from all areas, or across all seasons and years, precluding some direct comparisons.

Blubber samples from a total of 667 harbor seals have been analyzed (296 previously, 371 in the past year) for fatty acid composition. Of this total, blubber from 381 harbor seals was sampled in 1994-1998 (Table 2). 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 et al. 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 which was further divided into the same general locations as prey collections (see above and Fig. 1), and from other areas of the GOA: near Kodiak Island and in Southeast Alaska (Table 2). Not all areas were sampled in all years, seasons or among age classes, precluding some direct comparisons.

In addition to current field sampling undertaken in this Restoration Project, frozen archived blubber samples that had been taken before the decline in 1976 (n = 122), 1977 (n = 125) and 1978 (n = 23), as well as after the oil spill in and 1989-1993 (n = 16), were also analyzed during this past year (Table 3).

In 1997, the focus of our study changed slightly to concentrate on assessing aspects of foraging and body composition in young seals (primarily within the first year post-weaning). Thus in June of 1997 and 1998, a total of 65 animals were given deuterium oxide (D_2O), a heavy non-radioactive isotope of water, which allows accurate measurement of total body water and other body constituents (Oftedal and Iverson 1987; Iverson et al. 1993; Bowen and Iverson 1998). Animals were captured and weighed to the nearest 0.5 kg. Pups were checked for the presence of milk by gastric intubation, and all milk was removed if present to avoid delay in equilibration of isotope. Stomach contents of older animals were not checked or evaluated, however. An exact pre-weighed amount of D_2O (99.8% purity, Sigma) was delivered by gastric intubation using a 12-French stomach tube at 1 g/kg body mass. Syringe and stomach tube were then rinsed with two 5-cc quantities of fresh water; air was then blown through the tube as it was withdrawn to insure complete quantitative isotope delivery. Animals were held in nets for 2-4 hours and two serial blood samples were taken 20 min. apart at the end of this holding period to determine whether (and at what concentration) equilibration of isotope had occurred. Serum was collected from centrifuged blood samples and stored frozen until analysis at Dalhousie University.

Lipid and Fatty Acid Analysis

After recording length and mass of each whole prey, each was ground individually and lipids were quantitatively extracted in duplicate aliquots; fat content was expressed as an average of the two duplicates. In some cases when prey were too small to analyze separately, several 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).

Since the beginning of this Restoration Project all fish and other prey samples were extracted and analyzed using the Bligh and Dyer method (Bligh and Dyer 1959). This method has long been employed and frequently used in fisheries labs as well as in many other situations. It is considered to be one of the recommended methods, along with the method of Folch, Lees and Sloane-Stanley (1957), for extraction of lipids from animal tissue (Christie 1982; Ackman 1980, R. G. Ackman pers. comm.). The primary advantage of Bligh and Dyer is a reduction in solvent. During this project year, in the course of another study in our lab, we discovered that samples of a known very high fat content were significantly underestimated using Bligh and Dyer but not by the Folch method. Thus we undertook a detailed study to clarify this and found a significant but highly predictable relationship between true fat content (analyzed by Folch) and that analyzed using Bligh and Dyer (Iverson, Lang, Smith and Cooper, in prep.). Fatty acid composition is unaffected, however. This equation was used to correct the fat content of all prey samples that were previously analyzed using Bligh and Dyer. Thus, values reported in previous reports should be considered incorrect. All new samples are analyzed by Folch. Lipid has always been extracted from harbor seal blubber samples according to the method of Folch as modified by Iverson (1988) and 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, et al. (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 GC-mass spectrometry (Hewlett-Packard 6890 Gas Chromatograph, 1:20 split injection, Micromass Autospec oa-TOF mass spectrometer, operated at 1000 resolution, scanning masses 120 to 450). 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, by use of a guard column, and by frequent replacement. 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, replacement, 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.

Body Composition Analysis

For the study on body composition, total free-water was collected from blood sera by heat distillation according to the method of Oftedal and Iverson (1987) and D_2O concentration was determined by quantitative infrared spectrophotometry on a Perkin Elmer Fourier Transform IR Spectrophotometer (Oftedal and Iverson 1987). All samples were read in triplicate.

Equilibration was considered to have occurred when the isotope levels measured in the two serial blood samples taken during the equilibration period were within 0.01 percentage points D_2O concentration of each other. For one of the 35 animals studied this year (and five of the 30 animals studied last year), equilibration had not occurred and thus data were not available for these individuals. These individuals were non-pups and the delay in equilibration may have been due to the presence of food in the stomach. The other 34 animals (and 25 last year) had all equilibrated by the end of the holding period.

Isotope dilution space was converted to total body water (TBW) using the equation:

$$\text{TBW (kg)} = 0.003 + [0.968 \times (\text{dilution space})]$$

as derived by Bowen and Iverson (1998). TBW was then used to calculate total body fat (TBF) and total body protein (TBP) content using the equations:

$$\%\text{TBF} = 105.1 - (1.47 \times \%\text{TBW})$$

and

$$\%\text{TBP} = (0.42 \times \%\text{TBW}) - 4.75$$

as derived by Reilly and Fedak (1990) for grey seals (*Halichoerus grypus*).

Data Analysis and Interpretation

All data are presented as mean ± SEM, unless otherwise indicated. Fat content and fatty acid data were analyzed using regression and analysis of variance (ANOVA) on a limited subset of variables, and also using methods of classification and regression trees (CART) in S-plus according to methods described in Iverson et al. (1997a) and Smith et al. (1997). There are no restrictions in CART on the number of variables (fatty acids) that can be used in the analysis, thus the complete data sets of fatty acids were used. Although this has been described in previous reports, 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. Application of the SPLUS software is described in Clark and Pregibon (1992) and Venables and Ripley (1994).

Because of the extent and complexity of the present data sets, as well as extensive detail presented in past reports (please see Frost et al. 1996, 1997 and Iverson et al. 1998), only a small subset of final classification trees are presented and discussed in the current report. Model development and processes involved are presented in a separate section of the results.

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. 1997b), 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 classes were changed and corresponded to lengths of 5.0-12.0 cm, 12.1-24.0 cm, and 24.1-40.0 cm, respectively. Tomcod were also divided into two size classes of small and large (Table 1) Although within each squid species collected, a wide range of sizes was represented, there was little evidence from fatty acid data that splitting by size was appropriate.

Eulachon was able to be included in the data base for the first time and had the highest fat content of any species analyzed, averaging 19% fat, but reaching as high as 25% fat. Herring had the next highest average fat content (5-10% fat), but this ranged widely from 0.5 - 19.1%. The lowest fat contents (1%) tended to be found among some flatfish, shrimp and octopus. Confounding of collection distributions (i.e., all one size class from one season) precluded strict analysis of this in most species and trends have been discussed in detail in previous reports (e.g., Iverson et al. 1998). However, as illustrated most clearly in herring, the highest fat contents are found in the fall and lower contents in the spring and summer.

Prey Species - Fatty Acids

Approximately 70 fatty acids and isomers were routinely identified in all prey species (Table 4). Two additional components were formed from the ratio of two sets of important isomers as suggested by Iverson et al. (1997b): ratio of 20:1n-11 to 20:1n-9 (R20:1) and ratio of 22:1n-11 to 22:1n-9 (R22:1). In previous reports (see Iverson et al. 1998) differences between and within prey species in fatty acid composition have been well-illustrated and discussed. Thus for the current report only updated information - and that which applies to the modeling of seal diets - will be discussed. Refer to Table 4 and Iverson et al. 1998 for further details.

Despite variations within prey species, and often a confounding of sample collection (differences in size-classes, seasons, locations and years), prey continue to be readily and accurately distinguished from one another based upon their fatty acid signature. This can be illustrated using CART analysis, which compares all 70 fatty acids simultaneously across all species of prey (excluding prey with sample sizes less than 4) (Table 5). Despite a prey base that now contains over 1,000 individuals, the primary classification tree correctly identified 93.3% of all prey species in PWS by their fatty acid signatures alone. Although the tree itself is somewhat complex to present in the current report, groupings of species remained predictable. For instance, all flatfish (including yellowfin sole) are classified together down the far right node of the tree. Likewise, species of squid travel together and then separate. In general, herring, pollock, and sandlance require more splits and fatty acids in order to be correctly classified, suggesting more similarity in signatures among these three species.

The most extensive collection data remains for herring, providing the best opportunity to asses factors contributing to individual variability in fatty acid signatures. With a sample size of 332 individuals, all previous observed trends remain the same. For instance, despite seasonal variability in fat content, there do not appear to be evident seasonal or annual effects on fatty acid signatures (see Iverson et al. 1998). Size class remains the single largest factor affecting variability in signature (Fig. 2). For instance in the major fatty acids 20:1n-11 and 22:1n-11, about 80% of the variability was explained by length alone, while for 20:5n-3 and 22:6n-3, 50-58% of the variability was explained by length (Fig. 2). This year, herring was available from outside PWS near the Kodiak region and indeed these were comparable to general PWS herring and composition was well-predicted by size patterns (Fig. 2). The single exception remains herring collected from western (mainly NW) PWS. Fatty acid characteristics of NW-PWS herring differ from other PWS and Kodiak herring and are not well-predicted by the general size relationship, and hence have been excluded from those relationships (Fig. 2). Nevertheless, despite this variation (and primarily by size) in selected fatty acids, herring as a whole are still distinguished correctly from all other species with 98% accuracy (Table 5). Indeed, although differences within other species also remain apparent, species are readily differentiated from one another across species as a whole using fatty acid signatures, with an average of 93% accuracy.

Harbor Seal Fatty Acids

Tables 2 (recent samples) and 3 (archived samples) summarize the collection data for all blubber sampled and analyzed 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. In cases where animals were initially listed as "pups", but captured in either the fall (September, October) or early spring (March, April) , these were deemed to actually be half-year-olds and yearlings, respectively, as pups are weaned by July after about 25 days. "Pups" as contained herein refers only to actual suckling or newly weaned pups (within first few weeks) captured in June.

The same approximately 70 fatty acids and isomers found in PWS prey were routinely identified in harbor seal blubber samples across all locations and across several decades (Tables 6 and 7). A particularly promising finding was that archived blubber samples, taken from seals and stored frozen since the 1970s, showed little evidence of degradation. Indeed, any effects might be expected to be observed most strongly in losses of long-chain polyunsaturated fatty acids, but there was no evidence for this. In fact, in components such as 20:5n-3 and 22:6n-3 levels were generally higher in the archived samples than in the present-day samples.

Our previous reports have presented and discussed in detail variations observed in blubber fatty acid composition between seals among major locations of the GOA (i.e., PWS and elsewhere in the GOA), as well as on finer-scale regions within PWS or SEA (Iverson et al. 1998). Variability among demographic groups has also been addressed in detail. Hence, the current report will focus only on updated data and on some of the new broader-time scale comparisons, as well as data as it relates to modeling diets.

Since the harbor seals collected in southern PWS represent the only group to date with sampling extensive enough to evaluate differences in individuals across years, SC and SE seals were combined for the analysis of 1990s results. When only adults were included ($n = 107$), there was strong evidence that diets of seals (as indicated through fatty acid signatures) have differed between the years (Fig. 3). In particular 1994 and 1995 appeared to differ most with 1996 and 1997; adults were correctly identified to year by fatty acids with 96.3% accuracy. When all subadult classes (excluding suckling pups) were included with adults in this analysis ($n = 236$), a nearly identical result and classification was obtained with 96.2% of the animals correctly classified (Fig. 4).

It is useful to compare these changes with those possibly observed over a decadal scale and in relation to demographic groups. Given the large numbers of groups and sample sizes, in the present example only adults versus subadults that weighed <40 kg (most likely representing 2 year olds) are presented; also only animals sampled in south central areas of PWS and in the Kodiak Island area were used, since these areas are likely to be less confounded by large habitat differences involving differing fresh and saltwater inputs. Using five important indicator fatty acids or isomer ratios, it is clear that diets of harbor seals in the 1970s differed dramatically from those in the 1990s (Fig. 5). Although variation and changes over years are observed from 1994 to 1998 (and as illustrated in Figs. 3 and 4), these differences were far more minor than those which occurred after 1976 and 1977 in comparison to the 1990s ($P < 0.0001$). Differences between adults and subadults are also apparent in each decade, but those differences were generally more minor than between decades (Fig. 5). The results from CART analyses confirmed these observations (Fig. 6). A total of 97.6% of all seals (n = 375) were correctly identified both to their general location (Kodiak vs. PWS) and decade (1970s vs. 1990s) based on their blubber fatty acid signatures, indicating diets differed mostly over time, and secondarily with general GOA location (Fig. 6).

Harbor Seal Body Composition 1998

The body composition of 34 harbor seals captured in June 1998 from SC and SE PWS is reported in Table 8. Pups (n = 14; animals that were either about to be weaned or had recently been weaned) averaged 28 kg body mass and were comprised of 39% fat and 14% protein. Although body mass of these pups was slightly but significantly lighter than those in 1997, there was no difference in body fat content. In contrast, 1998 yearlings were significantly lighter than yearlings in 1997 but were also significantly fatter (Table 8). Older subadults in 1998 averaged a remarkably high 23-26% body fat, which again, appeared to be higher than those measured in 1997, however this could not be tested due to small sample sizes.

MODEL DEVELOPMENT TO PREDICT SEAL DIETS FROM FATTY ACID PROFILES: PROCEDURES AND RESULTS AND DISCUSSION

Initial Model Creation as applied to Free-Ranging PWS Seals

The use of fatty acids to elucidate trophic relationships or differences among groups of animals has previously been demonstrated (Iverson et al. 1997a,b; Iverson et al. 1998). The next stage, using fatty acids to actually estimate diet composition, requires the development of a statistical 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 eventually incorporate information on the widest range possible 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 somehow incorporate a weighting on individual fatty acids as a function of their ability to be biosynthesized by the predator, and, finally, a relative weighting of prey signatures that reflects the proximate fat content of each prey and size-class.

Although our current prey data base is not complete in a number of areas, it nevertheless is substantial in size and provides a solid basis with which to begin applying our model. As stated previously, the efforts to try to develop such a model are underway in conjunction with two ecosystem studies (the current PWS, Alaska study and that on the Scotian Shelf, Canada). The model development itself uses data from both of these studies but also relies heavily on information being gained from both past captive studies conducted at Dalhousie University's Aquatron facilities and from current studies being planned and conducted with captively held seals on Sable Island, NS. The following summarizes the initial work in this area and as it relates to the current Restoration Project. Most of the following is new from the previous report of Iverson et al. (1998).

The issue is to try to estimate the composition of a seal's diet based on the relationship of its fatty acid signature to that of the prey that made it up. The initial approach was to take a weighted mixture of the fatty acid profiles of the prey types and to choose the weighting which minimizes the distance from the seal or seals under consideration. Thus, we first began by defining the following quantities: we use j to label the fatty acid, l to label the seals and i to label the prey types. Then,

- Let y_{lj} represent the j th fatty acid for the l th seal, with the restriction that $\sum_j y_{lj} = 1$ for all l.
- Let x_{ij} represent the j th fatty acid for the i th prey type, with the restriction that $\sum_j x_{ij} = 1$ for all i.
- Let p_i represent the proportion of the seal's diet derived from prey type i, with the restriction that $\sum_i p_i = 1$.

The general problem is to find the weighted sum of the prey fatty acid profile, $\hat{y}$ with jth component $\hat{y}_j = \sum_i p_i x_{ij}$ which comes closest to matching the seal's fatty acid profile y_{lj}. Note that we require the same proportional weighting to hold across all the fatty acids j. We use optimization techniques to minimize the distance between the actual fatty acid signature and the predicted fatty acid signature profile $\hat{y}$.

The data set used in first trying out any models was a limited (n = 445) prey base from PWS and a small selected group (n = 30) of adults and subadults from central PWS. An average fatty acid profile was used for each prey species. Additionally, we restricted the fatty acids used in analyses to only those which could come from diet - that is, we included none that could be biosynthesized by the seal, even if also present in the prey. We then attempted calculating diets for both individuals as well as for a composite group of seals and at the same time came up with four different distance measures: (1) where distance is the absolute value of the log odds of the seal minus the log odds of the prey, which was motivated by the use of the log odds ratio in comparing two proportions; (2) the Euclidean distance and, finally (3) the forward and (4) backward Kulback-Leibler (KL) distance measures.

The calculations based on composite groups of seals were unsuccessful for a number of reasons and it was decided that the calculations for individuals were superior. Of the four distances, it was decided that the log odds ratio was performing the worst and was dropped. The forward and backward Kulback-Leibler distance measures performed the best:

$$(3) \quad \sum_j y_{lj} \log (y_{lj} / \hat{y}_{lj}) \quad \text{and} \quad (4) \sum_j \hat{y}_{lj} \log (\hat{y}_{lj} / y_{lj}).$$

Numerous iterations were run on various seals and data sets.

Optimization was initially done using Fortran and the NAG optimizer EO4UCF. However, time was taken to write some of the optimizing code in SPLUS (by C. Field). This has several advantages over Fortran, the most important being that the data management is considerably easier in SPLUS. Also, the SPLUS programming language is much easier to use The optimizer we used was nlminb (SPLUS).

Validations and Testing of the Model using Captive Studies

We then turned to using data from captive experiments to begin testing the model process to date. The data most recently used to develop the model are based on several captive studies of harp seals and grey seals (initially fed herring and then switched to diets of either pollock or mackerel or a mixed diet of mackerel and capelin) conducted at Dalhousie University's Aquatron facilities in 1994-1998. We continued to use subsets of dietary fatty acids only in calculations and we encountered some difficulty in predicting the actual known diets, in part due to this subset usage and in part due to some deficiencies in our distance measures. We thus introduced two new distance measures: (5) the sum of the KL forward and backward distances and (6) the squared distance applied to the arcsin square root of the proportion of each fatty acid.

We then made several important advances in the model process.

I. Bootstrapping to estimate standard errors: We needed to be able to assess the variability of an estimated diet due to variability in prey; that is, what error might occur due to using only an average of all the individuals of each prey type. Hence we developed a bootstrap sampling scheme. For each prey type, we select a bootstrap sample, compute the mean for each bootstrap sample, then estimate the diet using the bootstrap prey type mean, and repeat this a number of times. We can thus use the bootstrap samples to compute a standard error of the estimated diet for any individual seal. This kind of error estimate is time-consuming (requiring large computer capacity) but will be quite important in final reports and assessment of diets.

II. Truncation of distance measures: The fits for the distance measures used thus far all appeared to be overly sensitive to large deviations (i.e., greater weight placed on more abundant components). We thus created a truncated average KL and a truncated square distance, both of which performed better as assessed using sensitivity tests.

III. We then tested three different subsets of fatty acids to use in the model to see which performed the best: (a) all fatty acids detected in common between prey and seals, (b) only fatty acids that were known to be of dietary and only dietary origin (i.e., could not be biosynthesized by the seals), and (c) a combination of all the latter (group (b)) and some of the former (group (a), those which occur commonly in prey) into the most probable set of importance to be considered in dietary analysis. That is, group (c) contains all fatty acids of dietary origin plus the fatty acids that could and do arise from diet but that also can be biosynthesized by the seal; group (c) excludes those fatty acids which could only arise from biosynthesis in the seal. The fatty acids assigned to these groups were decided upon by consultation between S. J. Iverson and R. G. Ackman (Canadian Institute of Fisheries Technology).

In all cases, as tested with data from captive studies, groups (b) and (c) performed the best.

IV. Last, and probably most importantly, we developed what we call "calibration factors" (S. Iverson, C. Field, W. Blanchard and W. D. Bowen, unpublished). These factors are based on the notion that all fatty acids analyzed in a sample from a seal will provide information on the diet, however, some specific fatty acids provide information more directly and others less directly. That is, some fatty acids will originate in the seal both from direct transfer from a prey's fatty acids but also from biosynthesis in the seal (e.g., from excess protein consumed). In contrast, other fatty acids can originate only directly from intake them in the diet. Thus, several captive control studies of grey seals and harp seals, fed the same herring diet over many months, were conducted (1997 and 1998) and have been used to estimate calibration factors (weighting factors) of the degree to which a given fatty acid in the seal needs to be weighted to match its prey. The calibration factors are defined as follows:

$$c_j = \text{avg}_l \, y_{lj} / \text{avg}_i \, x_{ij}$$

As would be expected, the calibration factors determined for most group (b) fatty acids were near 1, whereas those from the mixed category differed consistently from 1. Next, the calibration factors were used in the squared distance measures and KL distance measures. These are currently ongoing studies, as we must assess the validity of the calibration factors on several different diets (captive studies planned for May-June 1999). Hence, the calibration factors may be further refined, but those currently developed have been tested successfully on dietary treatment groups (the previous captive studies where diets had been changed). Calibration factors appear to be one of the most important factors to include. The model algorithm was implemented to use the three sets of fatty acids and again found to perform best on groups (b) and (c). However, with the incorporation of calibration factors, the use of group (c) fatty acids appears to perform the most accurately. This later finding is also encouraging as it allows the use of more fatty acids and thus potentially allowing more resolution in diet estimation.

Finally, in practice, the algorithm is then run to find the estimated composite contribution of fatty acid signatures from prey to the signature of an individual seal. This result does not estimate diet, but the estimated contribution of fatty acid signatures of each prey type (i.e., it does not take into account the fat content of the prey). In order to convert these signature contributions to dietary proportions, the fat content of each prey type must be factored into the analysis and model. Thus, the average fat content was calculated for each species (or size classes used within species) and this is then used to calculate the amount of prey needed to make that signature contribution.

Results determined for PWS (and Kodiak) harbor seals

The diet estimates derived from fatty acid signature analysis presented in the current report are preliminary and likely represent more of what can be done, than what is the exact answer. As stated previously, in order for fatty acid signature analysis and the associated modeling to work successfully, i.e. to actually reconstruct the diet composition of a seal with accuracy, it requires a very detailed and extensive prey data base ("prey library") on the fatty acid signatures of all possible prey species and on the variability of these signatures within species. Obviously, if a prey type is not represented in the database, it will not be identified in any diet. Although the data base is currently quite large for some species, we may still be missing some species altogether, or may not have assessed the variability in species which do exist in the database (particularly with sample sizes of < 10). More importantly, the model requires further developmental work in several areas, which we plan to address in detail during the next year. Alternative competing diets using changes in the model parameters need to be thoroughly investigated in order to provide an error estimate for diets. An ability to truly add in a prey variance component is still underway and yet sorely needed. At the moment, for instance, the model is having some difficulty in reliably distinguishing pollock and sandlance from herring in PWS, and this is almost certainly because we are using composite prey averages. In part, computer power and time has been limiting. More time will be spent in this area in the next year. Additionally, as stated previously, the calibration factors developed have become quite important to the calculation process. These have largely been derived from several past captive studies with less than perfect validation conditions. We currently have planned several new captive studies to be conducted this spring with the aim to verify and optimize these factors. Thus, most of the final modeling and interpretation of harbor seal diets will be dealt with in the next (2000) report. However, given the above caveats, the following are current estimates and conclusions based on subsets of animals from the PWS and Kodiak Island data base.

Using the model as described above and group (c) fatty acids, mean contributions to harbor seal fatty acid signatures were estimated for a subset of animals: adults, yearlings and half-year olds in areas of PWS excluding NW-PWS, to get a general idea of what diet items appeared to be predominant (Table 9). Although we do not have any prey collected prior to 1994, we used our current prey data as a basis for applying to several PWS seals sampled in 1977-1989. In all cases, flatfish appeared as a consistent and prominent mean contributor (20-30%) to seal fatty acid signatures. This was primarily attributed to yellowfin sole; however, when yellowfin sole was removed from the data base, this contribution shifted to precisely the same sum of amounts of other flatfish species, primarily flathead sole and rex sole. Herring was detected as a prominent component of all diets, however, using alternate prey libraries and model parameters, it is clear that the current model has some trouble distinguishing herring, pollock and sandlance. Hence, for the moment, these are grouped together in Table 9. Switching from a composite prey average will likely reduce this problem, as suggested by tests on one or two individuals. When herring size classes are included in the model, the amounts of small and medium herring contribution (no large detected) sum to the same amount of herring predicted when no size classes are used in the model. Sandlance and pollock make up the rest of this contribution, but the exact amount is not yet clear. Rainbow smelt also appears prominently at 1-13% of signatures, however, currently only n = 4 of this species exists in the data base, hence the degree to which these represent the species as a whole is unknown. Octopus, pink salmon adults and pink salmon smolts, as well as some capelin appear only in the diets of adults, and not in the diets of yearlings or younger. Eulachon smelt appear quite prominently in many diets, especially those of yearlings and half-year olds, contributing up to 30% of some fatty acid signatures (Table 9).

When fat contents of prey species are taken into account, contributions to fatty acid signatures can be converted to model estimations of mass proportion in the diets consumed (Table 10). The same species identified in Table 9 appear in the diet, but in this case, species with lower fat contents such as pink salmon and flatfish must be eaten at higher amounts to contribute the proportion they do to signatures. Hence, flatfish increase to representing 24-50% of mean diets and pink salmon were detected to be quite high in some adult diets, especially prior to the 1990s. In contrast, eulachon decreases to only 1-7% of diet consumption; that is, only about 5% of eulachon needs to be consumed in the diet to make up 20% of the blubber fatty acid signature given most other prey consumed (Tables 9, 10).

Archived samples from harbor seals in the Kodiak Island area are far more plentiful than those available from PWS. Although we do not have a prey data base for the Kodiak Island area, results from harbor seal signatures (Iverson et al. 1988) as well as recent herring signature analysis (e.g., Fig. 2) suggest that prey signatures in the Kodiak area may be somewhat similar to that in central PWS. Again, we do not have an actual prey base from the 1970s, but given these caveats, we can use our current data base to examine possible differences that may have occurred in seal diets over decades. Thus, six adult harbor seals sampled in 1977 and eight in 1996 from Kodiak Island were modeled in detail using four different scenarios in the model and the prey library that it contained; the results of the four models were then combined and averaged (Fig. 7). Again predominant contributions to fatty acid signatures came from eulachon, flatfish, herring, and rainbow smelt, but also sandlance and squid. The proportion of herring consumed that was medium vs. small appears to have changed from the 1970s to the 1990s. Sandlance appeared to have decreased substantially from 1977 to 1996 and pollock to increase slightly. The other apparent trend was a higher diversity in prey species contributing to the signatures in 1977 vs. 1996 (Fig. 7). When fat contents of prey species are taken into account, estimations of mass proportion in the diets consumed (Fig. 8) suggested a consistent predominance of flatfish, followed by lower amounts of herring, rainbow smelt, sandlance, eulachon and pollock. Again, a higher diversity of prey species was apparent in 1977, with significant amounts of octopus, pink shrimp and various squid species predicted in diets (Fig. 8).

As stated previously, earlier indications from fatty acid patterns alone indicated that fine-scale structure of foraging distribution of harbor seals was apparent, 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 habitat within PWS. Hence this hypothesis was further examined in a final modeling exercise. As stated above, herring appears as a common diet item in seals in PWS (Tables 9, 10), yet it is clear that herring from NW-PWS differ quite readily from herring collected elsewhere in the PWS (Fig. 2). This factor was used to model diets of 11 harbor seals that were sampled in NW-PWS in the 1990's. These seals were modeled using 2 prey libraries: 1) that which contained no NW-PWS herring in the library while the rest of the herring were split into small, medium and large size classes, and 2) that which contained the above herring size classes in the library plus a fourth group labeled NW-PWS herring. In the first model (excluding NW-PWS herring from the library used), a total of 41.8% herring was predicted to make up fatty acid signatures across all seals (Fig. 9). This was further split into 1.0% large herring, 33.0% medium herring and 7.9% small herring. Other prey contributors to signatures included eulachon, flatfish, pink salmon (adults and smolts), pollock, rainbow smelt and squid. When the second model, including NW-PWS herring, was used, almost the exact same total quantity of herring (42.0%) was predicted to make up fatty acid signatures across all seals. However, in this case, 7.8% of the herring was instead identified as NW-PWS herring and the rest was further split into medium and small categories. The rest of the prey species identified remained at exactly the same levels as when predicted with the model that excluded NW-PWS herring from the library (Fig. 9).

When fat contents of the prey species are taken into account and estimations of mass proportion of prey in the diets consumed are calculated (using NW-PWS herring in the library), these can be divided across three demographic groups of the 11 seals (Fig. 10). In this case it can be seen that adults (n = 8) relied most heavily on eulachon, flatfish, some herring, pink salmon, pollock, rainbow smelt and squid. Only 1.4% (0.3% total) of the herring adults consumed was estimated to be NW-PWS herring. In contrast, of the herring the subadults and half-year olds were estimated to consume, 48% and 100% (respectively) of this herring was NW-PWS herring (Fig. 10). Again, as found in other areas of PWS (Tables 9, 10), the diversity of prey species in the diets of subadults and the half-year old was lower compared to adults, containing no salmon or pollock and little squid in the diets.

DISCUSSION AND CONCLUSIONS

Previous studies have suggested that various marine prey species may be readily distinguished from one another based on their fatty acid compositions, that fatty acids consumed in the diet can be directly deposited in adipose tissue, and hence that fatty acids may be used as trophic indicators in their predators (Iverson 1993). Lipids have been used as biological markers and general diet indicators in a number of studies on fish and copepods (e.g., Sargent *et al.* 1988; Fraser *et al.* 1989; St. John and Lund 1996; Kirsch *et al.* 1998). Moving up the food chain, milk and blubber fatty acids in free-ranging pinnipeds have been used recently as indicators of diet or of changes in diet (Iverson 1993; Iverson *et al.* 1997a; Iverson *et al.* 1997b; Smith *et al.* 1997). However, while previous studies have linked fatty acids to potential trophic levels and changes, with the development and implementation of our model, we present some of the first data which advances the use of fatty acids to the point of being able to use them in a quantitative manner to actually estimate species composition of the diets of individual seals. As discussed previously under the previous model development section, further development and refinement of the model and its parameters is required and planned for the 1999 research year; nevertheless, some compelling results are apparent from our preliminary estimates.

Although the prey base so far developed for PWS has grown in complexity and now contains over 1,000 individuals, prey are still able to be separated and identified to their species with an average of 93.3% accuracy by their fatty acid signatures alone (Table 5). Variability is still apparent within species, nevertheless species are still identifiable. As illustrated with herring, much of the variability can be explained by changes in size class (Fig. 2), which corresponds to the fact that diets of these fish change with size and age (e.g., NRC 1996). Although data for most species remain limited to test, it appears that season and year have minor affects on prey fatty acid composition, at least between the years analyzed of 1994 and 1998. However, in some species for which we have data, habitat differences may influence fatty acid patterns. The best example remains herring collected from the NW PWS, which largely differ from the patterns of PWS herring as a whole. NW waters may be more influenced by glacial freshwater input, hence may result in slightly different food web structures (e.g., Lalli and Parsons 1993). Nevertheless, herring as a whole (including NW-PWS herring) are still readily identified from most other species. The finding that herring, sandlance, and especially pollock are somewhat more difficult to separate than other species is consistent with findings of dietary overlap in these species in PWS. Willette *et al.* (1997) found evidence of very high dietary overlap primarily between herring and pollock and secondarily between these two species and sandlance in areas of PWS This would result in greater similarities in fatty acid signature of these species (Kirsch *et al.* 1998), even though they can still be distinguished from one another using CART. However, our finding that the current model has more difficulty distinguishing these species from one another in diet calculations, indicates that further work on model parameters and incorporation of prey variability will be required.

The analyses of archived blubber samples, taken from seals in the 1970s, were quite promising as they showed little evidence of degradation. Hence, these can be used to compare possible changes in diets of harbor seals over several decades, from a period of high population status (1970s) to a period of declining population status (1990s). The evidence is very compelling that diets have changed substantially over these decades as evidenced by large differences in blubber fatty acid signatures (Figs. 5, 6). Clearly, the intake of fatty acids in the diets of seals differed. Prey themselves might have changed quite substantially in fatty acid signatures, however, this seems unlikely. Despite the fact that a prey species signature will change with changes in diet (dietary fatty acids), even when these changes are dramatic, prey are still able to be distinguished by species as a whole (Kirsch *et al.* 1998). Thus, this suggests that seal diets have indeed changed.

Results from actually applying the model to these seal fatty acid signatures, suggest several things. One is that flatfish (and perhaps especially yellowfin sole) appear to be a large consistent proportion of the diet of most seals, both earlier and at present. The model appears to be quite robust to this conclusion, as even when we remove yellowfin sole from the library, the amounts shift over to other species of flatfish, all of which have fairly similar types of signatures (Table 5; and see Iverson *et al.* 1998). Even juveniles appear to rely on a consistent proportion of yellowfin sole and other flatfish. Although previous analyses of harbor seal stomach contents from the 1970s (Pitcher 1980a) do not suggest that flatfish are as important as with our model, discrepancies could result from methods used. Additionally, flatfish, especially yellowfin sole, represents one of the largest biomasses of finfish in the Bering Sea and GOA (NRC 1996), hence they should be amply available to harbor seals. Furthermore, recent data from underwater cameras (Crittercam, National Geographic) attached to harbor seals on the Scotian Shelf, suggest that flatfish are quite easy for harbor seals to catch and consume (W.D Bowen and S.J. Iverson, unpublished observations). This would argue for flatfish appearing consistently in the diets of less experienced juveniles as well.

Nevertheless, while flatfish may be a consistent item in the diet, it may not be nearly as important - per gram fish - as consuming a species such as eulachon. That is, flatfish are low-fat and may be easy for juveniles to catch. However, if juveniles can consume just 5-7% of high-fat eulachon in their diet, they can fatten far more readily, as illustrated by these amounts contributing 24-30% of their fatty acid signatures (e.g., Tables 9, 10). Thus, even if low-fat prey such as flatfish or pollock are currently the most abundant in the ecosystem, it may be that juveniles can make it by with just a small amount of consumption of a high fat prey. Certainly, juveniles studied in the past two years (1997-1998) have been found to be very high in body fat content (Table 8) and eulachon was prominent in all of these signatures (Table 9). Hence, diet composition tells us what biomass is eaten by seals, but the contribution to the fatty acid signature may tell us what is most important to survival.

Finally, the application of the model to harbor seal fatty acid signatures has suggested several findings about decades and demographic groups, as well as spatial scales of foraging. In summary, it appears that diets of harbors seals in PWS in the 1970s were generally lower in flatfish and higher in pink salmon than present day (although the sample size for the 1970s is quite small, Table 10), while diets of harbors seals at Kodiak Island in the 1970s were higher in sandlance and were more diverse than present day, containing substantial amounts of octopus, pink shrimp and squid in the 1970' (Fig. 8). Evidence also suggests that the diets of adults are more diverse than that of yearlings or half-year olds and contain prey such as octopus, pink salmon and squid. In contrast it would appear that juveniles do not catch these later items (and/or that these prey may be more difficult to catch) and instead depend on a more simple diet (Table

10). Juveniles may also have smaller spatial scales of foraging than adults, as illustrated by diets of the three subadults in NW-PWS containing predominantly herring from NW-PWS (Fig. 10). This later case was also an important example of the possible detailed extent to which fatty acid signature analysis can be used in assessing the foraging ecology and food dependence of free-ranging pinnipeds. Without having analyzed NW-PWS herring, the diets of NW-PWS seals would still have been predicted to contain herring (Fig. 9). However, with the inclusion of NW-PWS herring in the prey library, we predicted the exact same proportion of herring in the diets but we were additionally able to assess where that herring came from (Figs. 9, 10).

In conclusion, the current results of fatty acid signature analysis are very promising, informative and insightful. Results suggest that determining diets or changes in diets of harbor seals over time is possible using fatty acid signatures and may provide clues not only to changes in foraging patterns, but also to differences in local prey availability or preferences by individuals, as well as predominant species size classes, at the spatial and temporal scales that are essential to the nutrition of individual animals. However, as stated previously, the current estimates should be considered indeed as estimates, and future focus must be on further development and refinement of the model we have begun in order to have full confidence in our estimations. Briefly, this includes assessment of the prey library itself, incorporations and assessments of true prey variance components, consideration and testing of alternative competing diet estimations, and further confirmation and refinement of the calibration factors developed. These developments will allow a full analysis of changes that have occurred in harbor seal diets over years and across geographical regions in the GOA.

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Table 1: Collection data and Fat Content of Prey Species Analyzed (n = 1,052).

						Length (cm)		**Mass (g)**		**Fat Content (%)**	
Species		**n**	**Locations**	**Years**	**Seasons**	Mean ± SEM	range	Mean ± SEM	range	Mean ± SEM	range
Capelin		79	C,NE,NW,SC	1995,1996	all	12.8 ± 0.11	8.6 - 14.4	14.6 ± 0.54	2.2 - 25.8	1.9 ± 0.15	0.5 - 6.3
Chum		7	SE	1996	Sum	10.2 ± 0.68	8.3 - 14.0	10.6 ± 2.85	5.3 - 27.5	1.4 ± 0.09	1.1 - 1.9
Copper Rock Fish		1	NE	1995	Fall	20.2		173.9		2.2	
Eulachon Smelt		20	NE,SE	1996	Sp	15.1 ± 0.28	12.8 - 17.1	18.4 ± 1.49	9.5 - 30.9	19.0 ± 0.52	15.0 - 25.3
Flatfish	Flathead Sole	33	NW,SC,SE	1995,1996	Sum, Fall	17.0 ± 0.69	8.7 - 26.2	45.2 ± 5.73	5.0 - 168.8	1.6 ± 0.15	0.7 - 4.4
Flatfish	Rex Sole	23	SC,SE	1995,1996	all	18.9 ± 0.90	13.1 - 33.8	40.2 ± 9.41	3.0 - 234.0	1.1 ± 0.11	0.1 - 2.4
Flatfish	Rock Sole	1	NW	1997	Fall	23.8		144.71		.94	
Flatfish	Unknown Sp.	24	NE	1995	Fall	19.7 ± 0.57	15.6 - 26.2	61.8 ± 6.78	23.1 - 168.3	1.0 ± 0.12	0.4 - 2.1
Flatfish	Yellowfin Sole	17	SC,NE	1994,1996	Sum, Fall	25.1 ± 0.95	19.7 - 33.1	201.7 ± 25.97	93.5 - 436.8	3.0 ± 0.57	1.2 - 8.4
Greenling		2	SC	1996	Fall	36.5 ± 0.80	35.7 - 37.3	573.4 ± 8.11	565.3 - 581.5	1.3 ± 0.12	1.2 - 1.5
Herring	Large	76	SC,SE,Kodiak	1994 - 1998	all	22.4 ± 0.17	20.2 - 26.7	120.9 ± 3.93	62.7 - 208.0	9.7 ± 0.65	1.4 - 22.0
Herring	Medium	78	SC,SE	1994 - 1998	all	17.5 ± 0.20	14.2 - 20.1	54.7 ± 2.28	8.5 - 101.6	9.4 ± 0.55	1.9 - 26.3
Herring	Small	124	C,NE,SC,SE	1994 - 1997	all	10.7 ± 0.18	6.1 - 14.0	12.2 ± 0.64	1.4 - 27.3	4.8 ± 0.29	0.5 - 19.1
Herring	West	54	NW,SW	1995,1996	Sp,Sum	11.5 ± 0.15	9.0 - 14.6	13.8 ± 0.81	5.2 - 33.7	5.4 ± 0.39	1.1 - 12.6
Octopus		7	NE,SC	1994 - 1996	Sum, Fall	44.0 ± 6.53	23.0 - 71.6	722.0 ± 290.50	159.1 - 1858.0	1.2 ± 0.13	0.9 - 1.9
Pacific Cod		16	SE,SW	1994,1995	Sum, Fall	38.4 ± 17.6	17.3 - 302.0	84.9 ± 11.60	42.2 - 205.3	2.3 ± 0.39	0.6 - 5.3
Pink Salmon	Adult	5	NE	1996	Sum	47.8 ± 0.48	46.7 - 49.4	1438.9 ± 90.42	1238.7 - 1776.2	3.4 ± 0.58	2.2 - 5.0
Pink Salmon	Smolt	40	C,NE	1996	Sum	8.6 ± 0.24	6.7 - 12.3	6.2 ± 0.53	2.5 - 16.3	1.0 ± 0.05	0.6 - 2.1
Pollock	Large	12	NW,SE,SW	1995,1996	Sp, Fall	28.7 ± 1.09	24.5 - 37.7	163.9 ± 25.47	44.5 - 367.21	1.6 ± 0.15	1.0 - 2.3
Pollock	Medium	142	all	1995,1996	all	18.1 ± 0.21	12.6 - 23.5	44.2 ± 1.42	14.1 - 100.0	2.4 ± 0.12	0.6 - 7.5
Pollock	Small	32	all	1994,1995	all	8.3 ± 0.39	5.2 - 11.3	4.5 ± 0.53	0.8 - 12.1	1.7 ± 0.18	0.6 - 5.9

All values were derived from whole prey, ground and analyzed individually. When 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 (Sum) and Fall. .

* Each sample consisted of 23 individual shrimp ground together.

Table 1. Continued

						Length (cm)		**Mass (g)**		**Fat Content (%)**	
Species		**n**	**Locations**	**Years**	**Seasons**	Mean ± SEM	range	Mean ± SEM	range	Mean ± SEM	range
Rainbow Smelt		4	n/a	1994	n/a	20.5 ± 0.55	19.6 - 21.5	73.4 ± 12.3	52.1 - 108.4	3.6 ± 0.87	2.4 - 6.1
Rockfish		1	SC	1996	Fall	33.2		769.0		3.79	
Sandlance		80	C,NE,NW,SC,SE	1994 - 1997	Sp,Sum	10.7 ± 0.26	6.0 - 15.4	5.8 ± 0.40	0.5 - 13.6	3.7 ± 0.20	0.8 - 7.8
Sculpin		2	SC	1996,1997	Sum, Fall	27.1 ± 1.30	25.8 - 28.4	299.1 ± 65.30	233.8 - 364.4	1.0 ± 0.25	0.8 - 1.3
Shrimp	Pink Shrimp	15	NW,SE	1996	Sp,Sum	8.4 ± 0.16	7.5 - 10.0	2.8 ± 0.18	1.5 - 4.8	1.3 ± 0.11	0.7 - 2.1
Shrimp	Unknown Sp.	2*	SE	1994	Fall	n/a		n/a		1.1 ± 0.11	1.0 - 1.2
Squid	*B. magister*	12	NE,NW	1995	Fall	n/a		149.9 ± 86.1	2.1 - 811.1	6.7 ± 0.84	2.9 - 13.2
Squid	*R. pacifica*	22	SE	1995	Fall	n/a		14.9 ± 1.87	4.7 - 37.7	2.2 ± 0.09	1.1 - 3.1
Squid	Unknown Sp.	83	NW,SC,SE	1994 - 1996	all	26.1 ± 1.19	13.5 - 72.8	44.4 ± 5.46	2.2 - 345.4	2.1 ± 0.11	0.9 - 4.8
Tomcod	Large	18	NE,SC	1995,1996	Sum, Fall	19.7 ± 0.72	12.9 - 16.2	62.3 ± 10.77	28.7 - 214.8	1.3 ± 0.11	0.7 - 2.4
Tomcod	Small	20	n/a,SE	1996	Sum	7.7 ± 0.31	6.2 - 10.6	3.4 ± 0.55	1.4 - 10.8	1.2 ± 0..13	0.4 - 2.2

Table 2. Collection information for harbor seals sampled for fatty acids analysis, 1994-1998.

			Number of Individuals Sampled						
				Subadults					
Year	Area	Location	Adults	> 40 kg	< 40 kg	Yrlngs	Half Yrlngs	New Pups	Age Unk
1994	PWS	NE	-	1	-	-	2	-	-
		NW	3	1	-	-	-	-	-
		SC	13	8	7	-	2	-	-
		SE	1	-	1	-	1	-	-
	GOA		-	-	-	-	-	-	-
1995	PWS	NW	-	2	3	-	-	-	-
		SC	14	10	7	1	1	-	-
		SE	-	1	2	-	1	-	-
	GOA	Kodiak N.	4	2	-	2	-	-	-
		SEA	15	1	2	1	1	-	3
1996	PWS	SC	25	9	5	3	4	-	4
		SE	17	1	5	1	4	-	-
		SW	-	1	-	-	1	-	-
	GOA	Kodiak N.	8	-	1	-	1	-	-
		SCA	6	2	3	-	-	-	-
		SEA	9	2	3	-	-	-	10
1997	PWS	NE	1	-	-	-	-	-	-
		SC	10	8	3	5	-	16	-
		SE	-	2	-	2	-	2	-
	GOA	Kodiak N.	-	-	2	-	-	1	-
		Kodiak S.	-	2	-	-	-	10	-
		Kenai Pen.	-	-	-	1	-	-	-
	Bering Sea		-	2	-	-	-	-	-
1998	PWS	SC	18	8	1	16	-	14	-
		SE	9	3	-	7	-	-	-
	GOA		-	-	-	-	-	-	-
		Total	153	66	45	39	18	43	17

Animals from 1994 - 1997 which were initially listed as "pups" but captured either in the fall (September, October) or early spring (March, April) were considered separately from newly weaned pups and were considered as “half-year-olds” or “yearlings” respectively. In this table, “pups" refers only to actual suckling or newly weaned pups (within the first few weeks) captured in June. Some animals captured in June 1997 were also known to be yearlings. Subadults >40 kg and < 40 kg were combined for most analyses.

Table 3. Collection information for archived harbor seal blubber samples analyzed for fatty acids.

			Number of Individuals Sampled						
				Subadults			Half	New	Age
Year	Area	Location	Adults	> 40 kg	< 40 kg	Yrlngs	Yrlngs	Pups	Unk
1976	PWS		-	-	-	-	-	-	-
	GOA	Kayak Island	-	1	-	-	-	-	1
		Kenai Pen.	15	3	2	4	-	-	-
		Kodiak N.	30	6	-	2	1	-	-
		Kodiak S.	21	7	4	-	5	-	-
		Middleton Island	-	-	-	-	-	-	5
		SCA	10	-	-	-	-	-	5
1977	PWS	NE	3	-	-	1	-	-	-
	GOA	Barren Islands	4	-	-	-	-	-	-
		Kenai Pen.	25	1	-	2	-	-	-
		Kodiak N.	28	2	2	-	-	-	-
		Kodiak S.	42	1	3	3	-	-	-
		SCA	5	1	-	-	2	-	-
1978	PWS		-	-	-	-	-	-	-
	GOA	Cook Inlet	-	-	-	-	-	-	11
		Katmai	5	-	-	-	-	-	3
		Kenai Pen.	-	1	2	-	-	1	-
1989	PWS	C	1	-	-	-	-	-	-
		NW	2	1	-	-	-	-	-
		SC	2	-	-	-	-	-	1
	GOA		-	-	-	-	-	-	-
1990	PWS	NW	2	-	1	-	-	-	-
		SW	1	-	-	-	-	-	-
	GOA		-	-	-	-	-	-	-
1993	PWS	SW	1	1	-	-	-	-	3
	GOA		-	-	-	-	-	-	-
		Total	197	25	14	12	8	1	29

Animals which were initially listed as "pups" but captured either in the fall (September, October) or early spring (March, April) were considered separately from newly weaned pups and were considered as "half-year-olds" or "yearlings" respectively. In this table, "pups" refers only to actual suckling or newly weaned pups (within the first few weeks) captured in June. Subadults >40 kg and < 40 kg were combined for most analyses.

Table 4. Fatty acid composition of prey species (n=1052). Values are mean mass% of total fatty acids ± SEM. All values are derived from whole prey that were ground and analyzed individually. See Table 1 for collection and proximate analysis data. a) Capelin, chum salmon, copper rock fish, eulachon smelt, and unidentified flatfish.

	Capelin	Chum Salmon	Copper Rock Fish	Eulachon Smelt	Flatfish
					Flatfish Unk. Sp.
n	79	7	1	20	24
12:0	0.36 ± 0.044	0.02 ± 0.002	0.10	0.07 ± 0.002	0.01 ± 0.002
13:0	0.01 ± 0.001	0.00 ± 0.001	0.01	0.03 ± 0.001	0.02 ± 0.002
Iso14	0.02 ± 0.001	0.02 ± 0.003	0.01	0.03 ± 0.002	0.03 ± 0.003
14:0	5.05 ± 0.308	1.35 ± 0.211	3.44	8.62 ± 0.173	2.17 ± 0.124
14:1n-9	0.14 ± 0.010	0.05 ± 0.007	0.20	0.12 ± 0.007	0.24 ± 0.033
14:1n-7	0.00 ± 0.001	0.01 ± 0.002	0.03	0.03 ± 0.001	0.03 ± 0.004
14:1n-5	0.05 ± 0.005	0.01 ± 0.003	0.08	0.20 ± 0.006	0.03 ± 0.004
Iso15	0.08 ± 0.006	0.06 ± 0.008	0.12	0.16 ± 0.004	0.11 ± 0.007
Anti15	0.02 ± 0.003	0.02 ± 0.005	0.04	0.07 ± 0.002	0.04 ± 0.004
15:0	0.23 ± 0.009	0.23 ± 0.005	0.31	0.30 ± 0.007	0.40 ± 0.019
15:1n-8	0.00 ± 0.000	0.00 ± 0.000	0.01	0.01 ± 0.001	0.02 ± 0.006
15:1n-6	0.00 ± 0.001	0.00 ± 0.000	0.00	0.01 ± 0.001	0.03 ± 0.005
Iso16	0.19 ± 0.010	0.38 ± 0.022	0.19	0.08 ± 0.003	0.79 ± 0.039
16:0	15.56 ± 0.217	21.36 ± 0.317	17.22	16.68 ± 0.420	14.98 ± 0.183
16:1n-11	0.37 ± 0.013	0.29 ± 0.013	0.45	0.36 ± 0.014	0.44 ± 0.008
16:1n-9	0.16 ± 0.024	0.65 ± 0.053	0.25	0.27 ± 0.008	0.37 ± 0.015
16:1n-7	2.74 ± 0.168	2.09 ± 0.135	6.28	8.04 ± 0.373	5.11 ± 0.461
7Me16:0	0.23 ± 0.008	0.19 ± 0.011	0.26	0.28 ± 0.010	0.30 ± 0.009
16:1n-5	0.10 ± 0.005	0.08 ± 0.006	0.14	0.18 ± 0.003	0.23 ± 0.010
16:2n-6	0.04 ± 0.005	0.04 ± 0.003	0.23	0.05 ± 0.003	0.03 ± 0.006
Iso17	0.15 ± 0.021	0.07 ± 0.013	0.12	0.12 ± 0.003	0.15 ± 0.013
16:2n-4	0.20 ± 0.011	0.40 ± 0.037	0.41	0.21 ± 0.013	0.23 ± 0.029
16:3n-6	0.25 ± 0.026	0.06 ± 0.007	0.24	0.49 ± 0.030	0.40 ± 0.025
17:0	0.15 ± 0.012	0.33 ± 0.013	0.31	0.11 ± 0.004	0.28 ± 0.023
16:3n-4	0.24 ± 0.021	0.07 ± 0.005	0.21	0.22 ± 0.014	0.21 ± 0.036
17:1	0.03 ± 0.005	0.16 ± 0.004	0.38	0.33 ± 0.009	0.31 ± 0.037
16:3n-1	0.10 ± 0.006	0.25 ± 0.011	0.13	0.10 ± 0.002	0.11 ± 0.005
16:4n-1	0.51 ± 0.055	0.29 ± 0.008	0.35	0.16 ± 0.016	0.72 ± 0.042
18:0	2.48 ± 0.088	5.23 ± 0.158	4.15	2.43 ± 0.088	4.94 ± 0.155
18:1n-13	0.04 ± 0.005	0.01 ± 0.004	0.22	0.08 ± 0.006	0.10 ± 0.018
18:1n-11	0.59 ± 0.023	0.07 ± 0.011	0.43	0.38 ± 0.054	0.16 ± 0.012
18:1n-9	6.38 ± 0.267	9.16 ± 0.226	14.21	31.31 ± 1.012	8.68 ± 0.287
18:1n-7	2.17 ± 0.081	2.78 ± 0.103	3.85	5.01 ± 0.245	4.57 ± 0.173
18:1n-5	0.53 ± 0.010	0.42 ± 0.027	0.62	0.54 ± 0.018	0.34 ± 0.016
18:2d57	0.01 ± 0.001	0.13 ± 0.012	0.06	0.05 ± 0.003	0.02 ± 0.003
18:2n-7	0.00 ± 0.001	0.05 ± 0.003	0.02	0.05 ± 0.004	0.00 ± 0.003
18:2n-6	0.75 ± 0.025	1.35 ± 0.172	0.98	0.86 ± 0.022	0.77 ± 0.025
18:2n-4	0.16 ± 0.005	0.11 ± 0.007	0.14	0.07 ± 0.005	0.14 ± 0.015
18:3n-6	0.03 ± 0.003	0.12 ± 0.010	0.07	0.07 ± 0.002	0.13 ± 0.006
18:3n-4	0.05 ± 0.002	0.06 ± 0.006	0.06	0.08 ± 0.009	0.10 ± 0.011
18:3n-3	0.52 ± 0.037	0.68 ± 0.073	0.69	0.36 ± 0.020	0.26 ± 0.026
18:3n-1	0.10 ± 0.003	0.09 ± 0.006	0.14	0.04 ± 0.003	0.23 ± 0.016
18:4n-3	1.11 ± 0.098	0.61 ± 0.072	1.49	0.56 ± 0.048	0.78 ± 0.111
18:4n-1	0.19 ± 0.011	0.05 ± 0.003	0.11	0.07 ± 0.010	0.04 ± 0.006
20:0	0.13 ± 0.005	0.07 ± 0.005	0.11	0.14 ± 0.005	0.08 ± 0.003
20:1n-11	6.79 ± 0.447	0.21 ± 0.064	2.07	3.98 ± 0.431	1.30 ± 0.112

Table 4. Part a continued.

	Capelin	Chum Salmon	Copper Rock Fish	Eulachon Smelt	Flatfish
					Flatfish Unk. Sp.
20:1n-9	1.75 ± 0.091	0.46 ± 0.042	1.11	1.79 ± 0.085	1.08 ± 0.045
R20:1	3.73 ± 0.123	0.43 ± 0.111	1.87	2.17 ± 0.166	1.27 ± 0.139
20:1n-7	0.19 ± 0.010	0.15 ± 0.015	0.37	0.20 ± 0.009	1.07 ± 0.134
20:2n-9	0.05 ± 0.004	0.01 ± 0.012	0.10	0.09 ± 0.006	0.06 ± 0.004
20:2n-6	0.16 ± 0.007	0.24 ± 0.015	0.26	0.09 ± 0.003	0.20 ± 0.007
20:3n-6	0.03 ± 0.002	0.17 ± 0.014	0.06	0.03 ± 0.001	0.08 ± 0.002
20:4n-6	0.63 ± 0.050	2.04 ± 0.253	1.80	0.22 ± 0.008	5.05 ± 0.312
20:3n-3	0.05 ± 0.004	0.14 ± 0.011	0.10	0.02 ± 0.002	0.08 ± 0.009
20:4n-3	0.44 ± 0.016	0.63 ± 0.040	0.49	0.13 ± 0.009	0.32 ± 0.026
20:5n-3	12.98 ± 0.320	10.19 ± 0.505	9.38	1.52 ± 0.094	12.14 ± 0.325
22:1n-11	6.29 ± 0.505	0.12 ± 0.017	1.50	5.93 ± 0.668	0.62 ± 0.074
22:1n-9	0.34 ± 0.021	0.08 ± 0.017	0.24	0.69 ± 0.066	0.15 ± 0.013
R22:1	17.21 ± 0.774	1.65 ± 0.164	6.23	10.12 ± 1.368	4.53 ± 0.492
22:1n-7	0.07 ± 0.005	0.08 ± 0.011	0.12	0.13 ± 0.005	0.17 ± 0.011
22:2n-6	0.00 ± 0.001	0.00 ± 0.000	0.04	0.01 ± 0.003	0.09 ± 0.012
21:5n-3	0.35 ± 0.007	0.19 ± 0.013	0.22	0.15 ± 0.013	0.22 ± 0.016
22:4n-6	0.07 ± 0.007	0.11 ± 0.015	0.20	1.89 ± 0.449	0.47 ± 0.031
22:5n-6	0.16 ± 0.007	0.45 ± 0.033	0.32	0.14 ± 0.021	0.57 ± 0.022
22:4n-3	0.02 ± 0.002	0.04 ± 0.002	0.07	0.05 ± 0.009	0.09 ± 0.012
22:5n-3	1.50 ± 0.042	2.53 ± 0.049	1.33	0.21 ± 0.011	2.48 ± 0.059
22:6n-3	24.34 ± 0.948	31.81 ± 1.165	20.01	2.47 ± 0.106	22.68 ± 0.889
24:1	1.19 ± 0.037	0.86 ± 0.026	0.88	0.84 ± 0.051	1.19 ± 0.068

Table 4b. Flathead sole, rex sole, yellowfin sole, rock sole, greenling, and large herring.

	Flatfish				Greenling	Herring
	Flathead Sole	Rex Sole	Yellowfin Sole	Rock Sole		Large
n	33	23	17	1	2	76
12:0	0.03 ± 0.004	0.03 ± 0.004	0.04 ± 0.004	0.13	0.07 ± 0.000	0.09 ± 0.011
13:0	0.02 ± 0.001	0.04 ± 0.007	0.03 ± 0.003	0.02	0.02 ± 0.005	0.02 ± 0.001
Iso14	0.02 ± 0.003	0.02 ± 0.004	0.03 ± 0.002	0.07	0.02 ± 0.003	0.02 ± 0.001
14:0	2.45 ± 0.133	2.18 ± 0.188	3.91 ± 0.221	3.20	2.34 ± 0.057	7.94 ± 0.143
14:1n-9	0.22 ± 0.023	0.10 ± 0.010	0.35 ± 0.045	0.12	0.09 ± 0.020	0.22 ± 0.005
14:1n-7	0.05 ± 0.004	0.07 ± 0.006	0.07 ± 0.008	0.07	0.03 ± 0.000	0.01 ± 0.001
14:1n-5	0.05 ± 0.004	0.04 ± 0.005	0.10 ± 0.011	0.08	0.04 ± 0.000	0.11 ± 0.003
Iso15	0.14 ± 0.005	0.15 ± 0.012	0.22 ± 0.017	0.32	0.13 ± 0.005	0.16 ± 0.004
Anti15	0.06 ± 0.005	0.07 ± 0.007	0.11 ± 0.009	0.18	0.06 ± 0.008	0.05 ± 0.002
15:0	0.41 ± 0.012	0.78 ± 0.029	0.56 ± 0.018	0.59	0.49 ± 0.005	0.28 ± 0.007
15:1n-8	0.01 ± 0.002	0.01 ± 0.003	0.01 ± 0.002	0.02	0.00 ± 0.000	0.01 ± 0.001
15:1n-6	0.02 ± 0.003	0.03 ± 0.003	0.03 ± 0.004	0.02	0.01 ± 0.005	0.00 ± 0.001
Iso16	0.60 ± 0.021	0.68 ± 0.026	0.37 ± 0.050	0.80	0.28 ± 0.010	0.06 ± 0.004
16:0	15.43 ± 0.110	14.67 ± 0.168	12.93 ± 0.207	13.21	14.83 ± 0.202	14.05 ± 0.216
16:1n-11	0.54 ± 0.025	0.66 ± 0.031	0.88 ± 0.040	0.78	0.82 ± 0.025	0.42 ± 0.014
16:1n-9	0.35 ± 0.007	0.38 ± 0.010	0.38 ± 0.011	0.53	0.35 ± 0.003	0.14 ± 0.004
16:1n-7	7.84 ± 0.559	7.19 ± 0.666	10.36 ± 0.976	6.44	5.05 ± 0.130	5.06 ± 0.166
7Me16:0	0.48 ± 0.027	0.33 ± 0.018	0.28 ± 0.021	0.44	0.21 ± 0.005	0.23 ± 0.012
16:1n-5	0.35 ± 0.016	0.38 ± 0.026	0.35 ± 0.052	0.56	0.12 ± 0.005	0.07 ± 0.007
16:2n-6	0.05 ± 0.006	0.05 ± 0.006	0.20 ± 0.029	0.10	0.06 ± 0.000	0.09 ± 0.004
Iso17	0.20 ± 0.010	0.29 ± 0.030	0.19 ± 0.032	0.40	0.33 ± 0.015	0.08 ± 0.007
16:2n-4	0.35 ± 0.033	0.62 ± 0.059	0.64 ± 0.045	0.61	0.67 ± 0.015	0.34 ± 0.021
16:3n-6	0.44 ± 0.019	0.33 ± 0.049	0.42 ± 0.030	0.37	0.32 ± 0.017	0.37 ± 0.026
17:0	0.56 ± 0.069	0.91 ± 0.090	0.48 ± 0.045	0.52	0.89 ± 0.035	0.14 ± 0.010
16:3n-4	0.34 ± 0.023	0.19 ± 0.020	0.31 ± 0.035	0.35	0.28 ± 0.025	0.34 ± 0.020
17:1	0.26 ± 0.029	0.48 ± 0.018	0.38 ± 0.021	0.40	0.36 ± 0.015	0.17 ± 0.009
16:3n-1	0.25 ± 0.019	0.30 ± 0.030	0.20 ± 0.022	0.12	0.54 ± 0.025	0.09 ± 0.004
16:4n-1	0.73 ± 0.039	0.45 ± 0.024	0.50 ± 0.073	0.48	0.56 ± 0.047	0.54 ± 0.045
18:0	4.07 ± 0.101	4.88 ± 0.157	3.25 ± 0.156	4.25	5.43 ± 0.058	1.47 ± 0.043
18:1n-13	0.18 ± 0.026	0.51 ± 0.035	0.35 ± 0.058	0.49	0.58 ± 0.040	0.07 ± 0.006
18:1n-11	0.15 ± 0.018	0.14 ± 0.009	0.38 ± 0.064	0.10	0.14 ± 0.002	0.57 ± 0.024
18:1n-9	8.82 ± 0.344	5.04 ± 0.244	7.45 ± 0.949	6.55	7.98 ± 0.050	10.43 ± 0.376
18:1n-7	5.47 ± 0.158	5.35 ± 0.260	4.34 ± 0.196	4.97	5.19 ± 0.055	2.14 ± 0.080
18:1n-5	0.64 ± 0.032	0.36 ± 0.036	0.41 ± 0.039	0.46	0.34 ± 0.037	0.57 ± 0.009
18:2d57	0.03 ± 0.003	0.03 ± 0.003	0.04 ± 0.013	0.04	0.02 ± 0.020	0.02 ± 0.002
18:2n-7	0.03 ± 0.003	0.02 ± 0.004	0.02 ± 0.005	0.07	0.05 ± 0.003	0.01 ± 0.002
18:2n-6	0.75 ± 0.015	0.49 ± 0.062	0.78 ± 0.041	0.65	1.17 ± 0.033	0.81 ± 0.021
18:2n-4	0.17 ± 0.009	0.16 ± 0.017	0.23 ± 0.011	0.23	0.25 ± 0.002	0.12 ± 0.004
18:3n-6	0.10 ± 0.008	0.15 ± 0.009	0.12 ± 0.013	0.22	0.25 ± 0.005	0.06 ± 0.003
18:3n-4	0.07 ± 0.006	0.11 ± 0.017	0.13 ± 0.010	0.22	0.10 ± 0.005	0.05 ± 0.003
18:3n-3	0.32 ± 0.025	0.15 ± 0.017	0.38 ± 0.051	0.16	0.68 ± 0.018	0.68 ± 0.036
18:3n-1	0.12 ± 0.009	0.14 ± 0.021	0.17 ± 0.017	0.21	0.17 ± 0.002	0.06 ± 0.003
18:4n-3	0.90 ± 0.070	0.54 ± 0.066	1.09 ± 0.066	0.90	0.92 ± 0.045	1.69 ± 0.099
18:4n-1	0.07 ± 0.007	0.07 ± 0.007	0.13 ± 0.007	0.22	0.08 ± 0.003	0.15 ± 0.008
20:0	0.08 ± 0.005	0.10 ± 0.008	0.10 ± 0.010	0.14	0.13 ± 0.008	0.23 ± 0.005
20:1n-11	1.08 ± 0.076	1.42 ± 0.104	4.08 ± 0.807	1.65	1.11 ± 0.100	11.65 ± 0.344

Table 4b. Continued.

	Flatfish				Greenling	Herring
	Flathead Sole	Rex Sole	Yellowfin Sole	Rock Sole		Large
20:1n-9	1.01 ± 0.042	0.81 ± 0.058	1.39 ± 0.162	1.41	0.76 ± 0.030	2.76 ± 0.069
R20:1	1.10 ± 0.069	1.86 ± 0.153	2.61 ± 0.283	1.17	1.47 ± 0.190	4.40 ± 0.151
20:1n-7	1.14 ± 0.089	2.56 ± 0.167	2.05 ± 0.163	1.79	0.84 ± 0.057	0.22 ± 0.007
20:2n-9	0.04 ± 0.010	0.05 ± 0.007	0.13 ± 0.011	0.09	0.16 ± 0.005	0.09 ± 0.004
20:2n-6	0.26 ± 0.018	0.42 ± 0.032	0.39 ± 0.022	0.55	0.52 ± 0.020	0.14 ± 0.005
20:3n-6	0.07 ± 0.002	0.10 ± 0.003	0.12 ± 0.020	0.13	0.17 ± 0.008	0.03 ± 0.002
20:4n-6	3.10 ± 0.189	5.00 ± 0.233	2.58 ± 0.194	4.09	4.13 ± 0.290	0.35 ± 0.017
20:3n-3	0.10 ± 0.009	0.14 ± 0.018	0.14 ± 0.011	0.19	0.41 ± 0.043	0.06 ± 0.009
20:4n-3	0.39 ± 0.017	0.34 ± 0.021	0.47 ± 0.018	0.52	0.58 ± 0.053	0.45 ± 0.014
20:5n-3	14.99 ± 0.416	15.04 ± 0.362	14.60 ± 1.305	17.76	15.24 ± 0.070	6.95 ± 0.168
22:1n-11	0.49 ± 0.080	0.42 ± 0.026	2.12 ± 0.516	0.45	0.23 ± 0.073	13.97 ± 0.429
22:1n-9	0.17 ± 0.015	0.15 ± 0.017	0.26 ± 0.042	0.40	0.21 ± 0.085	0.58 ± 0.018
R22:1	2.65 ± 0.250	3.42 ± 0.363	6.18 ± 0.851	1.13	1.52 ± 0.983	25.13 ± 0.835
22:1n-7	0.23 ± 0.013	0.50 ± 0.034	0.24 ± 0.025	0.50	0.25 ± 0.073	0.18 ± 0.004
22:2n-6	0.02 ± 0.004	0.02 ± 0.007	0.03 ± 0.007	0.04	0.00 ± 0.000	0.02 ± 0.014
21:5n-3	0.34 ± 0.019	0.33 ± 0.031	0.37 ± 0.036	0.47	0.46 ± 0.000	0.24 ± 0.011
22:4n-6	0.37 ± 0.025	0.85 ± 0.039	0.51 ± 0.043	0.90	0.57 ± 0.008	0.06 ± 0.015
22:5n-6	0.46 ± 0.025	0.81 ± 0.049	0.41 ± 0.026	0.47	0.44 ± 0.043	0.09 ± 0.004
22:4n-3	0.02 ± 0.005	0.04 ± 0.006	0.06 ± 0.012	0.08	0.05 ± 0.000	0.06 ± 0.018
22:5n-3	2.69 ± 0.071	3.78 ± 0.091	3.18 ± 0.116	3.29	2.83 ± 0.213	0.80 ± 0.018
22:6n-3	17.84 ± 0.841	16.66 ± 0.704	12.59 ± 0.697	13.64	17.85 ± 0.365	9.94 ± 0.375
24:1	0.72 ± 0.041	0.50 ± 0.043	0.50 ± 0.064	0.62	0.79 ± 0.083	0.80 ± 0.034

Table 4c. Medium herring, small herring, west herring, octopus, and Pacific cod.

	Herring			Octopus	Pacific Cod
	Medium	Small	West		
n	78	124	54	7	16
12:0	0.08 ± 0.004	0.06 ± 0.003	0.05 ± 0.002	0.04 ± 0.008	0.02 ± 0.002
13:0	0.03 ± 0.001	0.03 ± 0.002	0.03 ± 0.002	0.01 ± 0.003	0.01 ± 0.001
Iso14	0.02 ± 0.001	0.03 ± 0.001	0.02 ± 0.001	0.04 ± 0.008	0.00 ± 0.001
14:0	6.89 ± 0.121	5.47 ± 0.176	9.06 ± 0.362	1.47 ± 0.146	1.57 ± 0.251
14:1n-9	0.31 ± 0.012	0.34 ± 0.011	0.48 ± 0.023	0.11 ± 0.036	0.08 ± 0.016
14:1n-7	0.02 ± 0.003	0.03 ± 0.001	0.02 ± 0.002	0.02 ± 0.009	0.01 ± 0.002
14:1n-5	0.09 ± 0.002	0.07 ± 0.003	0.10 ± 0.006	0.07 ± 0.015	0.03 ± 0.006
Iso15	0.21 ± 0.007	0.21 ± 0.007	0.16 ± 0.007	0.08 ± 0.012	0.07 ± 0.005
Anti15	0.08 ± 0.003	0.08 ± 0.003	0.06 ± 0.004	0.04 ± 0.011	0.02 ± 0.002
15:0	0.38 ± 0.009	0.48 ± 0.016	0.32 ± 0.010	0.32 ± 0.041	0.27 ± 0.010
15:1n-8	0.01 ± 0.001	0.01 ± 0.001	0.02 ± 0.002	0.01 ± 0.004	0.00 ± 0.001
15:1n-6	0.02 ± 0.003	0.00 ± 0.001	0.01 ± 0.002	0.04 ± 0.020	0.00 ± 0.002
Iso16	0.07 ± 0.004	0.15 ± 0.008	0.10 ± 0.008	0.81 ± 0.123	0.26 ± 0.021
16:0	18.00 ± 0.308	20.94 ± 0.146	18.93 ± 0.359	15.13 ± 0.594	14.75 ± 0.300
16:1n-11	0.49 ± 0.018	0.49 ± 0.009	0.41 ± 0.017	0.40 ± 0.040	0.41 ± 0.015
16:1n-9	0.18 ± 0.006	0.23 ± 0.007	0.12 ± 0.005	0.16 ± 0.028	0.38 ± 0.024
16:1n-7	6.01 ± 0.124	5.93 ± 0.166	6.54 ± 0.290	2.29 ± 0.587	2.91 ± 0.338
7Me16:0	0.27 ± 0.010	0.23 ± 0.007	0.27 ± 0.010	0.22 ± 0.060	0.18 ± 0.014
16:1n-5	0.12 ± 0.010	0.19 ± 0.006	0.12 ± 0.009	0.33 ± 0.079	0.14 ± 0.009
16:2n-6	0.10 ± 0.007	0.08 ± 0.004	0.11 ± 0.006	0.10 ± 0.055	0.11 ± 0.021
Iso17	0.20 ± 0.028	0.12 ± 0.003	0.25 ± 0.046	0.12 ± 0.022	0.07 ± 0.014
16:2n-4	0.28 ± 0.024	0.41 ± 0.013	0.31 ± 0.023	0.09 ± 0.046	0.56 ± 0.043
16:3n-6	0.31 ± 0.031	0.36 ± 0.018	0.38 ± 0.033	0.06 ± 0.025	0.12 ± 0.030
17:0	0.17 ± 0.008	0.25 ± 0.012	0.18 ± 0.018	0.84 ± 0.102	0.27 ± 0.025
16:3n-4	0.27 ± 0.017	0.31 ± 0.017	0.37 ± 0.030	0.09 ± 0.036	0.08 ± 0.028
17:1	0.19 ± 0.011	0.24 ± 0.009	0.15 ± 0.009	0.08 ± 0.019	0.28 ± 0.023
16:3n-1	0.09 ± 0.006	0.17 ± 0.007	0.14 ± 0.013	0.15 ± 0.102	0.23 ± 0.030
16:4n-1	0.54 ± 0.036	0.48 ± 0.041	0.95 ± 0.093	0.39 ± 0.153	0.28 ± 0.052
18:0	1.83 ± 0.047	2.61 ± 0.067	1.82 ± 0.077	4.44 ± 0.410	4.47 ± 0.231
18:1n-13	0.03 ± 0.003	0.05 ± 0.004	0.03 ± 0.005	0.44 ± 0.062	0.26 ± 0.034
18:1n-11	0.26 ± 0.017	0.09 ± 0.007	0.15 ± 0.019	0.17 ± 0.034	0.74 ± 0.145
18:1n-9	14.22 ± 0.435	11.97 ± 0.265	12.41 ± 0.415	3.28 ± 0.800	13.55 ± 0.795
18:1n-7	2.51 ± 0.062	2.90 ± 0.054	2.23 ± 0.068	4.10 ± 0.370	3.90 ± 0.137
18:1n-5	0.64 ± 0.020	0.55 ± 0.013	0.74 ± 0.016	0.46 ± 0.025	0.40 ± 0.019
18:2d57	0.05 ± 0.004	0.07 ± 0.004	0.05 ± 0.004	0.02 ± 0.006	0.05 ± 0.006
18:2n-7	0.03 ± 0.002	0.02 ± 0.002	0.01 ± 0.001	0.07 ± 0.019	0.02 ± 0.003
18:2n-6	0.99 ± 0.022	1.23 ± 0.038	0.80 ± 0.045	0.58 ± 0.065	0.60 ± 0.045
18:2n-4	0.14 ± 0.004	0.18 ± 0.006	0.21 ± 0.008	0.13 ± 0.028	0.12 ± 0.016
18:3n-6	0.06 ± 0.003	0.09 ± 0.002	0.08 ± 0.004	0.09 ± 0.025	0.06 ± 0.007
18:3n-4	0.06 ± 0.003	0.07 ± 0.003	0.07 ± 0.003	0.08 ± 0.022	0.08 ± 0.007
18:3n-3	0.97 ± 0.050	1.03 ± 0.045	0.52 ± 0.047	0.21 ± 0.049	0.34 ± 0.047
18:3n-1	0.08 ± 0.003	0.11 ± 0.003	0.08 ± 0.004	0.07 ± 0.023	0.16 ± 0.009
18:4n-3	2.20 ± 0.129	2.09 ± 0.095	1.83 ± 0.114	0.28 ± 0.084	0.41 ± 0.079
18:4n-1	0.16 ± 0.006	0.13 ± 0.008	0.22 ± 0.016	0.09 ± 0.017	0.06 ± 0.020
20:0	0.14 ± 0.006	0.10 ± 0.003	0.16 ± 0.006	0.19 ± 0.045	0.08 ± 0.005
20:1n-11	4.19 ± 0.357	0.76 ± 0.103	4.84 ± 0.417	1.50 ± 0.546	1.72 ± 0.332

Table 4c. Continued.

	Herring			Octopus	Pacific Cod
	Medium	Small	West		
20:1n-9	2.66 ± 0.179	0.90 ± 0.059	1.22 ± 0.063	3.81 ± 0.320	1.67 ± 0.192
R20:1	1.74 ± 0.149	0.90 ± 0.086	3.62 ± 0.217	0.41 ± 0.137	0.91 ± 0.129
20:1n-7	0.24 ± 0.008	0.22 ± 0.009	0.17 ± 0.005	1.01 ± 0.242	0.41 ± 0.066
20:2n-9	0.08 ± 0.004	0.06 ± 0.005	0.05 ± 0.007	0.11 ± 0.049	0.04 ± 0.008
20:2n-6	0.18 ± 0.005	0.23 ± 0.006	0.15 ± 0.010	0.57 ± 0.045	0.31 ± 0.015
20:3n-6	0.03 ± 0.002	0.04 ± 0.002	0.03 ± 0.002	0.06 ± 0.011	0.08 ± 0.005
20:4n-6	0.44 ± 0.017	0.69 ± 0.026	0.42 ± 0.031	5.60 ± 0.503	2.66 ± 0.220
20:3n-3	0.08 ± 0.004	0.10 ± 0.005	0.05 ± 0.006	0.73 ± 0.201	0.12 ± 0.008
20:4n-3	0.63 ± 0.027	0.59 ± 0.017	0.43 ± 0.021	0.27 ± 0.037	0.48 ± 0.054
20:5n-3	9.65 ± 0.211	12.38 ± 0.206	9.81 ± 0.289	18.27 ± 0.656	10.92 ± 0.527
22:1n-11	6.22 ± 0.444	1.11 ± 0.115	5.38 ± 0.435	1.16 ± 0.508	0.91 ± 0.204
22:1n-9	0.47 ± 0.030	0.24 ± 0.021	0.26 ± 0.011	0.76 ± 0.098	0.23 ± 0.027
R22:1	13.62 ± 0.810	4.63 ± 0.391	19.85 ± 1.423	1.26 ± 0.451	3.51 ± 0.602
22:1n-7	0.14 ± 0.005	0.14 ± 0.004	0.15 ± 0.003	0.24 ± 0.035	0.12 ± 0.014
22:2n-6	0.01 ± 0.002	0.00 ± 0.001	0.00 ± 0.001	0.13 ± 0.075	0.02 ± 0.009
21:5n-3	0.29 ± 0.008	0.29 ± 0.008	0.30 ± 0.011	0.47 ± 0.073	0.22 ± 0.026
22:4n-6	0.04 ± 0.003	0.04 ± 0.003	0.03 ± 0.005	0.56 ± 0.073	0.23 ± 0.029
22:5n-6	0.14 ± 0.005	0.20 ± 0.005	0.12 ± 0.008	0.46 ± 0.058	0.33 ± 0.037
22:4n-3	0.05 ± 0.005	0.03 ± 0.003	0.03 ± 0.002	0.03 ± 0.008	0.03 ± 0.004
22:5n-3	0.74 ± 0.017	0.83 ± 0.023	0.74 ± 0.025	2.45 ± 0.315	2.30 ± 0.187
22:6n-3	12.67 ± 0.342	19.24 ± 0.606	13.61 ± 0.947	21.57 ± 0.991	27.24 ± 2.114
24:1	0.90 ± 0.029	1.05 ± 0.070	0.83 ± 0.025	0.23 ± 0.068	1.13 ± 0.089

Table 4d. Pink salmon and pollock.

	Pink salmon		Pollock		
	Adult	Smolts	Large	Medium	Small
n	5	40	12	142	32
12:0	0.04 ± 0.006	0.02 ± 0.005	0.02 ± 0.005	0.08 ± 0.019	0.05 ±0.026
13:0	0.03 ± 0.004	0.02 ± 0.002	0.00 ± 0.001	0.01 ± 0.001	0.01 ±0.003
Iso14	0.02 ± 0.002	0.01 ± 0.002	0.00 ± 0.001	0.01 ± 0.001	0.02 ±0.004
14:0	2.96 ± 0.155	1.99 ± 0.104	3.04 ± 0.315	4.06 ± 0.119	2.60 ±0.212
14:1n-9	0.05 ± 0.006	0.05 ± 0.003	0.20 ± 0.027	0.18 ± 0.007	0.19 ±0.014
14:1n-7	0.02 ± 0.001	0.02 ± 0.002	0.01 ± 0.003	0.02 ± 0.001	0.01 ±0.002
14:1n-5	0.07 ± 0.005	0.00 ± 0.001	0.05 ± 0.006	0.06 ± 0.002	0.04 ±0.006
Iso15	0.15 ± 0.007	0.13 ± 0.007	0.09 ± 0.010	0.11 ± 0.003	0.11 ±0.009
Anti15	0.06 ± 0.002	0.06 ± 0.005	0.02 ± 0.005	0.02 ± 0.001	0.04 ±0.006
15:0	0.42 ± 0.039	0.58 ± 0.022	0.25 ± 0.020	0.26 ± 0.004	0.31 ±0.014
15:1n-8	0.00 ± 0.001	0.00 ± 0.001	0.00 ± 0.002	0.01 ± 0.001	0.00 ±0.001
15:1n-6	0.00 ± 0.000	0.00 ± 0.001	0.00 ± 0.004	0.01 ± 0.002	0.00 ±0.000
Iso16	0.15 ± 0.005	0.54 ± 0.016	0.18 ± 0.022	0.13 ± 0.007	0.30 ±0.014
16:0	12.65 ± 0.530	18.41 ± 0.123	16.73 ± 0.470	14.88 ± 0.225	17.79 ±0.323
16:1n-11	0.39 ± 0.028	0.57 ± 0.033	0.31 ± 0.017	0.34 ± 0.007	0.45 ±0.022
16:1n-9	0.27 ± 0.014	0.40 ± 0.018	0.16 ± 0.016	0.15 ± 0.004	0.22 ±0.010
16:1n-7	3.79 ± 0.172	2.32 ± 0.167	5.00 ± 0.522	5.65 ± 0.153	3.06 ±0.264
7Me16:0	0.32 ± 0.034	0.27 ± 0.008	0.24 ± 0.010	0.31 ± 0.006	0.24 ±0.042
16:1n-5	0.23 ± 0.023	0.22 ± 0.016	0.10 ± 0.018	0.10 ± 0.005	0.15 ±0.010
16:2n-6	0.03 ± 0.003	0.03 ± 0.004	0.05 ± 0.012	0.09 ± 0.005	0.09 ±0.011
Iso17	0.13 ± 0.012	0.12 ± 0.004	0.08 ± 0.014	0.07 ± 0.003	0.09 ±0.009
16:2n-4	0.34 ± 0.016	0.63 ± 0.038	0.31 ± 0.058	0.36 ± 0.025	0.45 ±0.028
16:3n-6	0.17 ± 0.013	0.06 ± 0.009	0.43 ± 0.085	0.34 ± 0.024	0.22 ±0.033
17:0	0.26 ± 0.091	0.47 ± 0.013	0.50 ± 0.155	0.30 ± 0.025	0.13 ±0.019
16:3n-4	0.41 ± 0.043	0.13 ± 0.013	0.24 ± 0.048	0.31 ± 0.028	0.55 ±0.067
17:1	0.01 ± 0.004	0.09 ± 0.014	0.16 ± 0.022	0.12 ± 0.006	0.16 ±0.027
16:3n-1	0.09 ± 0.039	0.23 ± 0.023	0.11 ± 0.025	0.07 ± 0.003	0.12 ±0.006
16:4n-1	0.11 ± 0.022	0.23 ± 0.009	0.34 ± 0.056	0.49 ± 0.049	0.41 ±0.070
18:0	3.91 ± 0.187	4.79 ± 0.107	3.59 ± 0.254	2.93 ± 0.079	3.87 ±0.130
18:1n-13	0.14 ± 0.014	0.06 ± 0.008	0.04 ± 0.016	0.08 ± 0.005	0.07 ±0.011
18:1n-11	1.09 ± 0.157	0.13 ± 0.018	0.51 ± 0.077	1.07 ± 0.054	0.55 ±0.064
18:1n-9	12.30 ± 0.889	6.61 ± 0.180	11.50 ± 0.748	8.86 ± 0.276	9.52 ±0.289
18:1n-7	2.82 ± 0.215	2.30 ± 0.068	4.57 ± 0.437	3.51 ± 0.141	3.16 ±0.228
18:1n-5	0.63 ± 0.075	0.40 ± 0.022	0.33 ± 0.018	0.48 ± 0.011	0.60 ±0.059
18:2d57	0.04 ± 0.003	0.11 ± 0.009	0.02 ± 0.005	0.03 ± 0.002	0.05 ±0.007
18:2n-7	0.06 ± 0.011	0.12 ± 0.023	0.03 ± 0.006	0.03 ± 0.002	0.04 ±0.005
18:2n-6	1.39 ± 0.083	1.32 ± 0.088	0.66 ± 0.058	0.67 ± 0.015	0.80 ±0.059
18:2n-4	0.11 ± 0.009	0.10 ± 0.011	0.15 ± 0.014	0.15 ± 0.004	0.12 ±0.008
18:3n-6	0.10 ± 0.007	0.12 ± 0.008	0.08 ± 0.006	0.08 ± 0.002	0.08 ±0.004
18:3n-4	0.09 ± 0.007	0.05 ± 0.009	0.08 ± 0.011	0.09 ± 0.003	0.08 ±0.010
18:3n-3	0.98 ± 0.108	1.13 ± 0.066	0.43 ± 0.088	0.48 ± 0.021	0.59 ±0.050
18:3n-1	0.08 ± 0.008	0.15 ± 0.012	0.08 ± 0.012	0.09 ± 0.003	0.13 ±0.008
18:4n-3	1.58 ± 0.141	0.89 ± 0.056	1.09 ± 0.208	1.49 ± 0.065	1.49 ±0.095
18:4n-1	0.15 ± 0.016	0.04 ± 0.006	0.14 ± 0.024	0.21 ± 0.012	0.11 ±0.022
20:0	0.07 ± 0.005	0.08 ± 0.003	0.07 ± 0.004	0.09 ± 0.003	0.07 ±0.005
20:1n-11	2.53 ± 0.244	0.35 ± 0.084	3.06 ± 0.574	6.14 ± 0.312	1.48 ±0.443

Table 4d. Continued.

	Pink salmon		Pollock		
	Adult	Smolts	Large	Medium	Small
20:1n-9	1.69 ± 0.137	0.52 ± 0.055	1.60 ± 0.140	2.15 ± 0.062	1.52 ±0.119
R20:1	1.49 ± 0.034	0.60 ± 0.086	1.81 ± 0.258	2.69 ± 0.097	0.72 ±0.156
20:1n-7	0.25 ± 0.060	0.22 ± 0.013	0.21 ± 0.014	0.21 ± 0.004	0.15 ±0.010
20:2n-9	0.08 ± 0.010	0.20 ± 0.036	0.07 ± 0.018	0.09 ± 0.003	0.09 ±0.005
20:2n-6	0.31 ± 0.033	0.29 ± 0.010	0.20 ± 0.016	0.19 ± 0.005	0.23 ±0.009
20:3n-6	0.11 ± 0.007	0.11 ± 0.008	0.05 ± 0.002	0.05 ± 0.001	0.05 ±0.002
20:4n-6	0.98 ± 0.026	1.48 ± 0.043	1.09 ± 0.088	0.76 ± 0.033	0.92 ±0.050
20:3n-3	0.15 ± 0.016	0.16 ± 0.007	0.06 ± 0.012	0.09 ± 0.015	0.09 ±0.004
20:4n-3	1.91 ± 0.185	1.09 ± 0.044	0.55 ± 0.055	0.63 ± 0.020	0.64 ±0.025
20:5n-3	12.87 ± 0.126	8.75 ± 0.257	12.92 ± 0.715	12.06 ± 0.215	12.89 ±0.338
22:1n-11	3.60 ± 0.435	0.27 ± 0.056	3.09 ± 0.733	6.19 ± 0.329	1.58 ±0.387
22:1n-9	0.43 ± 0.036	0.12 ± 0.019	0.60 ± 0.097	0.73 ± 0.050	0.46 ±0.047
R22:1	8.38 ± 0.429	2.40 ± 0.337	4.94 ± 0.805	9.41 ± 0.490	3.05 ±0.625
22:1n-7	0.08 ± 0.006	0.06 ± 0.008	0.14 ± 0.012	0.17 ± 0.006	0.13 ±0.012
22:2n-6	0.02 ± 0.010	0.05 ± 0.010	0.02 ± 0.005	0.02 ± 0.001	0.07 ±0.018
21:5n-3	0.33 ± 0.015	0.15 ± 0.008	0.38 ± 0.031	0.36 ± 0.010	0.31 ±0.021
22:4n-6	0.05 ± 0.004	0.10 ± 0.006	0.08 ± 0.016	0.08 ± 0.005	0.12 ±0.014
22:5n-6	0.14 ± 0.015	0.43 ± 0.037	0.21 ± 0.024	0.18 ± 0.009	0.23 ±0.008
22:4n-3	0.06 ± 0.004	0.07 ± 0.003	0.03 ± 0.013	0.09 ± 0.009	0.05 ±0.010
22:5n-3	4.40 ± 0.175	2.53 ± 0.030	1.22 ± 0.089	1.16 ± 0.021	0.97 ±0.037
22:6n-3	20.40 ± 0.430	36.02 ± 0.602	21.12 ± 1.441	18.15 ± 0.511	27.07 ±1.140
24:1	0.57 ± 0.062	0.72 ± 0.029	1.01 ± 0.077	1.05 ± 0.032	1.24 ±0.050

Table 4e. Rainbow smelt, rockfish, sandance, sculpin, and shrimp.

	Rainbow Smelt	Rockfish	Sandlance	Sculpin	Shrimp	
					Pink Shrimp	Shrimp Unk. Sp.
n	4	1	80	2	15	2
12:0	0.07 ± 0.009	0.10	0.07 ± 0.004	0.04 ± 0.010	0.16 ± 0.015	0.13 ± 0.005
13:0	0.01 ± 0.003	0.01	0.03 ± 0.001	0.01 ± 0.002	0.01 ± 0.003	0.04 ± 0.010
Iso14	0.01 ± 0.003	0.02	0.03 ± 0.001	0.03 ± 0.015	0.03 ± 0.002	0.09 ± 0.005
14:0	2.59 ± 0.349	3.02	5.39 ± 0.189	1.88 ± 0.928	3.02 ± 0.299	2.90 ± 0.110
14:1n-9	0.06 ± 0.013	0.14	0.32 ± 0.010	0.17 ± 0.115	0.08 ± 0.017	0.05 ± 0.005
14:1n-7	0.02 ± 0.000	0.05	0.03 ± 0.001	0.03 ± 0.010	0.01 ± 0.002	0.01 ± 0.005
14:1n-5	0.19 ± 0.046	0.09	0.06 ± 0.003	0.04 ± 0.005	0.06 ± 0.010	0.07 ± 0.010
Iso15	0.07 ± 0.010	0.14	0.24 ± 0.007	0.14 ± 0.067	0.16 ± 0.013	0.20 ± 0.030
Anti15	0.02 ± 0.003	0.06	0.10 ± 0.004	0.08 ± 0.050	0.06 ± 0.007	0.05 ± 0.010
15:0	0.27 ± 0.028	0.38	0.46 ± 0.015	0.35 ± 0.120	0.47 ± 0.023	0.73 ± 0.105
15:1n-8	0.01 ± 0.000	0.01	0.01 ± 0.001	0.01 ± 0.003	0.00 ± 0.001	0.00 ± 0.000
15:1n-6	0.00 ± 0.003	0.02	0.00 ± 0.001	0.02 ± 0.005	0.02 ± 0.004	0.04 ± 0.010
Iso16	0.10 ± 0.034	0.15	0.20 ± 0.007	0.25 ± 0.045	0.69 ± 0.042	0.67 ± 0.020
16:0	18.12 ± 0.387	17.08	19.07 ± 0.234	14.12 ± 0.940	15.79 ± 0.225	15.39 ± 1.245
16:1n-11	0.22 ± 0.024	0.40	0.56 ± 0.012	0.34 ± 0.110	0.26 ± 0.007	0.80 ± 0.070
16:1n-9	0.34 ± 0.036	0.43	0.21 ± 0.008	0.32 ± 0.053	0.20 ± 0.006	0.20 ± 0.010
16:1n-7	10.47 ± 1.651	8.93	5.09 ± 0.224	6.30 ± 1.295	7.11 ± 0.375	5.06 ± 0.320
7Me16:0	0.00 ± 0.000	0.21	0.26 ± 0.013	0.18 ± 0.023	0.15 ± 0.009	0.00 ± 0.000
16:1n-5	0.15 ± 0.010	0.30	0.21 ± 0.008	0.34 ± 0.100	0.40 ± 0.014	0.05 ± 0.005
16:2n-6	0.15 ± 0.038	0.06	0.09 ± 0.004	0.05 ± 0.023	0.01 ± 0.003	0.47 ± 0.025
Iso17	0.02 ± 0.003	0.24	0.16 ± 0.004	0.26 ± 0.080	0.26 ± 0.024	0.28 ± 0.035
16:2n-4	0.28 ± 0.105	0.42	0.62 ± 0.025	0.27 ± 0.040	0.15 ± 0.015	0.10 ± 0.010
16:3n-6	0.23 ± 0.141	0.32	0.31 ± 0.017	0.29 ± 0.150	0.19 ± 0.017	0.34 ± 0.060
17:0	0.23 ± 0.038	0.32	0.33 ± 0.019	0.41 ± 0.115	0.39 ± 0.025	0.50 ± 0.060
16:3n-4	0.04 ± 0.007	0.30	0.29 ± 0.020	0.21 ± 0.105	0.09 ± 0.014	0.14 ± 0.055
17:1	0.30 ± 0.043	0.37	0.19 ± 0.007	0.33 ± 0.032	0.55 ± 0.041	0.98 ± 0.250
16:3n-1	0.08 ± 0.009	0.08	0.21 ± 0.007	0.06 ± 0.018	0.15 ± 0.004	0.18 ± 0.010
16:4n-1	0.13 ± 0.031	0.32	0.54 ± 0.045	0.21 ± 0.145	0.10 ± 0.028	0.49 ± 0.010
18:0	3.80 ± 0.211	4.71	2.90 ± 0.073	5.05 ± 0.317	2.21 ± 0.065	2.71 ± 0.030
18:1n-13	0.10 ± 0.009	0.38	0.12 ± 0.012	0.40 ± 0.135	0.12 ± 0.017	0.11 ± 0.000
18:1n-11	0.10 ± 0.021	0.21	0.14 ± 0.017	0.08 ± 0.003	0.07 ± 0.010	0.20 ± 0.050
18:1n-9	18.42 ± 2.628	16.29	9.90 ± 0.369	10.45 ± 2.923	14.43 ± 0.276	10.91 ± 0.005
18:1n-7	4.76 ± 0.114	5.27	2.10 ± 0.051	8.01 ± 0.560	6.28 ± 0.163	5.63 ± 0.095
18:1n-5	0.46 ± 0.042	0.39	0.64 ± 0.020	0.33 ± 0.015	0.56 ± 0.016	0.50 ± 0.050
18:2d57	0.23 ± 0.109	0.04	0.09 ± 0.003	0.10 ± 0.013	0.04 ± 0.002	0.03 ± 0.000
18:2n-7	0.02 ± 0.003	0.04	0.02 ± 0.002	0.06 ± 0.010	0.02 ± 0.003	0.04 ± 0.010
18:2n-6	0.54 ± 0.181	0.66	1.50 ± 0.050	0.77 ± 0.060	0.78 ± 0.015	0.78 ± 0.015
18:2n-4	0.10 ± 0.013	0.24	0.17 ± 0.006	0.36 ± 0.145	0.20 ± 0.015	0.14 ± 0.000
18:3n-6	0.06 ± 0.015	0.13	0.10 ± 0.003	0.16 ± 0.040	0.08 ± 0.003	0.04 ± 0.005
18:3n-4	0.05 ± 0.006	0.13	0.06 ± 0.002	0.23 ± 0.113	0.13 ± 0.016	0.06 ± 0.035
18:3n-3	0.30 ± 0.134	0.27	1.34 ± 0.051	0.28 ± 0.023	0.31 ± 0.010	0.64 ± 0.025
18:3n-1	0.16 ± 0.027	0.11	0.17 ± 0.005	0.09 ± 0.020	0.03 ± 0.008	0.04 ± 0.010
18:4n-3	0.25 ± 0.049	0.80	3.01 ± 0.103	0.46 ± 0.213	0.22 ± 0.022	0.47 ± 0.065
18:4n-1	0.02 ± 0.003	0.14	0.12 ± 0.008	0.18 ± 0.090	0.09 ± 0.008	0.07 ± 0.000
20:0	0.10 ± 0.007	0.11	0.11 ± 0.004	0.13 ± 0.045	0.18 ± 0.006	0.20 ± 0.015
20:1n-11	0.40 ± 0.078	1.04	1.41 ± 0.276	0.88 ± 0.420	1.78 ± 0.220	1.98 ± 0.165

Table 4e. Continued.

	Rainbow Smelt	Rockfish	Sandlance	Sculpin	Shrimp	
					Pink Shrimp	Shrimp Unk. Sp.
20:1n-9	0.62 ± 0.139	0.98	0.99 ± 0.101	0.84 ± 0.032	1.16 ± 0.130	1.32 ± 0.080
R20:1	0.84 ± 0.330	1.06	1.09 ± 0.138	1.03 ± 0.461	1.59 ± 0.192	1.51 ± 0.216
20:1n-7	0.25 ± 0.148	0.71	0.26 ± 0.028	1.03 ± 0.535	0.87 ± 0.127	1.20 ± 0.225
20:2n-9	0.07 ± 0.006	0.08	0.13 ± 0.014	0.06 ± 0.038	0.08 ± 0.012	0.10 ± 0.015
20:2n-6	0.16 ± 0.017	0.25	0.30 ± 0.012	0.46 ± 0.100	0.35 ± 0.032	0.42 ± 0.015
20:3n-6	0.05 ± 0.014	0.06	0.04 ± 0.001	0.16 ± 0.000	0.08 ± 0.004	0.05 ± 0.005
20:4n-6	1.74 ± 0.467	1.92	0.71 ± 0.037	4.36 ± 1.060	3.11 ± 0.200	2.46 ± 0.140
20:3n-3	0.03 ± 0.008	0.06	0.12 ± 0.005	0.12 ± 0.000	0.08 ± 0.009	0.17 ± 0.020
20:4n-3	0.20 ± 0.011	0.38	0.72 ± 0.017	0.58 ± 0.168	0.39 ± 0.038	0.28 ± 0.010
20:5n-3	8.80 ± 0.535	11.53	13.59 ± 0.230	16.88 ± 2.293	15.98 ± 1.056	17.26 ± 0.170
22:1n-11	0.15 ± 0.012	0.67	1.74 ± 0.322	0.21 ± 0.015	2.11 ± 0.350	1.99 ± 0.095
22:1n-9	0.14 ± 0.028	0.41	0.25 ± 0.012	0.24 ± 0.035	1.03 ± 0.157	0.65 ± 0.090
R22:1	1.19 ± 0.182	1.62	5.46 ± 0.861	0.90 ± 0.071	2.29 ± 0.396	3.09 ± 0.282
22:1n-7	0.00 ± 0.000	0.16	0.13 ± 0.005	0.13 ± 0.030	0.29 ± 0.008	0.30 ± 0.005
22:2n-6	0.02 ± 0.000	0.02	0.02 ± 0.002	0.03 ± 0.000	0.00 ± 0.002	0.04 ± 0.020
21:5n-3	0.16 ± 0.017	0.30	0.35 ± 0.010	0.48 ± 0.150	0.20 ± 0.008	0.28 ± 0.030
22:4n-6	0.13 ± 0.029	0.33	0.05 ± 0.004	0.73 ± 0.120	0.22 ± 0.019	0.43 ± 0.070
22:5n-6	0.26 ± 0.064	0.25	0.25 ± 0.011	0.31 ± 0.018	0.22 ± 0.010	0.24 ± 0.020
22:4n-3	0.05 ± 0.011	0.09	0.04 ± 0.002	0.07 ± 0.005	0.04 ± 0.013	0.03 ± 0.005
22:5n-3	1.47 ± 0.208	2.06	0.77 ± 0.017	3.54 ± 0.138	1.16 ± 0.074	1.37 ± 0.150
22:6n-3	20.22 ± 2.652	14.02	19.22 ± 0.636	14.14 ± 3.465	12.81 ± 0.820	15.26 ± 0.105
24:1	0.90 ± 0.107	0.64	1.13 ± 0.030	0.56 ± 0.115	1.04 ± 0.060	0.78 ± 0.005

Table 4f. Squid and tomcod.

	Squid			Tomcod	
	B.Magister	*R.Pacifica*	Squid Unk. Sp.	Large	Small
n	12	22	82	18	20
12:0	0.08 ± 0.009	0.04 ± 0.003	0.16 ± 0.056	0.02 ± 0.002	0.02 ± 0.001
13:0	0.03 ± 0.004	0.01 ± 0.001	0.01 ± 0.002	0.00 ± 0.001	0.01 ± 0.000
Iso14	0.05 ± 0.006	0.03 ± 0.002	0.05 ± 0.006	0.01 ± 0.002	0.01 ± 0.001
14:0	4.93 ± 0.539	2.53 ± 0.068	2.36 ± 0.095	1.37 ± 0.103	2.27 ± 0.236
14:1n-9	0.14 ± 0.013	0.15 ± 0.009	0.11 ± 0.004	0.11 ± 0.024	0.27 ± 0.032
14:1n-7	0.04 ± 0.005	0.05 ± 0.006	0.05 ± 0.008	0.03 ± 0.004	0.02 ± 0.001
14:1n-5	0.14 ± 0.021	0.05 ± 0.003	0.09 ± 0.006	0.02 ± 0.003	0.01 ± 0.003
Iso15	0.18 ± 0.019	0.12 ± 0.006	0.05 ± 0.003	0.13 ± 0.015	0.12 ± 0.004
Anti15	0.10 ± 0.011	0.06 ± 0.004	0.02 ± 0.004	0.04 ± 0.006	0.04 ± 0.002
15:0	0.35 ± 0.036	0.43 ± 0.015	0.37 ± 0.033	0.48 ± 0.035	0.35 ± 0.015
15:1n-8	0.00 ± 0.001	0.02 ± 0.003	0.00 ± 0.001	0.01 ± 0.003	0.00 ± 0.001
15:1n-6	0.01 ± 0.001	0.03 ± 0.016	0.01 ± 0.001	0.01 ± 0.003	0.00 ± 0.000
Iso16	0.30 ± 0.037	0.67 ± 0.022	0.62 ± 0.024	0.32 ± 0.024	0.31 ± 0.025
16:0	16.36 ± 1.237	14.06 ± 0.244	19.12 ± 0.266	15.10 ± 0.160	17.96 ± 0.357
16:1n-11	0.45 ± 0.040	0.58 ± 0.019	0.28 ± 0.019	0.50 ± 0.038	0.53 ± 0.015
16:1n-9	0.21 ± 0.014	1.05 ± 0.071	0.11 ± 0.004	0.43 ± 0.024	0.30 ± 0.022
16:1n-7	4.93 ± 0.458	3.62 ± 0.249	3.13 ± 0.261	3.98 ± 0.325	2.82 ± 0.260
7Me16:0	0.30 ± 0.032	0.22 ± 0.005	0.21 ± 0.008	0.25 ± 0.014	0.28 ± 0.009
16:1n-5	0.20 ± 0.017	0.36 ± 0.017	0.17 ± 0.009	0.34 ± 0.034	0.22 ± 0.015
16:2n-6	0.05 ± 0.004	0.03 ± 0.002	0.01 ± 0.003	0.14 ± 0.044	0.05 ± 0.005
Iso17	0.10 ± 0.008	0.21 ± 0.012	0.06 ± 0.009	0.28 ± 0.025	0.13 ± 0.008
16:2n-4	0.21 ± 0.039	0.20 ± 0.017	0.20 ± 0.014	0.48 ± 0.038	0.66 ± 0.058
16:3n-6	0.46 ± 0.043	0.10 ± 0.011	0.21 ± 0.022	0.14 ± 0.036	0.15 ± 0.022
17:0	0.16 ± 0.013	0.54 ± 0.017	0.50 ± 0.066	0.61 ± 0.047	0.39 ± 0.032
16:3n-4	0.26 ± 0.038	0.04 ± 0.004	0.08 ± 0.013	0.32 ± 0.064	0.20 ± 0.008
17:1	0.22 ± 0.021	0.29 ± 0.024	0.08 ± 0.012	0.30 ± 0.068	0.09 ± 0.020
16:3n-1	0.14 ± 0.013	0.11 ± 0.003	0.19 ± 0.015	0.04 ± 0.008	0.11 ± 0.009
16:4n-1	0.33 ± 0.065	0.07 ± 0.004	0.14 ± 0.011	0.33 ± 0.067	0.25 ± 0.023
18:0	1.78 ± 0.052	3.60 ± 0.080	2.19 ± 0.031	4.91 ± 0.161	4.47 ± 0.129
18:1n-13	0.12 ± 0.009	0.28 ± 0.009	0.09 ± 0.003	0.88 ± 0.158	0.14 ± 0.040
18:1n-11	0.35 ± 0.099	0.51 ± 0.049	0.31 ± 0.029	0.50 ± 0.205	0.34 ± 0.049
18:1n-9	13.40 ± 1.277	4.04 ± 0.215	9.27 ± 0.422	8.26 ± 0.491	8.83 ± 0.325
18:1n-7	4.90 ± 0.305	4.44 ± 0.224	3.89 ± 0.183	5.19 ± 0.253	2.50 ± 0.064
18:1n-5	0.42 ± 0.032	0.52 ± 0.008	0.55 ± 0.017	0.35 ± 0.024	0.62 ± 0.050
18:2d57	0.04 ± 0.002	0.03 ± 0.003	0.02 ± 0.005	0.04 ± 0.010	0.07 ± 0.007
18:2n-7	0.06 ± 0.006	0.01 ± 0.002	0.05 ± 0.009	0.03 ± 0.006	0.04 ± 0.010
18:2n-6	1.15 ± 0.070	0.51 ± 0.019	0.74 ± 0.018	0.87 ± 0.162	1.01 ± 0.047
18:2n-4	0.12 ± 0.006	0.17 ± 0.006	0.13 ± 0.004	0.15 ± 0.016	0.19 ± 0.015
18:3n-6	0.10 ± 0.009	0.08 ± 0.002	0.05 ± 0.005	0.13 ± 0.013	0.12 ± 0.008
18:3n-4	0.12 ± 0.018	0.07 ± 0.006	0.03 ± 0.003	0.11 ± 0.017	0.08 ± 0.008
18:3n-3	0.98 ± 0.084	0.36 ± 0.023	0.31 ± 0.021	0.54 ± 0.107	0.68 ± 0.027
18:3n-1	0.06 ± 0.009	0.08 ± 0.005	0.07 ± 0.005	0.14 ± 0.018	0.18 ± 0.018
18:4n-3	1.59 ± 0.168	0.45 ± 0.057	0.57 ± 0.062	0.73 ± 0.115	1.21 ± 0.073
18:4n-1	0.08 ± 0.012	0.08 ± 0.003	0.05 ± 0.004	0.12 ± 0.039	0.07 ± 0.013
20:0	0.16 ± 0.004	0.14 ± 0.004	0.11 ± 0.011	0.08 ± 0.007	0.10 ± 0.011
20:1n-11	3.14 ± 0.649	3.44 ± 0.453	2.30 ± 0.208	0.91 ± 0.095	0.36 ± 0.042

Table 4f. Continued.

	Squid			Tomcod	
	B.Magister	*R.Pacifica*	Squid Unk. Sp.	Large	Small
20:1n-9	2.57 ± 0.364	4.54 ± 0.175	2.82 ± 0.091	0.93 ± 0.103	1.76 ± 0.259
R20:1	1.14 ± 0.095	0.72 ± 0.075	0.79 ± 0.054	1.09 ± 0.138	0.35 ± 0.090
20:1n-7	0.33 ± 0.016	0.68 ± 0.045	0.18 ± 0.009	1.13 ± 0.126	0.18 ± 0.036
20:2n-9	0.05 ± 0.008	0.05 ± 0.004	0.04 ± 0.011	0.05 ± 0.008	0.22 ± 0.018
20:2n-6	0.52 ± 0.032	0.64 ± 0.020	0.65 ± 0.024	0.56 ± 0.062	0.35 ± 0.024
20:3n-6	0.07 ± 0.003	0.05 ± 0.003	0.05 ± 0.007	0.15 ± 0.017	0.07 ± 0.008
20:4n-6	0.81 ± 0.062	2.18 ± 0.174	0.85 ± 0.031	3.25 ± 0.183	1.32 ± 0.175
20:3n-3	0.44 ± 0.049	1.03 ± 0.067	0.88 ± 0.041	0.24 ± 0.035	0.13 ± 0.010
20:4n-3	0.54 ± 0.039	0.34 ± 0.016	0.38 ± 0.015	0.51 ± 0.036	0.59 ± 0.019
20:5n-3	12.98 ± 0.901	18.95 ± 0.406	15.82 ± 0.189	15.49 ± 0.584	13.16 ± 0.270
22:1n-11	3.32 ± 0.816	3.18 ± 0.583	1.49 ± 0.146	0.25 ± 0.043	0.67 ± 0.139
22:1n-9	0.59 ± 0.052	0.54 ± 0.018	0.39 ± 0.017	0.12 ± 0.016	0.16 ± 0.021
R22:1	4.99 ± 0.765	5.51 ± 0.899	3.64 ± 0.286	2.45 ± 0.373	3.05 ± 0.479
22:1n-7	0.17 ± 0.014	0.21 ± 0.006	0.09 ± 0.004	0.11 ± 0.015	0.07 ± 0.003
22:2n-6	0.04 ± 0.007	0.04 ± 0.001	0.01 ± 0.001	0.08 ± 0.018	0.06 ± 0.009
21:5n-3	0.37 ± 0.025	0.27 ± 0.011	0.39 ± 0.008	0.31 ± 0.030	0.25 ± 0.013
22:4n-6	0.22 ± 0.104	0.26 ± 0.020	0.04 ± 0.010	0.79 ± 0.095	0.08 ± 0.016
22:5n-6	0.16 ± 0.013	0.29 ± 0.012	0.15 ± 0.004	0.46 ± 0.037	0.27 ± 0.015
22:4n-3	0.03 ± 0.006	0.02 ± 0.002	0.01 ± 0.008	0.03 ± 0.005	0.03 ± 0.003
22:5n-3	0.63 ± 0.053	1.47 ± 0.047	0.54 ± 0.014	4.09 ± 0.379	1.05 ± 0.092
22:6n-3	16.15 ± 1.022	19.82 ± 0.489	25.48 ± 0.919	20.31 ± 1.333	29.69 ± 1.280
24:1	0.60 ± 0.071	0.35 ± 0.016	0.44 ± 0.018	0.68 ± 0.093	0.91 ± 0.027

Table 5. Summary of CART analysis of all prey sampled to date. Data are for species shown in Table 4 for which n ≥ 4.

Species	correct / total	% correctly classified
Capelin	70 / 79	88.6 %
Chum	7 / 7	100.0 %
Eulachon Smelt	20 / 20	100.0 %
Flatfish		
Flathead Sole	31 / 33	93.9 %
Rex Sole	20 / 23	87.0 %
Unknown Sp.	23 / 24	95.8 %
Yellowfin Sole	13 / 17	76.5 %
Herring	327 / 333	98.2
Octopus	7 / 7	100.0 %
Pacific Cod	16 / 16	100.0 %
Pink Salmon		
Adult	5 / 5	100.0 %
Smolt	40 / 40	100.0 %
Pollock	169 / 189	89.4 %
Rainbow Smelt	0 / 4	0.0 %
Sandlance	71 / 80	88.8 %
Pink Shrimp	15 / 15	100.0 %
Squid		
B. magister	10 / 12	83.3 %
R. pacifica	19 / 22	86.4 %
Unknown Sp.	80 / 83	96.4 %
Tomcod	34 / 38	89.5 %
Total	977 / 1047	93.3 %

Table 6. Fatty acid composition of blubber from harbor seals collected during 1994-1998 (n = 364). Values are mean mass % of total fatty acids ± SEM. See Table 3 for summary of collection data.

	PRINCE WILLIAM SOUND				
	NE	NW	SC		
	All Groups	All Groups	Adults	Sub Adults	Yearlings
n	4	9	80	66	25
12:0	0.21 ± 0.026	0.16 ± 0.014	0.11 ± 0.003	0.12 ± 0.004	0.11 ± 0.005
13:0	0.01 ± 0.005	0.01 ± 0.002	0.02 ± 0.001	0.01 ± 0.001	0.02 ± 0.001
Iso14	0.01 ± 0.005	0.01 ± 0.004	0.02 ± 0.001	0.02 ± 0.001	0.02 ± 0.001
14:0	4.11 ± 0.282	3.96 ± 0.192	4.63 ± 0.128	5.62 ± 0.116	5.68 ± 0.159
14:1n-9	0.05 ± 0.021	0.09 ± 0.017	0.11 ± 0.004	0.13 ± 0.005	0.14 ± 0.006
14:1n-7	0.09 ± 0.012	0.10 ± 0.014	0.06 ± 0.002	0.08 ± 0.003	0.07 ± 0.004
14:1n-5	1.74 ± 0.274	2.33 ± 0.239	1.21 ± 0.047	1.73 ± 0.066	1.48 ± 0.104
Iso15	0.14 ± 0.024	0.10 ± 0.006	0.12 ± 0.002	0.12 ± 0.002	0.12 ± 0.003
Anti15	0.05 ± 0.017	0.04 ± 0.007	0.05 ± 0.002	0.05 ± 0.002	0.04 ± 0.002
15:0	0.34 ± 0.020	0.22 ± 0.008	0.26 ± 0.005	0.24 ± 0.004	0.24 ± 0.006
15:1n-8	0.00 ± 0.000	0.00 ± 0.002	0.01 ± 0.002	0.02 ± 0.003	0.01 ± 0.001
15:1n-6	0.09 ± 0.012	0.09 ± 0.007	0.06 ± 0.002	0.06 ± 0.003	0.05 ± 0.003
Iso16	0.08 ± 0.005	0.07 ± 0.005	0.07 ± 0.003	0.06 ± 0.003	0.06 ± 0.002
16:0	10.22 ± 0.399	7.78 ± 0.343	8.41 ± 0.199	9.09 ± 0.141	9.62 ± 0.218
16:1n-11	0.70 ± 0.127	0.54 ± 0.038	0.69 ± 0.029	0.61 ± 0.018	0.61 ± 0.022
16:1n-9	0.54 ± 0.066	0.56 ± 0.021	0.40 ± 0.008	0.41 ± 0.010	0.37 ± 0.013
16:1n-7	20.06 ± 1.852	21.87 ± 1.378	13.59 ± 0.297	16.62 ± 0.479	15.22 ± 0.668
7Me16:0	0.26 ± 0.011	0.26 ± 0.009	0.26 ± 0.004	0.26 ± 0.004	0.25 ± 0.006
16:1n-5	0.02 ± 0.018	0.03 ± 0.011	0.11 ± 0.010	0.09 ± 0.008	0.09 ± 0.013
16:2n-6	0.26 ± 0.084	0.17 ± 0.023	0.12 ± 0.010	0.12 ± 0.008	0.08 ± 0.004
Iso17	0.12 ± 0.019	0.05 ± 0.010	0.12 ± 0.006	0.08 ± 0.005	0.10 ± 0.005
16:2n-4	0.34 ± 0.030	0.15 ± 0.033	0.29 ± 0.014	0.24 ± 0.019	0.21 ± 0.012
16:3n-6	0.21 ± 0.018	0.41 ± 0.035	0.37 ± 0.017	0.46 ± 0.023	0.48 ± 0.018
17:0	0.21 ± 0.035	0.11 ± 0.009	0.17 ± 0.011	0.15 ± 0.012	0.14 ± 0.021
16:3n-4	0.11 ± 0.004	0.15 ± 0.024	0.25 ± 0.013	0.27 ± 0.009	0.28 ± 0.011
17:1	0.58 ± 0.031	0.44 ± 0.017	0.30 ± 0.023	0.27 ± 0.022	0.27 ± 0.019
16:3n-1	0.14 ± 0.008	0.08 ± 0.014	0.09 ± 0.005	0.08 ± 0.005	0.06 ± 0.006
16:4n-1	0.03 ± 0.019	0.13 ± 0.040	0.23 ± 0.018	0.29 ± 0.028	0.35 ± 0.032
18:0	1.23 ± 0.135	0.82 ± 0.063	1.08 ± 0.031	1.00 ± 0.027	1.16 ± 0.039
18:1n-13	0.30 ± 0.057	0.14 ± 0.034	0.36 ± 0.009	0.31 ± 0.009	0.32 ± 0.016
18:1n-11	1.73 ± 0.177	1.34 ± 0.194	2.90 ± 0.149	2.54 ± 0.126	2.38 ± 0.169
18:1n-9	22.03 ± 2.127	26.15 ± 1.887	23.97 ± 0.578	24.33 ± 0.668	23.05 ± 0.897
18:1n-7	4.22 ± 0.124	4.61 ± 0.234	3.89 ± 0.075	4.04 ± 0.095	4.04 ± 0.154
18:1n-5	0.48 ± 0.034	0.43 ± 0.015	0.48 ± 0.007	0.45 ± 0.006	0.44 ± 0.009
18:2d57	0.14 ± 0.035	0.11 ± 0.016	0.05 ± 0.004	0.07 ± 0.006	0.07 ± 0.005
18:2n-7	0.16 ± 0.041	0.16 ± 0.007	0.07 ± 0.004	0.10 ± 0.006	0.08 ± 0.004
18:2n-6	0.98 ± 0.097	1.03 ± 0.041	1.09 ± 0.017	0.98 ± 0.017	0.93 ± 0.019
18:2n-4	0.13 ± 0.022	0.14 ± 0.018	0.11 ± 0.003	0.11 ± 0.004	0.12 ± 0.005
18:3n-6	0.08 ± 0.014	0.06 ± 0.008	0.06 ± 0.003	0.06 ± 0.003	0.08 ± 0.003
18:3n-4	0.12 ± 0.013	0.12 ± 0.012	0.11 ± 0.005	0.12 ± 0.005	0.10 ± 0.005
18:3n-3	0.57 ± 0.100	0.56 ± 0.039	0.65 ± 0.018	0.58 ± 0.022	0.46 ± 0.017

Table 6. Continued.

	PRINCE WILLIAM SOUND				
	NE	NW	SC		
	All Groups	All Groups	Adults	Sub Adults	Yearlings
18:3n-1	0.05 ± 0.018	0.04 ± 0.008	0.05 ± 0.003	0.04 ± 0.003	0.04 ± 0.003
18:4n-3	0.82 ± 0.137	0.74 ± 0.036	0.99 ± 0.032	1.04 ± 0.041	0.92 ± 0.037
18:4n-1	0.12 ± 0.019	0.17 ± 0.012	0.16 ± 0.007	0.19 ± 0.009	0.18 ± 0.011
20:0	0.06 ± 0.010	0.04 ± 0.005	0.09 ± 0.003	0.08 ± 0.003	0.10 ± 0.007
20:1n-11	2.40 ± 0.086	2.46 ± 0.281	7.15 ± 0.282	6.80 ± 0.264	7.87 ± 0.513
20:1n-9	1.36 ± 0.176	1.32 ± 0.061	2.19 ± 0.060	1.90 ± 0.049	2.07 ± 0.068
R20:1	1.87 ± 0.280	1.89 ± 0.228	3.24 ± 0.077	3.54 ± 0.079	3.74 ± 0.155
20:1n-7	0.39 ± 0.088	0.21 ± 0.034	0.31 ± 0.020	0.21 ± 0.009	0.22 ± 0.012
20:2n-9	0.10 ± 0.033	0.06 ± 0.014	0.07 ± 0.004	0.07 ± 0.005	0.05 ± 0.004
20:2n-6	0.33 ± 0.023	0.17 ± 0.027	0.21 ± 0.008	0.17 ± 0.007	0.18 ± 0.008
20:3n-6	0.09 ± 0.004	0.08 ± 0.003	0.07 ± 0.003	0.06 ± 0.004	0.06 ± 0.003
20:4n-6	0.98 ± 0.102	0.61 ± 0.052	0.55 ± 0.026	0.48 ± 0.030	0.47 ± 0.036
20:3n-3	0.10 ± 0.020	0.09 ± 0.020	0.12 ± 0.032	0.07 ± 0.009	0.04 ± 0.004
20:4n-3	0.58 ± 0.114	0.52 ± 0.052	0.65 ± 0.028	0.45 ± 0.018	0.40 ± 0.021
20:5n-3	4.76 ± 0.545	4.50 ± 0.373	4.49 ± 0.140	4.04 ± 0.150	4.13 ± 0.239
22:1n-11	0.65 ± 0.258	0.35 ± 0.060	2.11 ± 0.136	2.50 ± 0.188	2.89 ± 0.258
22:1n-9	0.20 ± 0.062	0.13 ± 0.037	0.27 ± 0.023	0.21 ± 0.012	0.28 ± 0.016
R22:1	3.43 ± 1.023	3.95 ± 1.022	8.75 ± 0.414	11.72 ± 0.569	9.92 ± 0.550
22:1n-7	0.14 ± 0.081	0.04 ± 0.035	0.03 ± 0.002	0.03 ± 0.003	0.03 ± 0.005
22:2n-6	0.02 ± 0.015	0.01 ± 0.003	0.03 ± 0.005	0.02 ± 0.010	0.00 ± 0.000
21:5n-3	0.25 ± 0.015	0.24 ± 0.029	0.30 ± 0.006	0.28 ± 0.009	0.30 ± 0.013
22:4n-6	0.22 ± 0.034	0.10 ± 0.011	0.14 ± 0.010	0.10 ± 0.011	0.09 ± 0.011
22:5n-6	0.20 ± 0.046	0.11 ± 0.009	0.12 ± 0.004	0.10 ± 0.010	0.11 ± 0.017
22:4n-3	0.07 ± 0.011	0.05 ± 0.005	0.08 ± 0.003	0.06 ± 0.003	0.07 ± 0.009
22:5n-3	3.66 ± 0.459	3.26 ± 0.389	4.30 ± 0.153	2.70 ± 0.126	3.13 ± 0.186
22:6n-3	9.43 ± 1.565	8.97 ± 1.018	8.36 ± 0.311	6.14 ± 0.239	6.75 ± 0.378
24:1	0.07 ± 0.026	0.05 ± 0.008	0.11 ± 0.007	0.11 ± 0.007	0.11 ± 0.008

Table 6. Continued.

	PRINCE WILLIAM SOUND				
	SC		SE		
	Half Years	Pups	Adults	Sub Adults	Yearlings
n	7	30	27	15	10
12:0	0.14 ± 0.018	0.15 ± 0.003	0.10 ± 0.004	0.11 ± 0.008	0.11 ± 0.005
13:0	0.01 ± 0.003	0.02 ± 0.001	0.02 ± 0.001	0.02 ± 0.002	0.02 ± 0.002
Iso14	0.02 ± 0.003	0.02 ± 0.001	0.02 ± 0.001	0.02 ± 0.002	0.02 ± 0.001
14:0	5.65 ± 0.238	5.49 ± 0.144	4.47 ± 0.225	4.52 ± 0.198	5.31 ± 0.137
14:1n-9	0.11 ± 0.022	0.09 ± 0.003	0.14 ± 0.008	0.13 ± 0.009	0.14 ± 0.007
14:1n-7	0.09 ± 0.007	0.09 ± 0.003	0.07 ± 0.005	0.08 ± 0.004	0.07 ± 0.004
14:1n-5	1.96 ± 0.153	1.87 ± 0.066	1.22 ± 0.084	1.63 ± 0.120	1.43 ± 0.104
Iso15	0.13 ± 0.004	0.11 ± 0.002	0.14 ± 0.005	0.12 ± 0.004	0.13 ± 0.004
Anti15	0.05 ± 0.008	0.04 ± 0.002	0.06 ± 0.003	0.06 ± 0.003	0.05 ± 0.002
15:0	0.25 ± 0.008	0.25 ± 0.005	0.29 ± 0.015	0.26 ± 0.009	0.29 ± 0.016
15:1n-8	0.02 ± 0.009	0.01 ± 0.001	0.00 ± 0.002	0.00 ± 0.002	0.00 ± 0.001
15:1n-6	0.07 ± 0.008	0.06 ± 0.002	0.07 ± 0.006	0.08 ± 0.004	0.06 ± 0.004
Iso16	0.05 ± 0.008	0.07 ± 0.002	0.09 ± 0.006	0.08 ± 0.004	0.08 ± 0.004
16:0	10.01 ± 0.386	11.17 ± 0.148	8.48 ± 0.392	8.68 ± 0.305	9.47 ± 0.423
16:1n-11	0.58 ± 0.043	0.62 ± 0.016	0.66 ± 0.027	0.50 ± 0.042	0.59 ± 0.030
16:1n-9	0.42 ± 0.026	0.49 ± 0.018	0.44 ± 0.026	0.47 ± 0.023	0.42 ± 0.020
16:1n-7	19.52 ± 1.072	20.21 ± 0.380	14.61 ± 0.570	17.81 ± 0.741	15.22 ± 0.698
7Me16:0	0.29 ± 0.013	0.27 ± 0.004	0.25 ± 0.004	0.24 ± 0.007	0.24 ± 0.007
16:1n-5	0.08 ± 0.023	0.12 ± 0.012	0.16 ± 0.017	0.14 ± 0.023	0.13 ± 0.024
16:2n-6	0.11 ± 0.020	0.10 ± 0.002	0.07 ± 0.011	0.10 ± 0.020	0.07 ± 0.003
Iso17	0.06 ± 0.008	0.09 ± 0.004	0.15 ± 0.011	0.11 ± 0.013	0.13 ± 0.010
16:2n-4	0.25 ± 0.066	0.17 ± 0.007	0.29 ± 0.015	0.24 ± 0.027	0.29 ± 0.018
16:3n-6	0.41 ± 0.063	0.46 ± 0.027	0.37 ± 0.026	0.41 ± 0.029	0.40 ± 0.026
17:0	0.08 ± 0.016	0.11 ± 0.005	0.17 ± 0.013	0.15 ± 0.016	0.17 ± 0.045
16:3n-4	0.31 ± 0.024	0.26 ± 0.017	0.33 ± 0.037	0.27 ± 0.024	0.24 ± 0.020
17:1	0.14 ± 0.070	0.34 ± 0.018	0.29 ± 0.050	0.37 ± 0.055	0.37 ± 0.048
16:3n-1	0.07 ± 0.012	0.07 ± 0.005	0.09 ± 0.007	0.10 ± 0.024	0.10 ± 0.013
16:4n-1	0.25 ± 0.083	0.37 ± 0.034	0.22 ± 0.032	0.22 ± 0.028	0.23 ± 0.030
18:0	0.93 ± 0.043	1.03 ± 0.024	1.01 ± 0.060	1.00 ± 0.045	1.14 ± 0.091
18:1n-13	0.28 ± 0.014	0.37 ± 0.015	0.37 ± 0.017	0.23 ± 0.029	0.30 ± 0.020
18:1n-11	2.34 ± 0.254	2.87 ± 0.237	2.36 ± 0.209	1.73 ± 0.219	1.60 ± 0.176
18:1n-9	20.81 ± 1.863	21.55 ± 1.019	24.79 ± 0.925	26.16 ± 1.313	27.59 ± 1.686
18:1n-7	3.62 ± 0.162	4.20 ± 0.141	4.05 ± 0.177	4.37 ± 0.242	4.18 ± 0.210
18:1n-5	0.47 ± 0.016	0.46 ± 0.016	0.46 ± 0.010	0.45 ± 0.015	0.46 ± 0.016
18:2d57	0.11 ± 0.029	0.13 ± 0.010	0.04 ± 0.005	0.06 ± 0.011	0.08 ± 0.011
18:2n-7	0.10 ± 0.019	0.11 ± 0.004	0.06 ± 0.005	0.09 ± 0.015	0.08 ± 0.005
18:2n-6	0.94 ± 0.033	0.96 ± 0.026	1.16 ± 0.028	1.12 ± 0.039	1.08 ± 0.046
18:2n-4	0.13 ± 0.012	0.13 ± 0.007	0.12 ± 0.006	0.12 ± 0.006	0.12 ± 0.008
18:3n-6	0.07 ± 0.012	0.12 ± 0.003	0.06 ± 0.003	0.07 ± 0.005	0.09 ± 0.005
18:3n-4	0.16 ± 0.015	0.10 ± 0.008	0.13 ± 0.007	0.11 ± 0.011	0.11 ± 0.009
18:3n-3	0.59 ± 0.057	0.39 ± 0.017	0.66 ± 0.024	0.64 ± 0.040	0.60 ± 0.058
18:3n-1	0.03 ± 0.010	0.04 ± 0.002	0.04 ± 0.004	0.04 ± 0.005	0.05 ± 0.006

Table 6. Continued.

	PRINCE WILLIAM SOUND				
	SC		SE		
	Half Years	Pups	Adults	Sub Adults	Yearlings
18:4n-3	1.14 ± 0.092	0.88 ± 0.044	1.00 ± 0.057	0.92 ± 0.058	0.93 ± 0.102
18:4n-1	0.21 ± 0.025	0.21 ± 0.017	0.15 ± 0.013	0.14 ± 0.009	0.13 ± 0.015
20:0	0.05 ± 0.007	0.04 ± 0.003	0.07 ± 0.006	0.06 ± 0.006	0.09 ± 0.008
20:1n-11	5.46 ± 0.418	5.51 ± 0.376	5.13 ± 0.403	3.45 ± 0.328	4.95 ± 0.413
20:1n-9	1.68 ± 0.087	1.48 ± 0.065	1.92 ± 0.086	1.62 ± 0.093	1.92 ± 0.105
R20:1	3.30 ± 0.316	3.65 ± 0.114	2.63 ± 0.138	2.12 ± 0.146	2.63 ± 0.211
20:1n-7	0.18 ± 0.010	0.15 ± 0.010	0.31 ± 0.045	0.25 ± 0.040	0.26 ± 0.032
20:2n-9	0.09 ± 0.023	0.03 ± 0.004	0.06 ± 0.007	0.05 ± 0.006	0.06 ± 0.007
20:2n-6	0.20 ± 0.017	0.20 ± 0.008	0.22 ± 0.012	0.19 ± 0.015	0.20 ± 0.012
20:3n-6	0.06 ± 0.007	0.06 ± 0.002	0.07 ± 0.003	0.06 ± 0.005	0.06 ± 0.004
20:4n-6	0.53 ± 0.071	0.62 ± 0.049	0.55 ± 0.042	0.55 ± 0.045	0.50 ± 0.038
20:3n-3	0.16 ± 0.071	0.04 ± 0.004	0.09 ± 0.011	0.13 ± 0.056	0.06 ± 0.006
20:4n-3	0.48 ± 0.057	0.42 ± 0.026	0.71 ± 0.050	0.57 ± 0.061	0.52 ± 0.062
20:5n-3	4.85 ± 0.488	3.81 ± 0.208	5.06 ± 0.212	4.69 ± 0.302	4.02 ± 0.420
22:1n-11	1.79 ± 0.219	1.04 ± 0.115	1.79 ± 0.243	0.99 ± 0.151	1.76 ± 0.314
22:1n-9	0.15 ± 0.016	0.10 ± 0.012	0.23 ± 0.027	0.16 ± 0.019	0.29 ± 0.077
R22:1	12.10 ± 1.278	10.33 ± 0.599	8.00 ± 0.707	6.27 ± 0.632	7.72 ± 1.251
22:1n-7	0.01 ± 0.007	0.00 ± 0.001	0.03 ± 0.004	0.02 ± 0.005	0.03 ± 0.006
22:2n-6	0.01 ± 0.005	0.00 ± 0.002	0.01 ± 0.005	0.01 ± 0.003	0.00 ± 0.000
21:5n-3	0.29 ± 0.021	0.29 ± 0.012	0.29 ± 0.008	0.27 ± 0.017	0.26 ± 0.019
22:4n-6	0.09 ± 0.015	0.09 ± 0.015	0.12 ± 0.017	0.12 ± 0.017	0.09 ± 0.016
22:5n-6	0.09 ± 0.009	0.08 ± 0.005	0.13 ± 0.007	0.13 ± 0.010	0.12 ± 0.011
22:4n-3	0.06 ± 0.007	0.05 ± 0.004	0.08 ± 0.006	0.07 ± 0.006	0.07 ± 0.007
22:5n-3	3.04 ± 0.403	2.96 ± 0.182	4.18 ± 0.274	3.63 ± 0.327	2.87 ± 0.262
22:6n-3	7.36 ± 0.858	6.26 ± 0.357	8.94 ± 0.481	8.59 ± 0.634	7.34 ± 0.737
24:1	0.11 ± 0.036	0.02 ± 0.003	0.11 ± 0.011	0.10 ± 0.016	0.11 ± 0.017

Table 6. Continued.

	PRINCE WILLIAM SOUND			GULF OF ALASKA	
	SE		SW	Kenai Pen.	Kodiak N.
	Half Years	Pups	All Groups	All Groups	Adults
n	6	2	2	1	12
12:0	0.11 ± 0.028	0.14 ± 0.035	0.13 ± 0.055	0.09	0.08 ± 0.007
13:0	0.01 ± 0.003	0.02 ± 0.000	0.01 ± 0.002	0.02	0.02 ± 0.002
Iso14	0.02 ± 0.005	0.03 ± 0.003	0.03 ± 0.005	0.02	0.02 ± 0.003
14:0	5.21 ± 0.426	3.56 ± 0.488	5.15 ± 0.558	4.31	4.22 ± 0.104
14:1n-9	0.10 ± 0.015	0.09 ± 0.015	0.14 ± 0.015	0.18	0.14 ± 0.010
14:1n-7	0.10 ± 0.014	0.10 ± 0.015	0.11 ± 0.015	0.07	0.08 ± 0.004
14:1n-5	2.30 ± 0.513	1.86 ± 0.363	2.12 ± 0.445	1.04	1.39 ± 0.118
Iso15	0.11 ± 0.008	0.11 ± 0.008	0.11 ± 0.010	0.10	0.14 ± 0.011
Anti15	0.05 ± 0.008	0.06 ± 0.005	0.05 ± 0.005	0.04	0.06 ± 0.009
15:0	0.24 ± 0.021	0.25 ± 0.020	0.21 ± 0.023	0.26	0.27 ± 0.022
15:1n-8	0.01 ± 0.005	0.00 ± 0.003	0.00 ± 0.003	0.01	0.01 ± 0.002
15:1n-6	0.06 ± 0.014	0.09 ± 0.000	0.06 ± 0.000	0.05	0.08 ± 0.006
Iso16	0.07 ± 0.005	0.10 ± 0.018	0.07 ± 0.000	0.07	0.10 ± 0.016
16:0	10.07 ± 0.534	8.32 ± 1.918	8.70 ± 2.393	11.51	8.23 ± 0.291
16:1n-11	0.47 ± 0.035	0.49 ± 0.022	0.55 ± 0.125	0.47	0.71 ± 0.036
16:1n-9	0.54 ± 0.044	0.57 ± 0.058	0.50 ± 0.060	0.38	0.44 ± 0.019
16:1n-7	20.88 ± 2.432	19.59 ± 4.290	20.05 ± 4.988	14.97	15.68 ± 0.633
7Me16:0	0.27 ± 0.013	0.24 ± 0.015	0.23 ± 0.008	0.21	0.28 ± 0.026
16:1n-5	0.11 ± 0.033	0.27 ± 0.040	0.17 ± 0.005	0.06	0.17 ± 0.035
16:2n-6	0.10 ± 0.030	0.09 ± 0.015	0.07 ± 0.020	0.08	0.09 ± 0.019
Iso17	0.08 ± 0.014	0.16 ± 0.045	0.09 ± 0.010	0.13	0.12 ± 0.032
16:2n-4	0.21 ± 0.039	0.29 ± 0.048	0.19 ± 0.002	0.16	0.23 ± 0.038
16:3n-6	0.35 ± 0.064	0.24 ± 0.030	0.40 ± 0.055	0.70	0.52 ± 0.032
17:0	0.14 ± 0.029	0.15 ± 0.010	0.26 ± 0.143	0.11	0.16 ± 0.025
16:3n-4	0.27 ± 0.060	0.14 ± 0.002	0.18 ± 0.005	0.29	0.41 ± 0.037
17:1	0.23 ± 0.099	0.58 ± 0.030	0.37 ± 0.030	0.33	0.16 ± 0.056
16:3n-1	0.07 ± 0.034	0.16 ± 0.010	0.10 ± 0.010	0.05	0.05 ± 0.006
16:4n-1	0.13 ± 0.032	0.12 ± 0.005	0.18 ± 0.028	0.37	0.30 ± 0.029
18:0	1.05 ± 0.120	0.95 ± 0.023	0.70 ± 0.090	1.62	1.00 ± 0.057
18:1n-13	0.21 ± 0.034	0.34 ± 0.055	0.30 ± 0.038	0.14	0.28 ± 0.036
18:1n-11	1.29 ± 0.158	2.18 ± 0.140	2.08 ± 0.120	0.38	1.59 ± 0.119
18:1n-9	27.04 ± 2.582	25.01 ± 4.265	31.10 ± 10.30	24.89	24.88 ± 1.335
18:1n-7	4.58 ± 0.243	4.55 ± 0.583	4.82 ± 0.705	6.27	4.82 ± 0.297
18:1n-5	0.44 ± 0.014	0.45 ± 0.018	0.40 ± 0.055	0.28	0.40 ± 0.017
18:2d57	0.14 ± 0.025	0.11 ± 0.025	0.08 ± 0.010	0.07	0.05 ± 0.009
18:2n-7	0.15 ± 0.034	0.10 ± 0.018	0.11 ± 0.025	0.11	0.07 ± 0.009
18:2n-6	0.96 ± 0.043	1.20 ± 0.065	1.08 ± 0.032	0.93	1.04 ± 0.040
18:2n-4	0.10 ± 0.007	0.11 ± 0.013	0.09 ± 0.015	0.19	0.13 ± 0.011
18:3n-6	0.08 ± 0.009	0.10 ± 0.023	0.07 ± 0.020	0.09	0.05 ± 0.005
18:3n-4	0.12 ± 0.017	0.08 ± 0.010	0.07 ± 0.007	0.11	0.13 ± 0.009
18:3n-3	0.46 ± 0.060	0.51 ± 0.025	0.47 ± 0.032	0.53	0.61 ± 0.044

Table 6. Continued.

	PRINCE WILLIAM SOUND			GULF OF ALASKA	
	SE		SW	Kenai Pen.	Kodiak N.
	Half Years	Pups	All Groups	All Groups	Adults
18:3n-1	0.04 ± 0.007	0.06 ± 0.010	0.03 ± 0.002	0.05	0.05 ± 0.004
18:4n-3	0.70 ± 0.092	0.63 ± 0.027	0.72 ± 0.080	0.98	0.88 ± 0.056
18:4n-1	0.11 ± 0.013	0.09 ± 0.015	0.10 ± 0.028	0.14	0.18 ± 0.018
20:0	0.05 ± 0.010	0.05 ± 0.018	0.04 ± 0.005	0.06	0.06 ± 0.005
20:1n-11	3.06 ± 0.482	3.55 ± 0.957	4.00 ± 0.678	2.35	4.35 ± 0.488
20:1n-9	1.35 ± 0.129	1.31 ± 0.330	1.39 ± 0.112	1.17	1.74 ± 0.120
R20:1	2.27 ± 0.274	2.69 ± 0.052	2.85 ± 0.256	2.00	2.47 ± 0.207
20:1n-7	0.20 ± 0.050	0.27 ± 0.095	0.10 ± 0.007	0.23	0.35 ± 0.066
20:2n-9	0.08 ± 0.040	0.03 ± 0.010	0.00 ± 0.000	0.04	0.04 ± 0.005
20:2n-6	0.24 ± 0.041	0.26 ± 0.002	0.19 ± 0.060	0.20	0.21 ± 0.020
20:3n-6	0.06 ± 0.013	0.08 ± 0.008	0.04 ± 0.000	0.05	0.06 ± 0.004
20:4n-6	0.63 ± 0.171	0.76 ± 0.045	0.38 ± 0.095	0.50	0.59 ± 0.069
20:3n-3	0.09 ± 0.053	0.06 ± 0.000	0.05 ± 0.023	0.06	0.07 ± 0.007
20:4n-3	0.36 ± 0.073	0.55 ± 0.010	0.30 ± 0.040	0.38	0.55 ± 0.052
20:5n-3	3.42 ± 0.552	3.70 ± 0.013	2.92 ± 0.677	8.07	6.25 ± 0.415
22:1n-11	0.97 ± 0.333	0.37 ± 0.175	0.70 ± 0.030	0.56	1.08 ± 0.145
22:1n-9	0.18 ± 0.029	0.11 ± 0.045	0.08 ± 0.010	0.09	0.14 ± 0.014
R22:1	5.37 ± 1.577	3.38 ± 0.217	8.84 ± 0.730	6.59	7.99 ± 0.927
22:1n-7	0.02 ± 0.007	0.00 ± 0.000	0.00 ± 0.000	0.03	0.02 ± 0.003
22:2n-6	0.01 ± 0.008	0.03 ± 0.015	0.00 ± 0.000	0.00	0.03 ± 0.005
21:5n-3	0.22 ± 0.022	0.26 ± 0.010	0.23 ± 0.040	0.54	0.34 ± 0.015
22:4n-6	0.13 ± 0.056	0.20 ± 0.058	0.05 ± 0.005	0.07	0.14 ± 0.026
22:5n-6	0.10 ± 0.024	0.16 ± 0.025	0.06 ± 0.013	0.09	0.12 ± 0.009
22:4n-3	0.04 ± 0.007	0.08 ± 0.005	0.04 ± 0.005	0.06	0.06 ± 0.005
22:5n-3	2.52 ± 0.610	4.94 ± 0.650	2.03 ± 0.625	4.22	4.59 ± 0.329
22:6n-3	6.21 ± 1.247	8.96 ± 0.258	4.96 ± 1.715	8.25	8.62 ± 0.557
24:1	0.09 ± 0.036	0.05 ± 0.033	0.04 ± 0.010	0.07	0.08 ± 0.011

Table 6. Continued.

	GULF OF ALASKA			BERING SEA
	Southeast Alaska			
	Peril St. All Groups	Sitka All Groups	Stephen's Passage All Groups	All Groups
n	14	9	14	2
12:0	0.09 ± 0.009	0.12 ± 0.006	0.08 ± 0.009	0.10 ± 0.015
13:0	0.02 ± 0.002	0.02 ± 0.002	0.02 ± 0.001	0.02 ± 0.002
Iso14	0.02 ± 0.002	0.02 ± 0.001	0.02 ± 0.002	0.02 ± 0.003
14:0	3.37 ± 0.190	3.91 ± 0.201	3.09 ± 0.166	2.53 ± 0.055
14:1n-9	0.14 ± 0.010	0.10 ± 0.028	0.12 ± 0.011	0.09 ± 0.005
14:1n-7	0.07 ± 0.004	0.06 ± 0.008	0.08 ± 0.006	0.08 ± 0.015
14:1n-5	1.12 ± 0.074	0.96 ± 0.166	1.69 ± 0.165	0.95 ± 0.072
Iso15	0.11 ± 0.006	0.14 ± 0.009	0.09 ± 0.005	0.12 ± 0.015
Anti15	0.05 ± 0.004	0.05 ± 0.004	0.05 ± 0.005	0.05 ± 0.010
15:0	0.24 ± 0.014	0.32 ± 0.022	0.21 ± 0.012	0.24 ± 0.008
15:1n-8	0.00 ± 0.001	0.00 ± 0.000	0.01 ± 0.002	0.00 ± 0.003
15:1n-6	0.07 ± 0.003	0.05 ± 0.002	0.09 ± 0.005	0.07 ± 0.010
Iso16	0.07 ± 0.007	0.09 ± 0.010	0.06 ± 0.004	0.12 ± 0.030
16:0	8.22 ± 0.311	9.84 ± 0.445	6.71 ± 0.449	6.89 ± 0.355
16:1n-11	0.51 ± 0.032	0.65 ± 0.066	0.50 ± 0.043	0.45 ± 0.048
16:1n-9	0.45 ± 0.010	0.45 ± 0.027	0.50 ± 0.019	0.54 ± 0.060
16:1n-7	15.43 ± 0.662	13.67 ± 0.966	18.97 ± 1.247	14.55 ± 0.398
7Me16:0	0.23 ± 0.006	0.29 ± 0.021	0.22 ± 0.007	0.22 ± 0.007
16:1n-5	0.18 ± 0.012	0.23 ± 0.021	0.04 ± 0.003	0.13 ± 0.015
16:2n-6	0.06 ± 0.004	0.06 ± 0.010	0.15 ± 0.019	0.06 ± 0.000
Iso17	0.11 ± 0.009	0.13 ± 0.021	0.03 ± 0.002	0.20 ± 0.032
16:2n-4	0.23 ± 0.014	0.24 ± 0.037	0.09 ± 0.007	0.39 ± 0.020
16:3n-6	0.38 ± 0.033	0.42 ± 0.073	0.61 ± 0.043	0.20 ± 0.010
17:0	0.20 ± 0.038	0.18 ± 0.026	0.09 ± 0.009	0.13 ± 0.005
16:3n-4	0.47 ± 0.027	0.50 ± 0.036	0.49 ± 0.049	0.11 ± 0.005
17:1	0.02 ± 0.004	0.03 ± 0.002	0.50 ± 0.042	0.61 ± 0.073
16:3n-1	0.07 ± 0.010	0.10 ± 0.009	0.03 ± 0.003	0.14 ± 0.050
16:4n-1	0.17 ± 0.040	0.27 ± 0.065	0.29 ± 0.029	0.07 ± 0.028
18:0	1.17 ± 0.032	1.51 ± 0.130	0.80 ± 0.039	0.98 ± 0.120
18:1n-13	0.21 ± 0.029	0.25 ± 0.050	0.02 ± 0.010	0.32 ± 0.098
18:1n-11	1.55 ± 0.203	1.53 ± 0.237	1.34 ± 0.131	1.16 ± 0.498
18:1n-9	25.57 ± 1.192	21.97 ± 1.649	28.83 ± 1.451	28.22 ± 1.248
18:1n-7	5.30 ± 0.379	4.67 ± 0.280	4.97 ± 0.200	4.88 ± 0.018
18:1n-5	0.37 ± 0.018	0.36 ± 0.030	0.34 ± 0.018	0.48 ± 0.015
18:2d57	0.03 ± 0.005	0.03 ± 0.018	0.06 ± 0.004	0.11 ± 0.002
18:2n-7	0.07 ± 0.005	0.06 ± 0.007	0.12 ± 0.007	0.07 ± 0.020
18:2n-6	1.22 ± 0.053	1.28 ± 0.084	1.05 ± 0.083	1.39 ± 0.130
18:2n-4	0.14 ± 0.009	0.14 ± 0.015	0.14 ± 0.007	0.12 ± 0.005
18:3n-6	0.05 ± 0.004	0.05 ± 0.012	0.05 ± 0.002	0.08 ± 0.003
18:3n-4	0.16 ± 0.007	0.16 ± 0.013	0.13 ± 0.009	0.07 ± 0.000
18:3n-3	0.66 ± 0.047	0.84 ± 0.082	0.54 ± 0.053	0.51 ± 0.017

Table 6. Continued.

	GULF OF ALASKA			BERING SEA
	Southeast Alaska			
	Peril St. All Groups	Sitka All Groups	Stephen's Passage All Groups	All Groups
18:3n-1	0.04 ± 0.004	0.03 ± 0.009	0.05 ± 0.005	0.07 ± 0.015
18:4n-3	0.82 ± 0.065	1.42 ± 0.288	0.68 ± 0.041	0.61 ± 0.023
18:4n-1	0.15 ± 0.016	0.15 ± 0.021	0.19 ± 0.013	0.07 ± 0.005
20:0	0.04 ± 0.003	0.04 ± 0.005	0.05 ± 0.002	0.06 ± 0.000
20:1n-11	2.88 ± 0.401	2.37 ± 0.411	2.50 ± 0.338	3.73 ± 1.978
20:1n-9	2.09 ± 0.208	2.09 ± 0.328	1.97 ± 0.200	2.59 ± 0.127
R20:1	1.40 ± 0.178	1.16 ± 0.157	1.23 ± 0.125	1.48 ± 0.836
20:1n-7	0.31 ± 0.025	0.31 ± 0.043	0.25 ± 0.022	0.41 ± 0.020
20:2n-9	0.04 ± 0.004	0.06 ± 0.005	0.02 ± 0.002	0.03 ± 0.007
20:2n-6	0.24 ± 0.009	0.26 ± 0.023	0.15 ± 0.016	0.28 ± 0.015
20:3n-6	0.08 ± 0.005	0.08 ± 0.005	0.09 ± 0.006	0.09 ± 0.020
20:4n-6	0.66 ± 0.036	0.78 ± 0.067	0.49 ± 0.031	0.60 ± 0.053
20:3n-3	0.09 ± 0.006	0.10 ± 0.012	0.07 ± 0.009	0.08 ± 0.008
20:4n-3	0.65 ± 0.061	0.80 ± 0.099	0.56 ± 0.069	0.61 ± 0.085
20:5n-3	6.21 ± 0.312	7.43 ± 0.822	5.77 ± 0.319	4.83 ± 1.380
22:1n-11	0.81 ± 0.137	1.01 ± 0.193	0.32 ± 0.047	0.81 ± 0.208
22:1n-9	0.20 ± 0.015	0.19 ± 0.036	0.12 ± 0.024	0.22 ± 0.027
R22:1	4.19 ± 0.819	6.30 ± 1.078	2.90 ± 0.285	3.90 ± 1.447
22:1n-7	0.04 ± 0.018	0.02 ± 0.007	0.01 ± 0.009	0.00 ± 0.000
22:2n-6	0.04 ± 0.009	0.03 ± 0.011	0.03 ± 0.006	0.00 ± 0.000
21:5n-3	0.37 ± 0.008	0.39 ± 0.037	0.36 ± 0.012	0.32 ± 0.000
22:4n-6	0.12 ± 0.015	0.16 ± 0.029	0.08 ± 0.008	0.17 ± 0.030
22:5n-6	0.13 ± 0.008	0.15 ± 0.022	0.10 ± 0.009	0.20 ± 0.012
22:4n-3	0.08 ± 0.005	0.07 ± 0.007	0.06 ± 0.005	0.09 ± 0.015
22:5n-3	5.64 ± 0.341	5.25 ± 0.637	4.52 ± 0.327	5.67 ± 0.718
22:6n-3	9.41 ± 0.701	10.76 ± 1.046	8.26 ± 0.715	10.82 ± 1.855
24:1	0.10 ± 0.006	0.08 ± 0.013	0.05 ± 0.005	0.11 ± 0.007

Table 7. Fatty acid composition of archived harbor seal blubber (n = 286). Values are mean mass % of total fatty acids ± SEM. See Table 4 for summary of collection data.

	PRINCE WILLIAM SOUND		GULF OF ALASKA		
	1977	1989-93	1976&77		
	All Groups	All Groups	SCA	Kenai Pen.	Kodiak N.
n	4	16	30	56	71
12:0	0.11 ± 0.012	0.12 ± 0.004	0.09 ± 0.006	0.09 ± 0.004	0.10 ± 0.002
13:0	0.02 ± 0.005	0.02 ± 0.002	0.02 ± 0.001	0.02 ± 0.001	0.02 ± 0.001
Iso14	0.01 ± 0.007	0.01 ± 0.002	0.02 ± 0.001	0.02 ± 0.001	0.02 ± 0.001
14:0	3.82 ± 0.537	4.61 ± 0.238	4.68 ± 0.203	4.63 ± 0.114	4.71 ± 0.104
14:1n-9	0.09 ± 0.016	0.14 ± 0.009	0.13 ± 0.005	0.12 ± 0.003	0.14 ± 0.003
14:1n-7	0.07 ± 0.012	0.06 ± 0.004	0.06 ± 0.002	0.05 ± 0.002	0.06 ± 0.002
14:1n-5	1.52 ± 0.410	1.28 ± 0.116	1.00 ± 0.055	0.81 ± 0.058	0.89 ± 0.036
Iso15	0.10 ± 0.005	0.13 ± 0.005	0.14 ± 0.005	0.12 ± 0.003	0.13 ± 0.004
Anti15	0.04 ± 0.001	0.04 ± 0.002	0.06 ± 0.003	0.05 ± 0.002	0.06 ± 0.003
15:0	0.25 ± 0.023	0.25 ± 0.014	0.29 ± 0.010	0.25 ± 0.008	0.25 ± 0.006
15:1n-8	0.00 ± 0.000	0.00 ± 0.000	0.01 ± 0.001	0.01 ± 0.000	0.01 ± 0.000
15:1n-6	0.07 ± 0.008	0.05 ± 0.003	0.05 ± 0.003	0.04 ± 0.002	0.04 ± 0.002
Iso16	0.06 ± 0.003	0.07 ± 0.002	0.10 ± 0.005	0.08 ± 0.004	0.09 ± 0.002
16:0	8.20 ± 0.937	8.61 ± 0.410	10.47 ± 0.306	11.32 ± 0.170	10.99 ± 0.204
16:1n-11	0.59 ± 0.026	0.69 ± 0.024	0.50 ± 0.031	0.45 ± 0.018	0.44 ± 0.010
16:1n-9	0.55 ± 0.046	0.41 ± 0.022	0.38 ± 0.013	0.34 ± 0.010	0.35 ± 0.009
16:1n-7	15.80 ± 2.133	14.25 ± 0.742	13.28 ± 0.393	12.66 ± 0.438	13.30 ± 0.240
7Me16:0	0.25 ± 0.015	0.29 ± 0.010	0.21 ± 0.006	0.21 ± 0.011	0.21 ± 0.004
16:1n-5	0.07 ± 0.018	0.08 ± 0.006	0.13 ± 0.010	0.07 ± 0.005	0.06 ± 0.002
16:2n-6	0.06 ± 0.011	0.06 ± 0.003	0.05 ± 0.002	0.06 ± 0.002	0.07 ± 0.001
Iso17	0.10 ± 0.007	0.11 ± 0.004	0.14 ± 0.008	0.12 ± 0.005	0.14 ± 0.004
16:2n-4	0.30 ± 0.030	0.29 ± 0.011	0.28 ± 0.021	0.22 ± 0.015	0.24 ± 0.010
16:3n-6	0.25 ± 0.040	0.31 ± 0.021	0.38 ± 0.019	0.46 ± 0.015	0.51 ± 0.012
17:0	0.15 ± 0.009	0.12 ± 0.009	0.15 ± 0.013	0.13 ± 0.008	0.13 ± 0.005
16:3n-4	0.12 ± 0.017	0.16 ± 0.013	0.18 ± 0.012	0.24 ± 0.012	0.24 ± 0.007
17:1	0.43 ± 0.032	0.35 ± 0.014	0.39 ± 0.020	0.28 ± 0.014	0.28 ± 0.008
16:3n-1	0.03 ± 0.006	0.03 ± 0.002	0.12 ± 0.007	0.09 ± 0.005	0.10 ± 0.005
16:4n-1	0.14 ± 0.034	0.25 ± 0.028	0.20 ± 0.022	0.29 ± 0.024	0.36 ± 0.015
18:0	0.95 ± 0.130	0.98 ± 0.049	1.29 ± 0.051	1.46 ± 0.031	1.30 ± 0.028
18:1n-13	0.36 ± 0.014	0.36 ± 0.013	0.18 ± 0.019	0.22 ± 0.012	0.25 ± 0.011
18:1n-11	2.17 ± 0.266	2.63 ± 0.273	0.69 ± 0.051	1.14 ± 0.108	1.23 ± 0.064
18:1n-9	25.24 ± 2.309	21.01 ± 1.040	27.08 ± 0.973	24.04 ± 0.879	22.83 ± 0.558
18:1n-7	3.80 ± 0.422	3.93 ± 0.121	5.00 ± 0.199	5.52 ± 0.175	5.18 ± 0.116
18:1n-5	0.41 ± 0.043	0.43 ± 0.009	0.39 ± 0.018	0.38 ± 0.021	0.38 ± 0.009
18:2d57	0.08 ± 0.023	0.05 ± 0.007	0.08 ± 0.006	0.06 ± 0.004	0.06 ± 0.002
18:2n-7	0.07 ± 0.020	0.05 ± 0.003	0.07 ± 0.003	0.08 ± 0.003	0.08 ± 0.002
18:2n-6	1.13 ± 0.064	1.10 ± 0.040	1.39 ± 0.049	1.05 ± 0.028	0.97 ± 0.021
18:2n-4	0.09 ± 0.002	0.11 ± 0.006	0.12 ± 0.008	0.15 ± 0.007	0.17 ± 0.005
18:3n-6	0.03 ± 0.018	0.06 ± 0.003	0.09 ± 0.003	0.09 ± 0.002	0.08 ± 0.002
18:3n-4	0.05 ± 0.015	0.05 ± 0.005	0.12 ± 0.008	0.09 ± 0.004	0.11 ± 0.004
18:3n-3	0.66 ± 0.072	0.65 ± 0.031	0.60 ± 0.024	0.50 ± 0.016	0.45 ± 0.019

Table 7. Continued.

	PRINCE WILLIAM SOUND		GULF OF ALASKA		
	1977	1989-93	1976&77		
	All Groups	All Groups	SCA	Kenai Pen.	Kodiak N.
18:3n-1	0.04 ± 0.004	0.05 ± 0.004	0.06 ± 0.005	0.05 ± 0.003	0.05 ± 0.002
18:4n-3	0.85 ± 0.045	1.13 ± 0.076	1.15 ± 0.073	1.11 ± 0.042	0.99 ± 0.046
18:4n-1	0.10 ± 0.004	0.15 ± 0.011	0.12 ± 0.011	0.15 ± 0.009	0.19 ± 0.009
20:0	0.05 ± 0.004	0.05 ± 0.006	0.08 ± 0.004	0.08 ± 0.004	0.07 ± 0.002
20:1n-11	4.18 ± 0.446	5.35 ± 0.469	3.50 ± 0.277	4.23 ± 0.314	3.92 ± 0.208
20:1n-9	1.81 ± 0.114	2.50 ± 0.203	1.76 ± 0.075	1.70 ± 0.060	2.11 ± 0.071
R20:1	2.33 ± 0.265	2.19 ± 0.144	1.95 ± 0.104	2.43 ± 0.111	1.92 ± 0.087
20:1n-7	0.18 ± 0.025	0.17 ± 0.015	0.32 ± 0.038	0.27 ± 0.014	0.32 ± 0.014
20:2n-9	0.02 ± 0.012	0.03 ± 0.003	0.07 ± 0.005	0.06 ± 0.004	0.06 ± 0.003
20:2n-6	0.24 ± 0.033	0.20 ± 0.012	0.27 ± 0.014	0.22 ± 0.008	0.20 ± 0.006
20:3n-6	0.07 ± 0.014	0.06 ± 0.003	0.06 ± 0.004	0.06 ± 0.002	0.06 ± 0.002
20:4n-6	0.49 ± 0.028	0.54 ± 0.038	0.65 ± 0.074	0.51 ± 0.032	0.53 ± 0.020
20:3n-3	0.10 ± 0.023	0.08 ± 0.006	0.08 ± 0.004	0.07 ± 0.003	0.06 ± 0.002
20:4n-3	0.68 ± 0.182	0.68 ± 0.057	0.54 ± 0.035	0.48 ± 0.021	0.44 ± 0.019
20:5n-3	4.52 ± 0.398	5.44 ± 0.280	5.40 ± 0.259	7.02 ± 0.285	7.27 ± 0.183
22:1n-11	0.93 ± 0.249	1.58 ± 0.214	1.14 ± 0.201	1.29 ± 0.154	1.23 ± 0.088
22:1n-9	0.16 ± 0.019	0.21 ± 0.021	0.22 ± 0.021	0.22 ± 0.015	0.23 ± 0.016
R22:1	5.93 ± 1.840	7.78 ± 0.745	5.17 ± 0.510	6.05 ± 0.435	5.53 ± 0.289
22:1n-7	0.01 ± 0.005	0.01 ± 0.003	0.03 ± 0.006	0.03 ± 0.002	0.04 ± 0.002
22:2n-6	0.01 ± 0.005	0.01 ± 0.005	0.00 ± 0.001	0.00 ± 0.000	0.00 ± 0.001
21:5n-3	0.28 ± 0.020	0.33 ± 0.011	0.35 ± 0.014	0.43 ± 0.015	0.47 ± 0.008
22:4n-6	0.09 ± 0.014	0.11 ± 0.011	0.16 ± 0.026	0.11 ± 0.014	0.11 ± 0.007
22:5n-6	0.11 ± 0.020	0.11 ± 0.006	0.16 ± 0.017	0.11 ± 0.007	0.11 ± 0.004
22:4n-3	0.05 ± 0.028	0.07 ± 0.005	0.08 ± 0.005	0.07 ± 0.004	0.06 ± 0.002
22:5n-3	5.40 ± 1.167	5.26 ± 0.309	3.91 ± 0.230	4.45 ± 0.198	5.29 ± 0.155
22:6n-3	11.22 ± 2.451	11.39 ± 0.444	9.09 ± 0.433	9.14 ± 0.443	8.97 ± 0.278
24:1	0.05 ± 0.020	0.07 ± 0.007	0.12 ± 0.008	0.12 ± 0.005	0.13 ± 0.006

Table 7. Continued

	GULF OF ALASKA	
	1976, 1977	1978
	Kodiak S.	All Groups
n	86	23
12:0	0.10 ± 0.002	0.10 ± 0.008
13:0	0.02 ± 0.001	0.02 ± 0.001
Iso14	0.02 ± 0.001	0.01 ± 0.001
14:0	4.61 ± 0.094	5.16 ± 0.251
14:1n-9	0.15 ± 0.004	0.15 ± 0.006
14:1n-7	0.06 ± 0.001	0.07 ± 0.005
14:1n-5	0.83 ± 0.032	1.10 ± 0.116
Iso15	0.15 ± 0.005	0.11 ± 0.003
Anti15	0.08 ± 0.005	0.04 ± 0.002
15:0	0.27 ± 0.006	0.22 ± 0.005
15:1n-8	0.01 ± 0.000	0.01 ± 0.001
15:1n-6	0.04 ± 0.001	0.04 ± 0.004
Iso16	0.10 ± 0.003	0.07 ± 0.004
16:0	11.39 ± 0.192	10.90 ± 0.360
16:1n-11	0.45 ± 0.010	0.43 ± 0.023
16:1n-9	0.34 ± 0.007	0.37 ± 0.013
16:1n-7	13.49 ± 0.215	14.36 ± 0.931
7Me16:0	0.22 ± 0.005	0.21 ± 0.010
16:1n-5	0.08 ± 0.004	0.12 ± 0.009
16:2n-6	0.06 ± 0.001	0.07 ± 0.005
Iso17	0.16 ± 0.006	0.11 ± 0.005
16:2n-4	0.24 ± 0.011	0.19 ± 0.013
16:3n-6	0.50 ± 0.013	0.51 ± 0.021
17:0	0.13 ± 0.005	0.09 ± 0.006
16:3n-4	0.23 ± 0.007	0.22 ± 0.018
17:1	0.30 ± 0.008	0.30 ± 0.016
16:3n-1	0.11 ± 0.004	0.08 ± 0.003
16:4n-1	0.34 ± 0.013	0.35 ± 0.048
18:0	1.32 ± 0.026	1.37 ± 0.060
18:1n-13	0.21 ± 0.011	0.16 ± 0.020
18:1n-11	0.93 ± 0.044	0.75 ± 0.094
18:1n-9	21.97 ± 0.431	28.21 ± 1.454
18:1n-7	5.44 ± 0.107	5.88 ± 0.196
18:1n-5	0.39 ± 0.012	0.33 ± 0.013
18:2d57	0.07 ± 0.002	0.08 ± 0.008
18:2n-7	0.08 ± 0.002	0.08 ± 0.004
18:2n-6	1.15 ± 0.036	0.82 ± 0.028
18:2n-4	0.15 ± 0.004	0.13 ± 0.008
18:3n-6	0.09 ± 0.001	0.07 ± 0.003
18:3n-4	0.09 ± 0.003	0.12 ± 0.005
18:3n-3	0.55 ± 0.025	0.33 ± 0.015
18:3n-1	0.06 ± 0.002	0.04 ± 0.004

Table 7. Continued

	GULF OF ALASKA	
	1976, 1977	1978
	Kodiak S.	All Groups
18:4n-3	1.01 ± 0.043	0.70 ± 0.039
18:4n-1	0.16 ± 0.005	0.17 ± 0.018
20:0	0.07 ± 0.002	0.07 ± 0.007
20:1n-11	2.88 ± 0.126	3.95 ± 0.487
20:1n-9	2.18 ± 0.163	1.48 ± 0.058
R20:1	1.63 ± 0.081	2.62 ± 0.267
20:1n-7	0.35 ± 0.017	0.28 ± 0.018
20:2n-9	0.06 ± 0.003	0.05 ± 0.005
20:2n-6	0.22 ± 0.006	0.17 ± 0.010
20:3n-6	0.07 ± 0.002	0.05 ± 0.003
20:4n-6	0.56 ± 0.023	0.50 ± 0.047
20:3n-3	0.07 ± 0.003	0.04 ± 0.003
20:4n-3	0.48 ± 0.018	0.31 ± 0.020
20:5n-3	7.89 ± 0.166	4.99 ± 0.296
22:1n-11	1.16 ± 0.085	1.00 ± 0.187
22:1n-9	0.20 ± 0.009	0.16 ± 0.012
R22:1	5.74 ± 0.266	6.17 ± 0.881
22:1n-7	0.04 ± 0.002	0.02 ± 0.003
22:2n-6	0.00 ± 0.001	0.00 ± 0.001
21:5n-3	0.47 ± 0.007	0.38 ± 0.019
22:4n-6	0.12 ± 0.010	0.10 ± 0.013
22:5n-6	0.12 ± 0.005	0.10 ± 0.010
22:4n-3	0.07 ± 0.003	0.05 ± 0.005
22:5n-3	5.26 ± 0.127	4.13 ± 0.337
22:6n-3	9.40 ± 0.248	7.44 ± 0.425
24:1	0.14 ± 0.005	0.09 ± 0.01

Table 8. Comparison of body composition of harbor seals sampled in southcentral and southeast Prince William Sound, June 1997 and 1998, as determined by isotope dilution (n = 59).

Age Group	Mass (kg)	%Body Water	% Body Protein	%Body Fat
1998				
Pups (n = 14)	28.4 ± 0.71	45.1 ± 1.37	14.2 ± 0..58	39.1 ± 2.01
Yearlings (n = 15)	33.6 ± 0.72	53.3 ± 0.61	17.6 ± 0.25	27.0 ± 0
2 yr old (n = 3)	41.1 ± 0.12	54.2 ± 1.89	18.0 ± 0.79	25.7 ± 2.76
Subadult (n = 2)	39.9 ± 4.10	56.0 ± 3.49	18.8 ± 1.47	23.1 ± 5.12
1997				
Pups (n = 12)	31.8 ± 0.97	42.7 ± 0.56	13.2 ± 0.24	42.6 ± 0.82
Yearlings (n = 6)	37.7 ± 1.04	56.0 ± 0.59	18.8 ± 0.25	23.1 ± 0.87
2-3 yr old (n = 2)	43.4 ± 2.75	57.8 ± 1.07	19.5 ± 0.45	20.5 ± 1.56
Subadult (n = 5)	41.5 ± 1.50	59.6 ± 1.76	20.3 ± 0.74	17.8 ± 2.58

Table 9. Mean initial estimated contributions (%) of prey fatty acid signatures to harbor seal diet signatures in PWS.

Year	Age	n	Capelin	Eulachon	Flatfish[1]	Herring/ Pollock/ Sandlance[2]	Octopus	Pink salmon (adults)	Pink salmon (smolts)	Rainbow smelt[3]	Shrimp	Squid
1977	Adult	3	0.0	6.5	25.4	31.8	0.0	1.7	11.8	22.0	0.0	0.9
1977	Yearling	1	0.0	24.2	34.6	34.8	0.0	0.0	0.0	6.4	0.0	0.0
1989	Adult	4	0.0	1.8	23.1	55.4	0.0	2.8	3.4	13.1	0.0	0.5
1994	Adult	14	0.0	5.3	34.9	47.7	0.0	0.3	1.1	8.9	0.0	1.7
1994	Halfyear	5	0.0	15.2	40.3	31.6	0.0	0.0	0.0	12.9	0.0	0.0
1995	Adult	14	0.5	6.9	30.2	50.8	0.0	0.7	1.6	8.2	0.0	1.1
1995	Yearling	1	0.0	0.3	39.0	54.2	0.0	0.0	0.0	6.4	0.0	0.0
1995	Halfyear	2	0.0	24.0	29.4	37.1	0.0	0.0	0.0	9.6	0.0	0.0
1996	Adult	42	0.0	10.0	28.2	53.8	0.3	0.4	0.9	5.4	0.0	0.9
1996	Yearling	4	0.0	12.3	32.8	44.7	0.0	0.0	0.0	10.2	0.0	0.0
1996	Halfyear	8	0.0	19.0	34.2	38.1	0.0	0.0	0.0	8.8	0.0	0.0
1997	Adult	11	0.0	19.5	24.5	47.1	0.0	1.6	0.0	7.3	0.0	0.0
1997	Yearling	7	0.0	29.5	23.7	46.0	0.0	0.0	0.0	0.8	0.0	0.0
1998	Adult	18	0.0	15.0	21.7	56.1	0.0	2.6	0.1	3.8	0.0	0.7
1998	Yearling	16	0.0	10.0	26.5	62.3	0.0	0.0	0.0	1.2	0.0	0.1

NW-PWS seals excluded. Species of n = 1 not included in model; see Table 1 for species included but not detected.

[1] Flatfish identified primarily as yellowfin sole, although may contain some flathead sole and rex sole.

[2] Current model (using composite prey averages) not yet distinguishing well enough between PWS herring, pollock and sandlance; however, the largest proportion appears to be herring, followed by sandlance; pollock appears to be minor.

[3] Only n = 4 individuals in prey base, hence the degree to which these represent the species is unknown.

Table 10. Mean initial illustrative diets of harbor seals in PWS derived from fatty acid signatures.

						Herring/ Pollock/		Pink salmon		Rainbow		
Year	Age	n	Capelin	Eulachon	Flatfish[1]	Sandlance[2]	Octopus	(adults)	(smolts)	smelt[3]	Shrimp	Squid
1977	Adult	3	0.0	1.0	24.3	21.2	0.0	1.5	33.8	17.5	0.0	0.7
1977	Yearling	1	0.0	5.6	50.9	35.7	0.0	0.0	0.0	7.8	0.0	0.0
1989	Adult	4	0.0	0.3	26.9	44.9	0.0	2.8	11.9	12.7	0.0	0.4
1994	Adult	14	0.0	1.0	42.8	40.8	0.0	0.3	4.2	9.1	0.0	1.7
1994	Halfyear	5	0.0	3.2	53.4	29.2	0.0	0.0	0.0	14.2	0.0	0.0
1995	Adult	14	1.0	1.4	37.4	43.9	0.0	0.7	6.1	8.5	0.0	1.1
1995	Yearling	1	0.0	0.1	47.4	46.0	0.0	0.0	0.0	6.5	0.0	0.0
1995	Halfyear	2	0.0	5.6	43.8	38.6	0.0	0.0	0.0	11.9	0.0	0.0
1996	Adult	42	0.0	2.1	36.8	49.0	1.1	0.4	3.6	5.9	0.0	1.0
1996	Yearling	4	0.0	2.6	44.1	41.9	0.0	0.0	0.0	11.4	0.0	0.0
1996	Halfyear	8	0.0	4.2	48.1	37.4	0.0	0.0	0.0	10.3	0.0	0.0
1997	Adult	11	0.0	4.5	36.1	48.4	0.0	2.1	0.0	8.9	0.0	0.0
1997	Yearling	7	0.0	7.6	38.8	52.5	0.0	0.0	0.0	1.0	0.0	0.0
1998	Adult	18	0.0	3.4	31.2	56.3	0.0	3.3	0.3	4.6	0.0	0.9
1998	Yearling	16	0.0	2.2	36.5	59.9	0.0	0.0	0.0	1.4	0.0	0.1

Estimated diets calculated from fatty acid signature model (Table 9) and relative fat contents of prey (Table 1). NW-PWS seals excluded.

[1] Flatfish identified primarily as yellowfin sole, although may contain some flathead sole and rex sole.

[2] Current model (using composite prey averages) not yet distinguishing well enough between PWS herring, pollock and sandlance; however, the largest proportion appears to be herring, followed by sandlance, pollock appears to be minor.

[3] Only n = 4 individuals in prey base, hence the degree to which these represent the species is unknown.

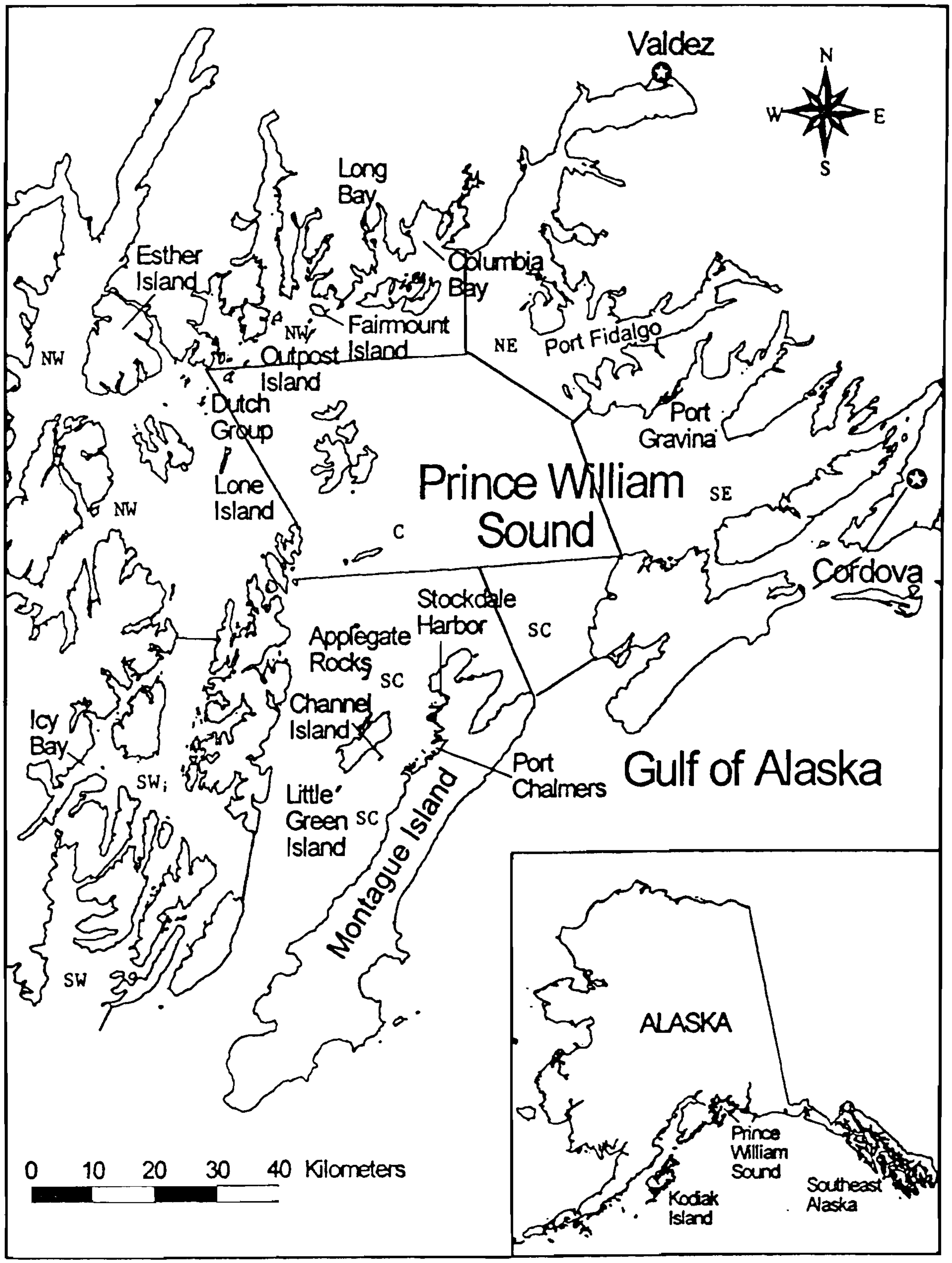


Figure 1. Prince William Sound (PWS), Alaska, showing major locations of harbor seals and prey sampled. General locations are indicated by boundary markers which coincide with fisheries zones.

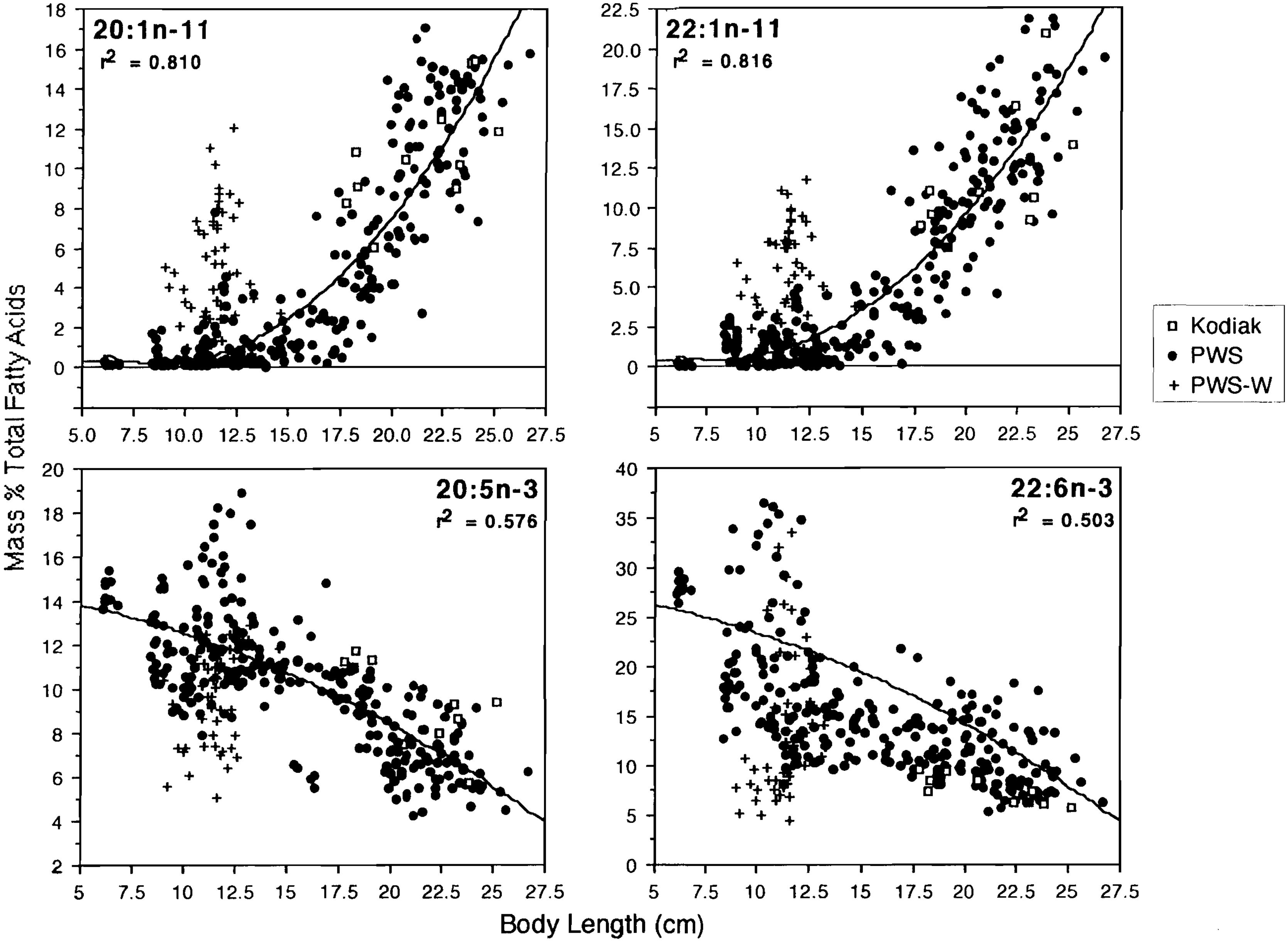
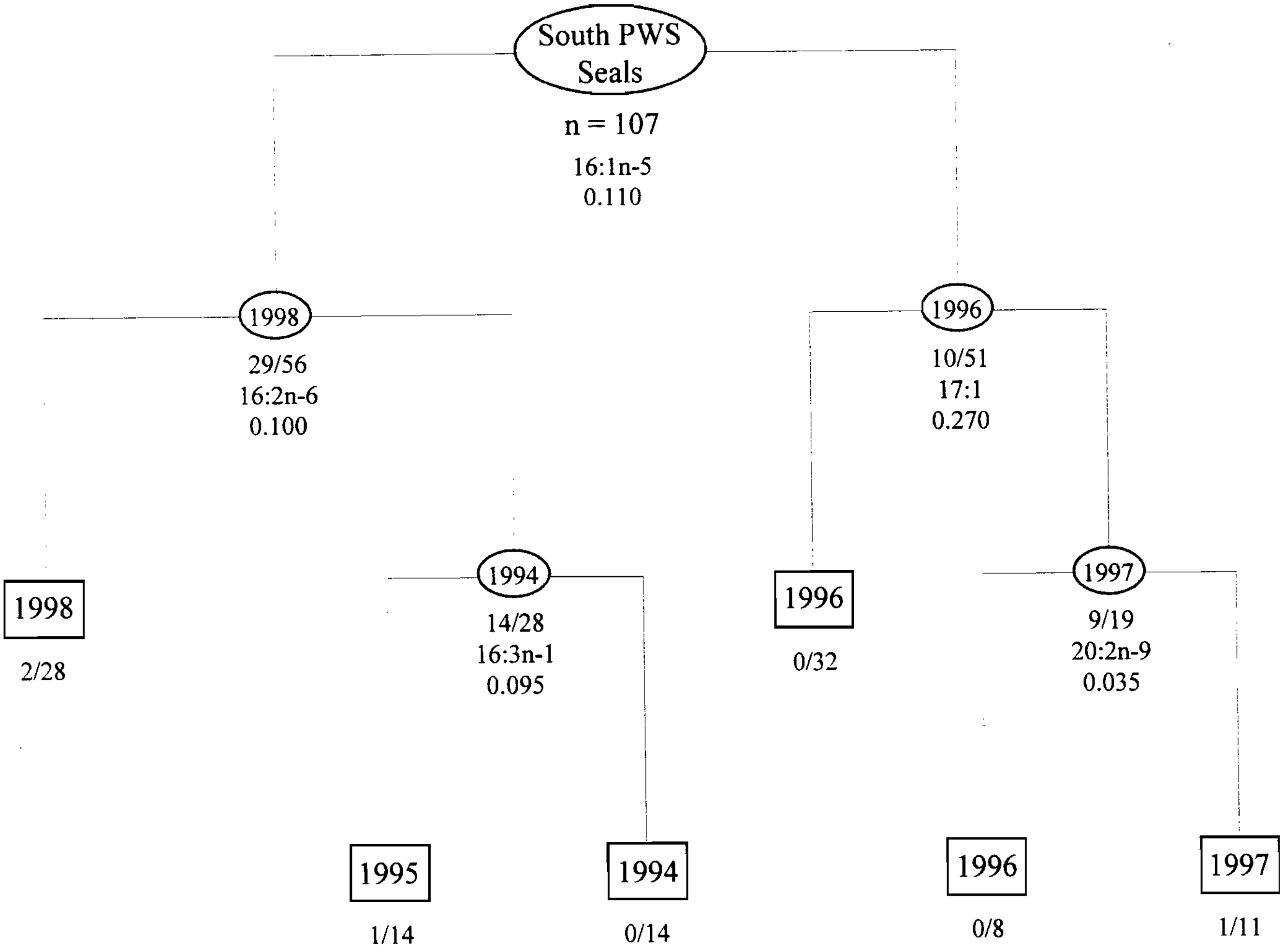
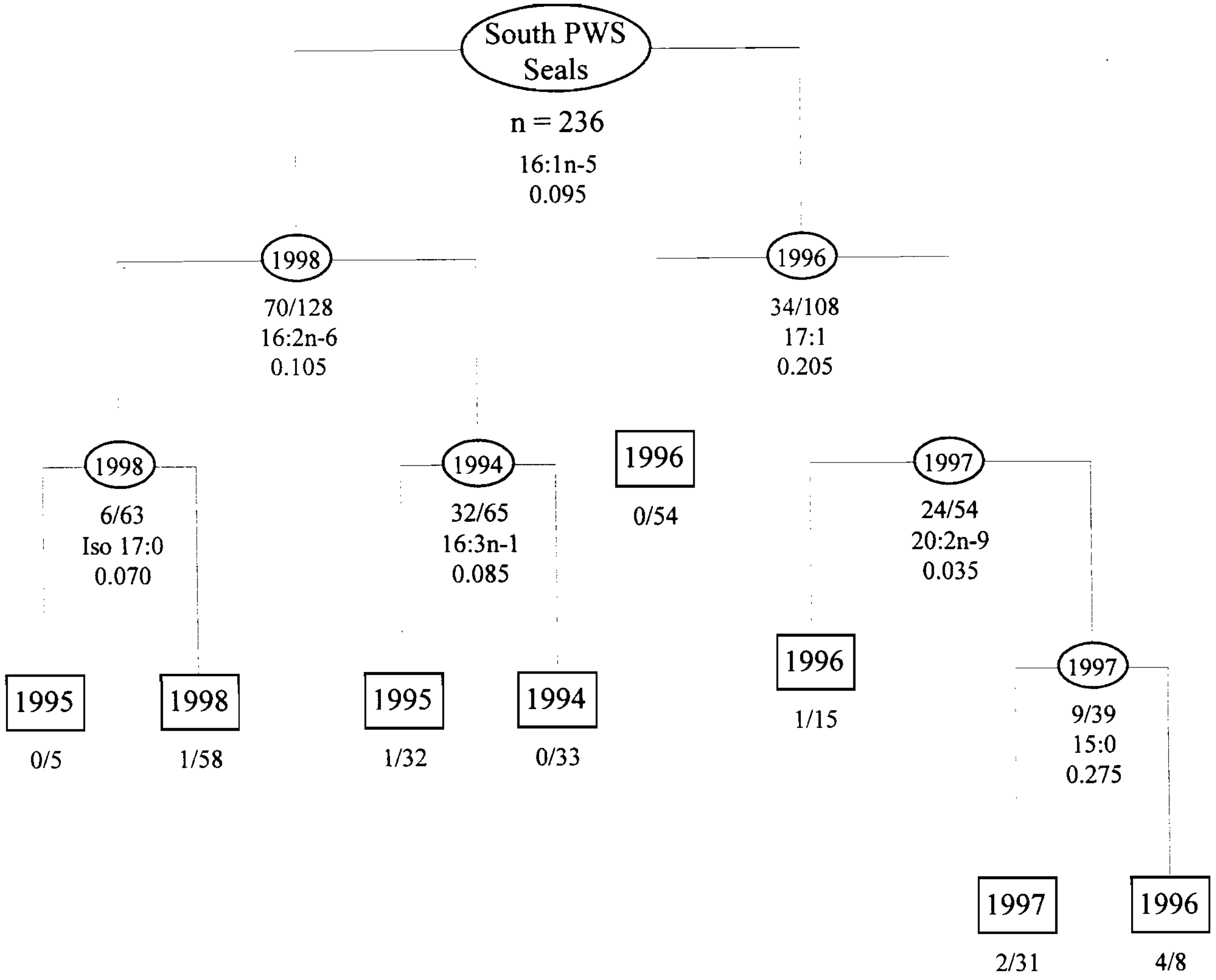


Figure 2. Variation in four selected fatty acids in herring (n = 332) as a function of body length. Herring from northwestern PWS (PWS-W) are excluded from regression equations ($P < 0.0001$ for all). Data are across all seasons and years 1994-1998; however variability is primarily explained by size class (e.g., see Iverson et al. 1998).



Summary	correct/total	% correctly classified
1994	14/14	100%
1995	13/14	92.9%
1996	40/42	95.2%
1997	10/10	100%
1998	26/27	96.3%
Total	103/107	96.3%
Misclassified	4	

Figure 3: Classification tree of adult Harbor Seals from South (SC & SE) PWS by year.



Summary	correct/total	% correctly classified
1994	33/33	100%
1995	36/37	97.3%
1996	72/74	97.3%
1997	29/30	96.7%
1998	57/62	91.9%
Total	227/236	96.2%
Misclassified	9	

Figure 4: Classification tree of all Harbor Seals (*ie*. Adults, subadults, yearlings and half-year olds) from South (SC & SE) PWS by year.

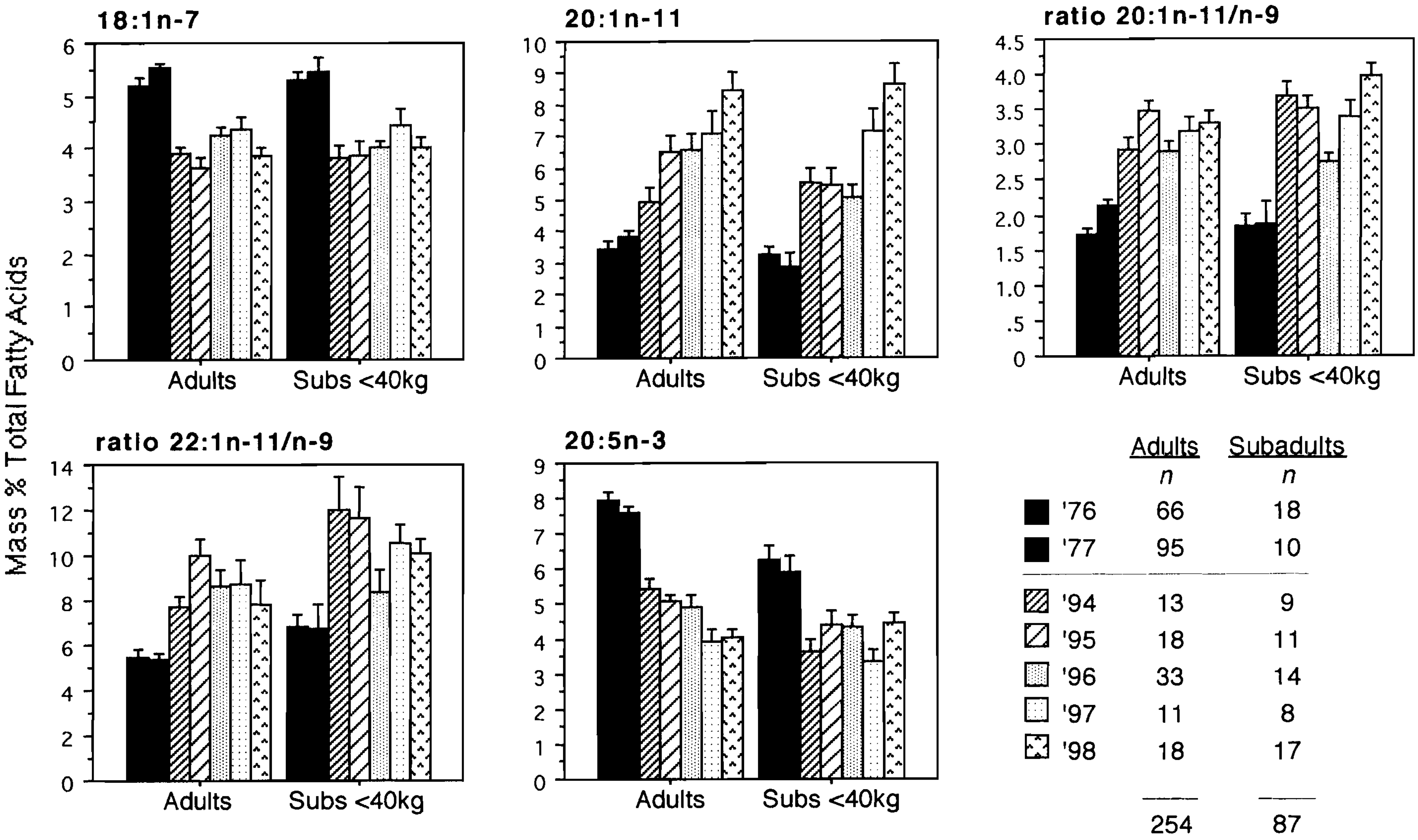
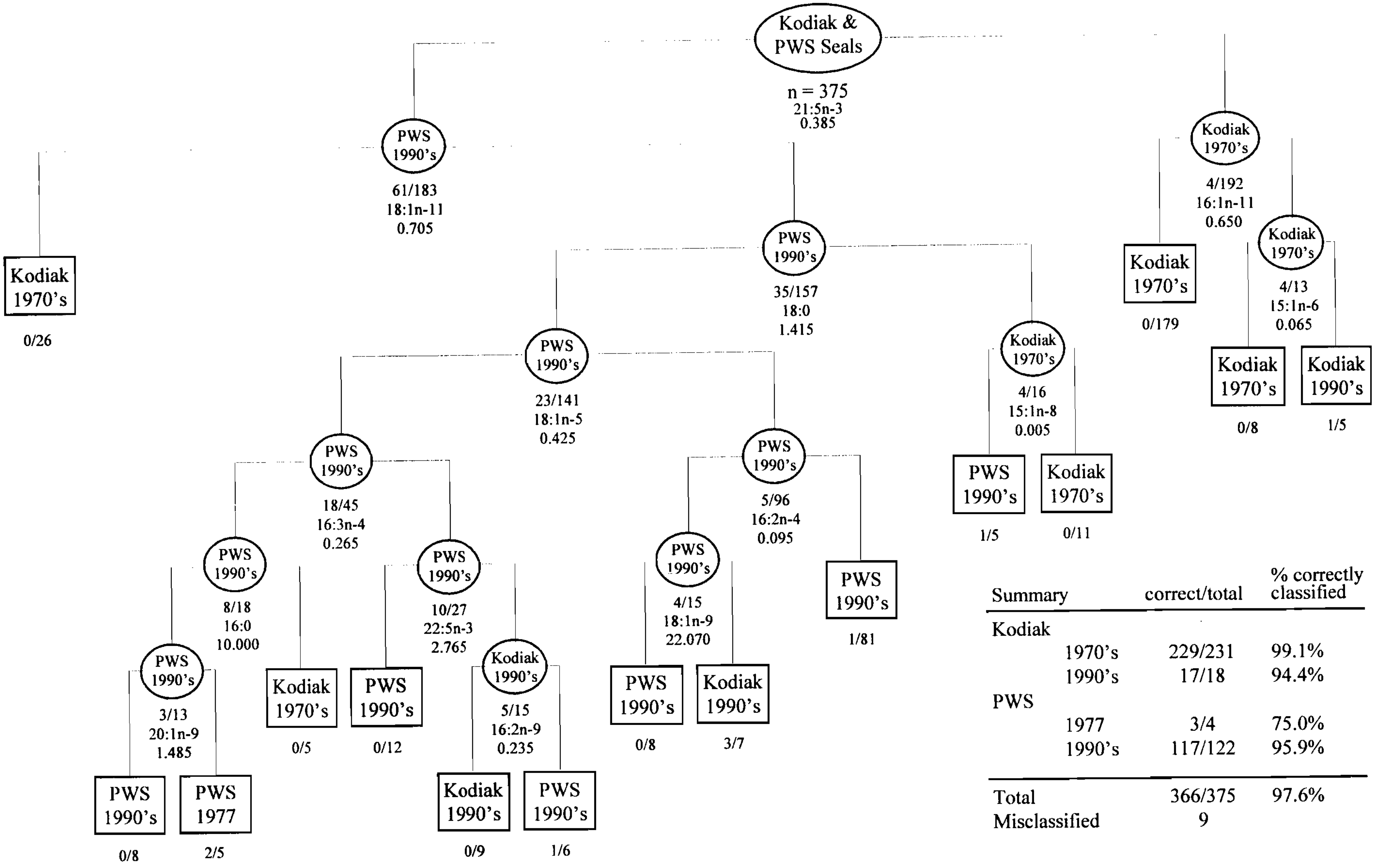


Figure 5. Variation in selected fatty acids in habor seal blubber (n = 341) sampled in south central PWS and Kodiak Island areas in the late 1970's and during the mid 1990's. Year differences were found for all components ($P < 0.0001$; in general 1976 and 1977 differed from 1994-1998); differences between adults and subadults that were less than 40 kg body mass were found for ratio 20:1n-11/n-9 ($P = 0.050$), and ratio 22:1n-11/n-9 and 20:5n-3 ($P < 0.0001$; 2-way ANOVA).



Summary		correct/total	% correctly classified
Kodiak			
	1970's	229/231	99.1%
	1990's	17/18	94.4%
PWS			
	1977	3/4	75.0%
	1990's	117/122	95.9%
Total		366/375	97.6%
Misclassified		9	

Figure 6: Classification tree of all Harbor Seals (excluding pups) from the Kodiak Island area and PWS in the 1970's and 1990's.

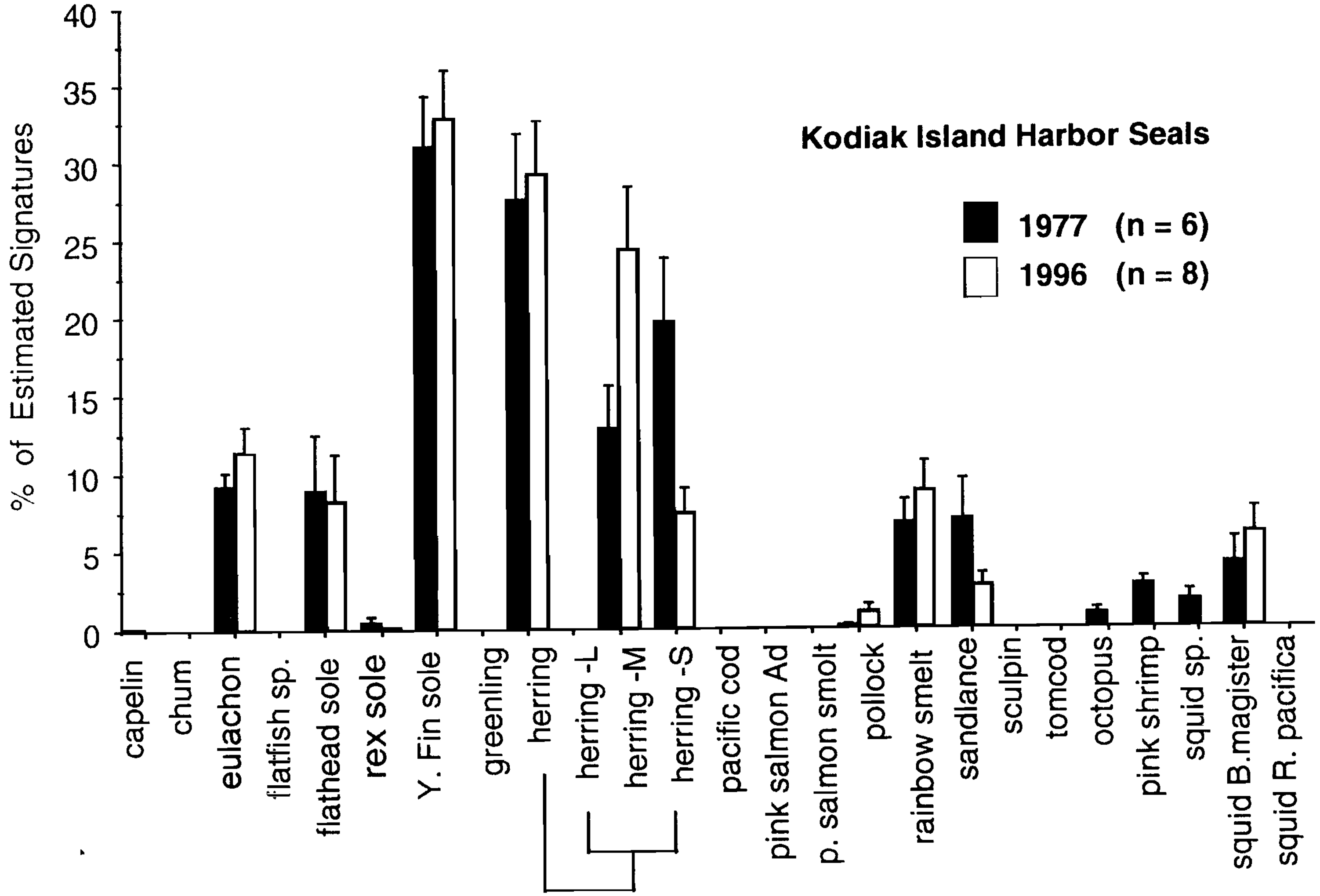


Figure 7. Initial estimated contributions of prey fatty acid signatures to harbor seal diets (n = 14) at Kodiak Island during two decades. Results averaged from several models. Herring represents the sum of herring-L + herring-M + herring-S.

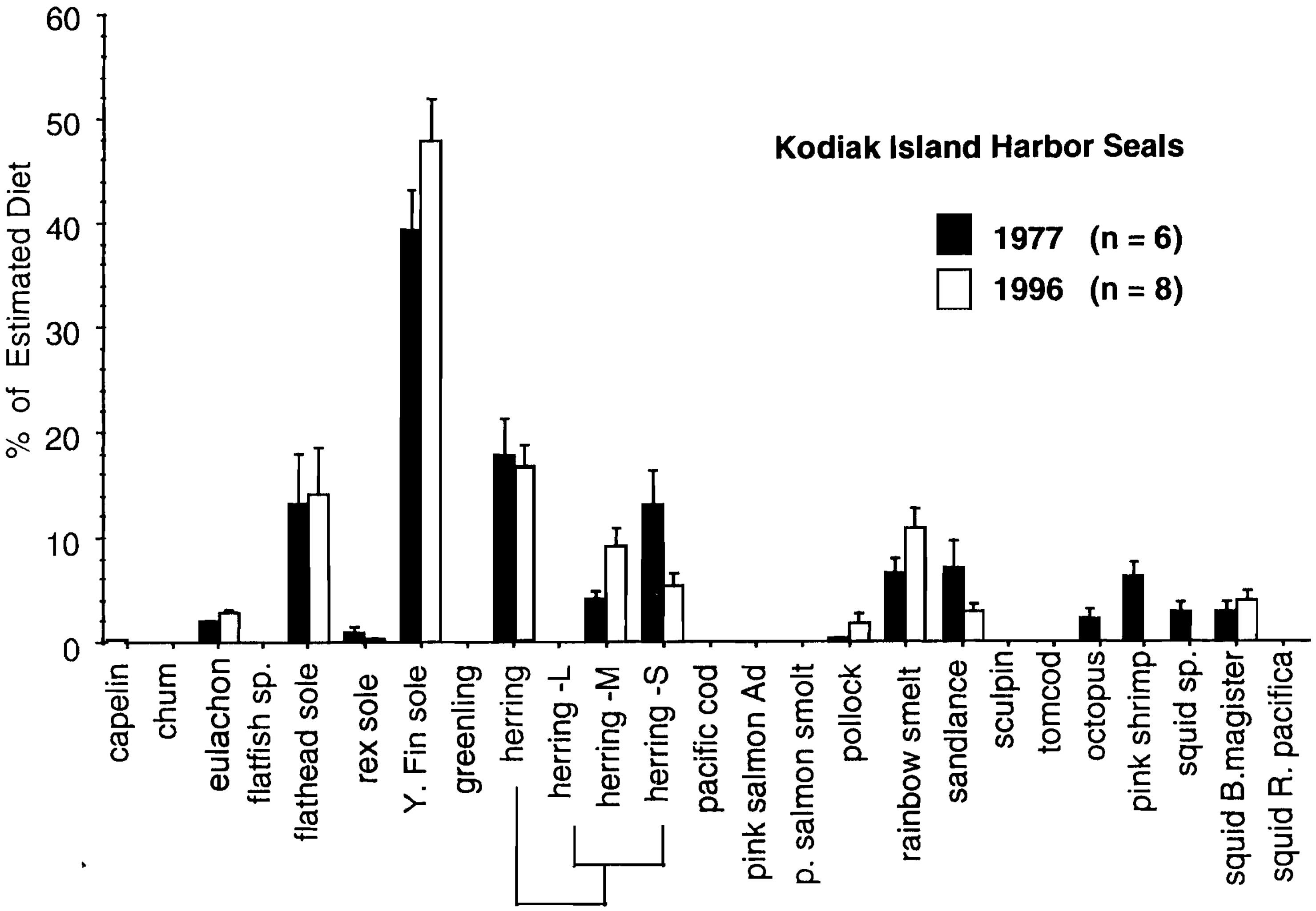


Figure 8. Initial illustrative and estimated diets of of harbor seals (n = 14) at Kodiak Island during two decades. Results averaged from several models. Herring represents the sum of herring-L + herring-M + herring-S. Estimated diets calculated from fatty acid signature modeling and relative fat contents of prey (Table 1).

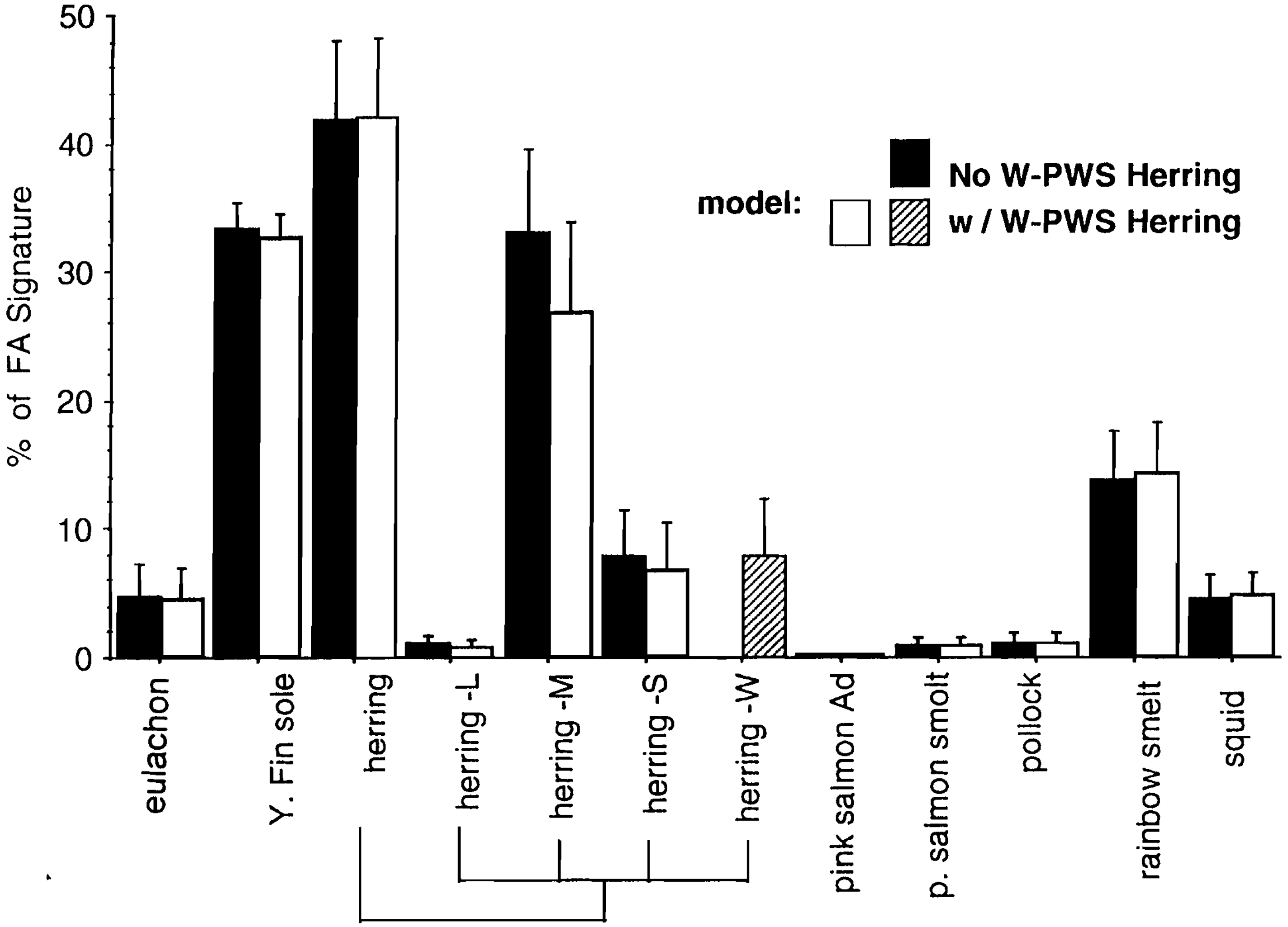


Figure 9. Initial estimated contributions of prey fatty acid signatures to harbor seal diets (n = 11) in NW-PWS. Results are from two models: one includes no herring from NW-PWS in data base; the second includes herring from NW-PWS as a separate category of herring. Herring represents the sum of herring-L + herring-M + herring-S + herring-W.

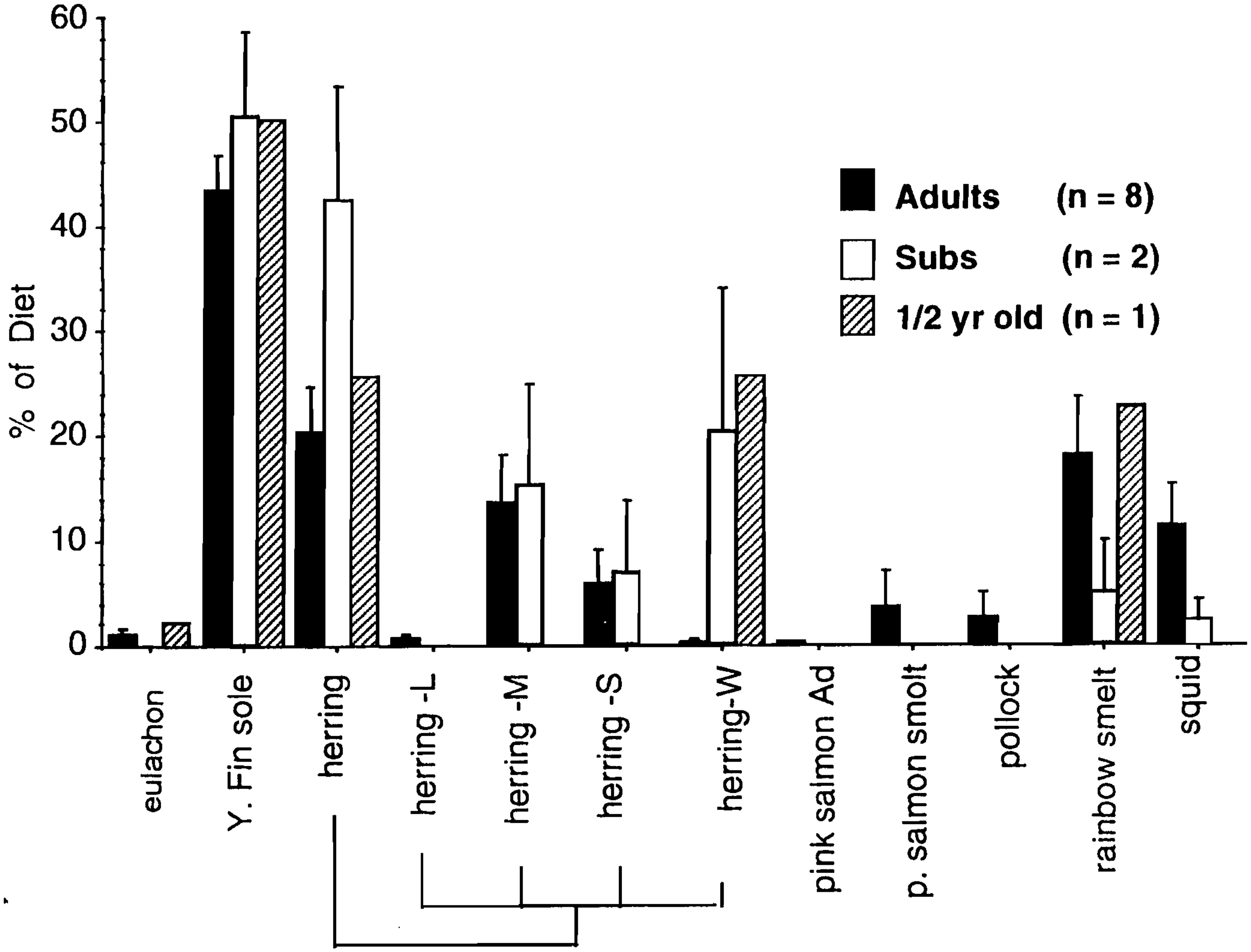


Figure 10. Initial illustrative and estimated diets of harbor seals (n = 11) in NW-PWS. Results are the model that includes herring from NW-PWS as a separate category of herring. Herring represents the sum of herring-L + herring-M + herring-S + herring-W. Estimated diets calculated from fatty acid signature modeling and relative fat contents of prey (Table 1).

CHAPTER FOUR

BAYESIAN HIERARCHICAL MODELS FOR ESTIMATING HARBOR SEAL TRENDS IN PRINCE WILLIAM SOUND, ALASKA

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OBJECTIVE 1

Monitor the abundance and trends of harbor seals at trend count sites in oiled and unoiled areas of PWS to determine whether the PWS harbor seal population has declined, stabilized, or increased since the EVOS.

This report to be cited as:

Ver Hoef, J. M. and K. J. Frost. 1999. Bayesian hierarchical models for estimating harbor seal trends in Prince William Sound, Alaska. Pages 104 -125 *in* Monitoring, habitat use, and trophic interactions of harbor seals in Prince William Sound, Alaska. Annual Report to the *Exxon Valdez* Oil Spill Trustee Council. Restoration Study 98064. Alaska Department of Fish and Game, Division of Wildlife Conservation, Fairbanks, AK.

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ABSTRACT

Bayesian hierarchical models were used to assess trends of harbor seals, *Phoca vitulina richardsi*, in Prince William Sound, Alaska, following the 1989 *Exxon Valdez* oil spill. Data consisted of 4-10 replicate observations per year at 25 sites over 12 years. In previous work, Poisson regression was used to adjust counts to a standardized date, time of day, and time relative to low tide. Then linear regression was used to assess trend for the adjusted counts. The whole procedure was bootstrapped to assess significance of trends. We found several problems with this method. First, the number of estimated parameters was very large. Second, we wished to develop models for each site, but it was difficult to combine trend estimates from each site into an overall assessment of trend. The Bayesian hierarchical model helped solve these problems by using a Poisson regression model for each of the 25 sites, where the mean of the Poisson distribution depended on the factors: 1) year, 2) time of year, 3) time of day, and 4) time relative to low tide. Then, the 25 site parameters for each factor in the Poisson mean were given a normal distribution. Results showed that at most sites, 1) counts decreased yearly, 2) counts decreased throughout August and September, 3) counts decreased throughout the day, and 4) counts were at a maximum just a few minutes before low tide; however, there was considerable variation among sites. To get overall trend we used a weighted average of the trend at each site, where the weights depended on the overall abundance of a site. The overall trend indicated a continued significant decrease in the harbor seal population. Comparison of methods showed similar parameter estimates, but the Bayesian hierarchical model allowed more flexible use of trend indices in a single statistical framework.

Key words: aerial surveys, *Exxon Valdez* oil spill, generalized linear model, harbor seal, *Phoca vitulina richardsi*, Poisson regression, population monitoring, Prince William Sound, trend analysis

INTRODUCTION

Monitoring programs to track long-term changes in population size are important for applied ecological studies. There are often several statistical methods to analyze such data. One of the most fundamental differences among statistical methods occurs when making a choice between Bayesian and classical (frequentist) methods. While there are strong philosophical differences, in practice results can be quite similar, and the choice can be made on practical considerations. In this paper we develop Bayesian hierarchical models for Poisson regression, along with its classical counterpart, and show that the Bayesian approach gives similar results on individual sites but has considerably more flexibility for combining sites.

Harbor seals (*Phoca vitulina richardsi*) are one of the most common marine mammal species in Prince William Sound (PWS), Alaska, and adjacent parts of the Gulf of Alaska. PWS has over 4,800 km of coastline, consisting of many fiords, bays, islands, and offshore rocks. The exact number of harbor seals inhabiting the region is unknown, but is at least several thousand (Hill and DeMaster 1998). Between 1984 and 1988 the number of seals counted at haulout sites in eastern and central PWS declined by about 40% (Frost et al. 1994a). Subsequent to the *Exxon Valdez* oil spill as part of damage assessment and restoration science studies programs, monitoring of the harbor seal population was continued by flying aerial surveys during 1990-1998.

Many studies have demonstrated effects of time of day, date, and tide on the hauling out behavior of harbor seals (Schneider and Payne 1983, Stewart 1984, Harvey 1987, Pauli and Terhune 1987, Yochem *et al.* 1987, Thompson and Harwood 1990, Moss 1992). The data to describe those behavioral patterns has usually come from continuous or repetitive visual observations of seal haulouts, or from telemetry studies. Information derived from such studies has been used in the design of harbor seal surveys, to the extent that survey programs are generally designed to occur on dates and at times when the greatest number of seals is expected to be out of the water and available for counting (Pitcher 1990, Harvey *et al.* 1990, Olesiuk *et al* 1990, Huber 1995). However, once a "survey window" has been established counts have usually been treated as replicates during analyses, and the possible effects of other factors on annual abundance estimates have been ignored.

This paper presents an analysis of aerial survey counts of harbor seals in PWS. The objectives are to develop Bayesian hierarchical models to: 1) estimate trends at individual sites; 2) estimate trends in the study area as a whole; and 3) compare Bayesian results to classical methods of Poisson regression.

METHODS

Aerial Surveys

We conducted aerial surveys along a trend count route that covered 25 harbor seal haulout sites in eastern and central PWS (see Chapter 1, Figure 1). The route included 7 sites that were substantially affected by the *Exxon Valdez* oil spill and 18 unoiled sites that were outside of the primary affected area (Frost *et al.* 1994a). Surveys were flown during the molting period (August-September) in 1984 and 1988-1998.

Visual counts of seals were conducted from a single-engine fixed-wing aircraft (Cessna 185) at altitudes of 200-300 m, usually with the aid of 7-power binoculars. Counts were usually conducted from two hours before low tide to two hours after low tide. A survey normally included counts at all 25 sites, but occasionally some sites could not be counted because of poor weather or a rapidly rising tide. For each survey the date, time and height of low tide, and time of sunrise and sunset were recorded. Each site was circled until the observer was confident that an accurate count had been made, and the time of the count was recorded. For larger groups of seals (generally those of 40 or more) color photographs were taken using a hand-held 35-mm camera, and seals were counted from images projected on a white surface. Each year several survey flights, usually 7-10, were made. The total number of counts for all sites and all years exceeds 2,000.

Prior to further data analysis, the covariates: date, time of day, and time relative to low tide were standardized by subtracting the mean and dividing by the standard deviation. For this preliminary analysis, the effect of year was standardized by setting 1993 as year 0. In the future, year may be centered differently. Specifically, the covariates were adjusted as follows:

$\text{Year}_{\text{std}} = \text{Year} - 1993$
$\text{Date}_{\text{std}} = (\text{Date} - 28.84\ \text{min})/7.56\ \text{min}$
$\text{Time-of-day}_{\text{std}} = (\text{Time-of-day} - 755.88\ \text{min})/200.60\ \text{min}$
$\text{Time-relative-to-low-tide}_{\text{std}} = (\text{Time-relative-to-low-tide} + 1.99\ \text{min})/61.24\ \text{min}$

Previous Methods – Poisson Regression for All Sites Combined

Frost *et al.* (1999) used a generalized linear model (McCullagh and Nelder 1989) with a log link function and a Poisson distribution to analyze the factors that may affect the number of seals hauled out and available to be counted during surveys. The model may be written as: $\Pr(Z_{tij} = z) = \exp(-\lambda_{tij})\lambda_{tij}^{z}/z!$ with $ln(\lambda_{tij}) = \beta'\mathbf{x}_{tij}$ where β is a parameter vector and $\mathbf{x}_{tij}$ is a vector containing information on the state of covariates: year, site, time of tide, height of tide, time of day, date for the j^{th} flight at site i in year t. Loglikelihood ratios were used to obtain a parsimonious model. Then the count data were adjusted to a standardized set of covariates. The adjusted counts were the expected counts at each site for each year as if each was made under optimal conditions. Next, to assess overall trend, linear regression and Poisson regression models were fitted to the adjusted yearly count estimates. The analysis of Frost *et al.* (1999) was complicated because they first adjusted yearly counts for each site to a standardized date, time of day, and time relative to low tide, then summed over sites to get a yearly index, and then used the index in a trend regression analysis. Under these circumstances, it is difficult to pass the uncertainty associated with adjusting the counts to the trend analysis. Therefore, they used bootstrap methods (Efron and Tibshirani 1993, Manly 1997) for the whole procedure.

Poisson Regression for Sites Separately

One of the goals of the study was to allow separate analyses of sites after sufficient data were collected. A separate Poisson regression model can be developed for each site. Most sites had 80–90 observations from all years. The model developed for each site was $\Pr(Z_{tij} = z) = \exp(-\lambda_{tij})\lambda_{tij}^{z}/z!$ with $ln(\lambda_{tij}) = \beta_i'\mathbf{x}_{tij}$ where β_i is a parameter vector for the ith location, and $\mathbf{x}_{tij}$ is a vector containing information on the state of covariates: year, site, time of tide, height of tide, time of day, date for the j^{th} flight at site i in year t. The difference between this model and the Poisson regression for all sites combined is that, here, each site has its own response to year and the other factors: time of year, time of day, time of tide, and height of tide. Now, we no longer need to sum the sites by location parameters to get trend, but it is more difficult to combine the trend parameters from each site.

Bayesian Hierarchical Model

The hierarchical Bayesian model begins with Poisson regression for each site separately. Write $f(Z_{tij}) = \exp(-\lambda_{tij})\lambda_{tij}^{z} / z!$ with $ln(\lambda_{tij}) = \beta_i'\mathbf{x}_{tij}$, and assuming independence, then jointly

$$f(\mathbf{z}|\ \beta_1,\ldots,\beta_{25}) \equiv \Pi f(Z_{tij}).$$

Let β_{pi} be the pth component of the vector β_i. For this study, we have the following parameters for the ith site,

β_{0i} = intercept
β_{1i} = year
β_{2i} = date
β_{3i} = $(\text{date})^2$
β_{4i} = time of day
β_{5i} = $(\text{time of day})^2$
β_{6i} = time relative to low tide
β_{7i} = $(\text{time relative to low tide})^2$

In the next level of the hierarchy, we will give the parameters for each factor a distribution: where

$$f(\beta_{p,1}, \ldots, \beta_{p,25} \mid \mu_p, \sigma_p^2)$$

for $p = 0, 1, \ldots, 7$,and the result is a normal distribution with mean μ_p and variance σ_p^2. In the third and final level of the hierarchy, we give noninformative prior distributions: $f(\mu_p)$ is a normal distribution with mean 0 and variance 1,000,000 and $f(\sigma_p^2)$ is a gamma distribution with parameters 0.001 and 0.001. Using this setup, Bayes theorem allows us to write the posterior distribution:

$$f(\beta_1,\ldots,\beta_{25}, \mu_1, \ldots,\mu_7, \sigma_1^2, \ldots, \sigma_7^2|\ \mathbf{z}) \propto f(\mathbf{z}|\ \beta_1,\ldots,\beta_{25})\Pi f(\beta_{p,1}, \ldots, \beta_{p,25} \mid \mu_p, \sigma_p^2) f(\mu_p) f(\sigma_p^2)$$

It is difficult to obtain an analytical solution to the above equation; however the modern techniques of Markov Chain Monte Carlo (MCMC, see e.g. Gilks *et al.* 1996) allow us to obtain samples from the posterior distribution. From these samples we can compute functions and summaries of the posterior distribution, such as expectation, standard errors, quantiles, etc. The resulting tables use covariates on their standardized scale, but the figures show the effects back on the original scale. Standardizing the covariates helps to stabilize the Markov Chain Monte Carlo methods.

From the posterior distribution, several parameters have particular interest. The parameters $\beta_{1,1}, \ldots, \beta_{1,25}$ are the slope parameters for all 25 sites, and μ_p is their mean, which is an overall indication of trend among all sites. However, μ_p is not entirely satisfactory because it weights all sites equally (actually, it depends on their sample sizes – in this study, they are all relatively equal). In order to give sites with greater abundance more weight, we can consider the following:

$$\tau_1 = \frac{\sum_{i=1}^{25} \beta_{0i}\beta_{1i}}{\sum_{i=1}^{25} \beta_{0i}}$$

In fact, we can compute τ_p for any of the coefficients β_{pi}. The beauty of the hierarchical Bayes method using MCMC is that we can make inference on τ_p very easily – we simply use the samples from the posterior distributions of β_{0i} and β_{pi} to compute the posterior distribution of τ_p.

The statistical package SPLUS was used to do Poisson regression, and the statistical package BUGS was used for the Bayesian hierarchical model. For the MCMC, we let the chain "burn in" for 10,000 samples, and then computed the means, standard errors, and percentiles based on the next 10,000 simulations. We started the chain from several different points and obtained very similar results, and examination of the trace of the chain did not reveal any irregularities. Typically the autocorrelation for each parameter dropped to near zero after 30 iterations.

RESULTS

Comparison of Bayesian Hierarchical Model to Classical Poisson Regression

From previous work (Frost *et al.* 1999), four primary factors significantly affected the counts of seals during aerial survey: year, date, time of day, and time of count relative to low tide. These four factors we used in all site specific models. Using Poisson regression for each site separately, we obtained the parameter estimates given in Table 1. The parameter estimates divided by their standard errors are given in Table 2. The values in Table 2 can be compared to values from a standard normal distribution to assess the importance of the factor in the model. In this paper we focus on the Bayesian hierarchical models, but we provide Tables 1 and 2 for comparison to the Bayesian hierarchical models.

All β parameter estimates using the Bayesian hierarchical model are given in Table 3, and the parameter estimates divided by their standard errors are given in Table 4. It is apparent when comparing Tables 1 to 3, and when comparing Tables 2 to 4, that the Bayesian hierarchical model estimates and inferences are very similar to Poisson regression.

Estimates for each Site Separately

Figure 1 shows the fitted trend model for each site, along with the raw values. The raw values are not corrected for the state of the other covariates, so we should expect some lack of fit. Nevertheless, it appears that a single coefficient for trend may not be sufficient, especially for sites 4, 16, and 18. Some values above 200 are cut off in order to make the graph more readable. As seen from Table 3 and 4, most sites have had significant decreasing trends, but there is some variation. The most drastic decrease occurred at location 1, which experienced a proportional change of exp(-0.4845) = 0.616, or almost a 40% per year decline. On the other hand, site 25 experienced a proportional change of exp(0.0242)=1.024, or about a 2% per year increase. Most sites experienced significant change, but no change was detectable at sites 3, 19, and 23, at $\alpha = 0.05$ (Table 4).

Graphical depiction of the effect of date at each site is given in Fig. 2. The date effect has two parameters, including a date^2 effect. There are a variety of responses to date, with most sites showing decreasing counts with date, or some maximum count before or around late August. At a few sites, there appeared to be no significant effect of date (sites 14 and 21, see Table 4). The effect of time of day for all sites is given in Fig. 3. Again, there are a variety of responses, with most sites showing decreasing counts with time of day, or some maximum in early or midday Sites 4, 7, 11, and 20 showed no significant response to time of day, and several other sites had a weak response (Table 4). The effect of time relative to low tide is given in Fig. 4. There are a variety of responses, but the individual responses are mostly not as strong as seen for trend, date, or time of day (Table 4). Many sites do not show a significant effect.

Estimates for Site Combined

Table 5 shows the parameter estimates and 95% credibility intervals for μ_p, for $p = 0, 1, \ldots, 7$. Table 6 shows the parameter estimates and 95% credibility intervals for τ_p, for $p = 1, 2, \ldots, 7$. Graphical depiction of the effects of year, date, time of day, and time relative to low tide are given in Fig. 5. From Table 5, there is, on average, a decrease of exp(-0.128) = 0.88, or about a 12% per year for the unweighted mean, and from Table 6 a decrease of exp(-0.079) = 0.92 or about 8 % per year if we give more weight to larger sites. From Table 5, the date for counting the most seals, averaged over all sites, is 30 August; from Table 6 the date for counting the most seals, where larger sites get more weight, is 20 August. The fitted model for the effect of date on the proportional change in counts is depicted in Fig. 5. From Table 5, the time of day for counting the most seals, averaged over all sites, is shortly after 9:00 AM; from Table 6 the time of day for counting the most seals, where larger sites get more weight, is shortly before 8:00 AM. The fitted model for the effect of time of day on the proportional change in counts is depicted in Fig. 5. From Table 5, the time relative to low tide for counting the most seals, averaged over all sites, is ½ minute before low tide; from Table 6 the time relative to low tide for counting the most seals, where larger sites get more weight, is 7 ½ minutes before low tide. The fitted model for the effect of time relative to low tide on the proportional change in counts is depicted in Fig. 5.

DISCUSSION

Comparison of Bayesian Hierarchical Model to Classical Poisson Regression

As mentioned in the introduction, there has often been acrimonious debate over whether or not to use Bayesian methods. The main objection to Bayesian methods is the specification of a prior distribution, which can allow prior knowledge or belief to enter into an analysis, and some feel this lacks objectivity. However, the use of very flat, vague priors, as we have done in this study, removes the influence of the prior. Also, when there is a lot of data, the data overwhelms the prior. In fact, we tried priors with different values, and as long as the variance of the prior was large, the results were the same. Tables 1 – 4 also show that the use of Bayesian methods gives almost exactly the same inference as using more classical Poisson regression. However, from a practical standpoint, there are two very attractive features of the Bayesian hierarchical model: 1) because of the hierarchical structure, we can group parameters and make inferences on the groups as well as the individual parameters, and 2) it is easy to create functions of parameters (e.g., τ_p) and make inference on these functions (e.g., Table 6). Conceptually, the closest "non-Bayesian" analysis to the Bayesian hierarchical model would be the bootstrap. For example, bootstrap samples could be used to generate a distribution for all parameter estimates in Table 1. Using all of these estimates, we could form estimates and confidence intervals for τ_p. The strength of the bootstrap method is that it is quite free of assumptions; because the Bayesian hierarchical model specifies a distribution for the parameters, it should be more powerful if the model is valid.

Estimates for each Site Separately

Bayesian methods often produce an effect called "shrinkage." For example, notice from Table 5 that $\mu_0 = 2.215$. Shrinkage occurs because the β_{0i} parameters want to "shrink" back towards 2.215. The effect of shrinkage becomes stronger as parameter estimates get farther from the mean. Thus, in Table 3 that β_{01} for site 1 is estimated to be -0.0823 while in Table 1 site 1 β_{01} is estimated to be -0.1962. Likewise in Table 3, for site 11 $\beta_{0,11}$ is estimated to be -1.0220 while in Table 1 site $\beta_{0,11}$ is estimated to be -1.2288. Thus, we see a small shrinkage effect toward the mean. For most other sites and factors, there was little shrinkage because sample sizes were large and no sites had large deviations. Thus, Tables 1 and 3 are quite similar, as are Tables 2 and 4.

Estimates for Site Combined

There were some differences between μ_p and τ_p, as seen in Tables 5 and 6 and Fig. 5. For example, when it comes to individual seal biology such as response of hauling out to time of day or time relative to low tide, we see very little difference between μ_p and τ_p. However, when it comes to factors that may be affected by sex and age composition, namely total counts and changes by date, we see considerable differences between μ_p and τ_p if we weight the larger sites differently. Therefore, weighting can make a difference and be a useful measure. The weighting and standardization requires some discussion. We chose the "zero" year to be 1993, so weighting occurs relative to the abundance (β_{0i}) in 1993. By choosing a different year as the "zero" year, weighting would be different. For example, if 1984 were the "zero" year, then site 18 would get a larger weight than site 20, but if 1998 were the zero year, site 20 would get a larger weight than site 18.

Significance to Monitoring Studies

There are basically two ways to deal with the effect of covariates on monitoring harbor seals, or any other species. One would be to design the survey to avoid the effects of covariates. For example, if we could always survey on the same dates, at the same tide condition, the same time of day, etc., then these factors would not influence counts. Unfortunately, it is not possible to design such a sampling scheme because of the way date, tides, and weather vary. The other approach is to make adjustments or allowances for covariates. Poisson regression does this.

The significance of the Bayesian hierarchical model is that it allowed us to model each site separately, which is probably more biologically realistic than assuming that all sites respond the same to a covariate. The problem of how to then combine information from sites is solved by grouping covariate parameters and giving them a distribution in the hierarchical model. The PWS harbor seal data demonstrates the utility and flexibility of the Bayesian hierarchical model.

Future direction

The analyses reported in this chapter are preliminary. They were conducted primarily as a means to develop methods for applying Bayesian analysis to harbor seal survey data, not as a final trend analysis. For this reason data regarding the effects of covariates on counts, as well as estimates of rates of decline, should not be considered final. Until additional Bayesian analyses are conducted, results from the Poisson regression described in Chapter 1 should be used for trend analysis.

For this analysis, year was centered in 1993 (mid way in the dataset) and all trend data from 1984-1998 were included. The resulting estimate of an 8% annual rate of decline is much higher than the 2.5% annual decline estimated in Chapter 1, in large part because of the inclusion of counts made during 1984-1988. The Chapter 1 analysis includes only data from 1990-1998, when the rate of decline had slowed substantially. In future Bayesian analyses, the trend analysis will not include 1984-1989, and will be centered on a different manner. Future parameter estimates will also be calculated using only surveys conducted after 1990. For earlier surveys, variables such as time of count and time relative to low tide were interpolated estimates, and less accurate than the real-time data collected in recent years. It is likely that some of the apparent inconsistencies between analyses in the relationship of counts to date and time are due to the inclusion of these pre-1990 datasets.

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Table 1. Poisson regression parameter estimates for factors affecting counts of hauled out harbor seals in Prince William Sound.

Location i	β_{0i}	β_{1i}	β_{2i}	β_{3i}	β_{4i}	β_{5i}	β_{6i}	β_{7i}
1	-0.1962	-0.5185	1.2134	-0.5365	-0.3663	-0.2795	0.4748	-0.2538
2	2.5497	-0.0256	-0.1772	0.0995	-0.4885	0.1090	0.0324	-0.1014
3	3.6468	-0.0032	-0.1348	0.0639	-0.1772	-0.0244	0.0851	-0.0316
4	4.3014	-0.0716	-0.3922	0.0369	-0.0171	-0.0080	0.0157	-0.0433
5	1.4209	-0.1931	0.3319	-0.4767	-0.3965	0.0389	-0.1606	-0.0779
6	2.8786	-0.2136	-0.0435	-0.1291	0.0853	-0.1995	-0.0629	0.0072
7	0.0646	-0.2955	-0.3288	0.0971	-0.0325	-0.2058	-0.1567	-0.0861
8	1.7532	-0.2315	0.3103	-0.3063	-0.2500	-0.3707	0.1534	0.0407
9	2.5991	-0.1131	0.3388	-0.2678	0.2543	-0.0653	-0.0533	-0.0597
10	1.4326	-0.2383	0.5834	-0.1106	0.1152	-0.0508	0.0718	-0.0481
11	-1.2288	-0.3961	0.5158	0.0661	-0.0786	-0.1138	0.0665	0.0817
12	3.6209	-0.0642	-0.2941	0.0353	-0.1293	0.0159	-0.0455	0.0381
13	3.4078	-0.1223	-0.2691	0.0084	0.0183	-0.2052	-0.0296	-0.0326
14	3.6855	-0.0847	-0.0162	0.0198	-0.1427	-0.0059	-0.0109	-0.0321
15	3.6321	-0.1174	-0.1493	-0.0270	-0.1212	0.1159	0.0644	-0.0516
16	4.5532	-0.0923	-0.3513	0.1523	0.1434	-0.1133	0.0396	0.0055
17	3.2393	-0.0885	0.1318	-0.1708	-0.2767	0.0428	-0.0809	-0.0152
18	4.1459	-0.1557	-0.6258	0.0511	-0.2251	0.1050	0.0380	-0.0531
19	3.8447	0.0084	0.2064	-0.0598	0.1320	-0.2480	-0.0182	0.1759
20	4.6105	0.0160	-0.0136	-0.0687	0.0259	-0.0139	0.0073	-0.0777
21	3.5899	-0.0432	0.0049	-0.0368	-0.0653	0.0330	-0.0937	-0.0282
22	2.3109	-0.1908	0.7723	-0.3363	-0.0367	0.1165	-0.0070	-0.0278
23	3.4281	0.0019	-0.4166	0.1508	-0.1055	-0.0722	0.0738	-0.1157
24	3.8211	-0.0711	0.0129	-0.0591	-0.0205	0.0502	-0.0846	-0.0180
25	3.8980	0.0234	0.0943	-0.0348	-0.2243	0.0618	-0.0764	-0.3243

Table 2. Poisson regression model parameter estimates divided by standard errors for factors affecting counts of hauled out harbor seals in Prince William Sound.

Location i	β_{0i}	β_{1i}	β_{2i}	β_{3i}	β_{4i}	β_{5i}	β_{6i}	β_{7i}
1	-0.8652	-21.7459	7.4060	-5.8486	-4.8651	-4.0667	6.8329	-5.4032
2	36.5983	-2.8933	-4.6275	4.0119	-16.6841	3.7359	1.2533	-5.0849
3	89.6727	-0.5401	-5.7267	3.9112	-9.5021	-1.3048	5.5837	-2.7868
4	153.0919	-19.4725	-24.0596	2.8536	-1.3235	-0.6206	1.4397	-5.8241
5	13.3033	-15.4544	3.5930	-6.4779	-7.4309	0.6650	-2.8346	-3.2630
6	57.4569	-33.8218	-1.2065	-4.0093	3.0683	-6.1906	-2.2568	0.6025
7	0.3609	-14.4987	-2.8205	1.0863	-0.3612	-1.8978	-1.3785	-1.7261
8	20.0357	-21.0426	3.7857	-5.3538	-4.7593	-5.7791	2.9075	1.7192
9	45.4965	-12.5718	7.0090	-7.3712	6.5434	-1.7504	-1.1631	-2.3466
10	17.1180	-21.0014	7.8666	-2.5322	2.5400	-1.0480	1.3268	-1.6704
11	-4.5152	-12.5717	2.5431	0.6078	-0.7193	-0.9178	0.5602	1.4338
12	111.4696	-12.9599	-13.2171	2.1175	-5.9528	0.7504	-1.6268	2.2915
13	90.3872	-21.5180	-10.0663	0.4059	0.7072	-7.3750	-0.9164	-1.5437
14	116.5510	-17.4707	-0.7045	1.3039	-6.5987	-0.2570	-0.4090	-1.7709
15	113.8606	-25.0230	-6.6283	-1.6877	-5.9188	5.1137	2.5653	-2.7339
16	217.4755	-26.5133	-25.0665	14.6587	10.6137	-8.0221	2.4600	0.3987
17	76.4986	-13.0897	4.0496	-7.7002	-10.3539	1.3524	-2.9845	-0.6740
18	156.0077	-39.0685	-32.8364	3.4307	-15.6949	7.0193	2.4140	-3.9583
19	111.7065	1.3194	7.7409	-3.2859	5.2361	-8.8344	-0.7062	7.7570
20	191.2769	3.6066	-0.7915	-5.7453	1.8161	-0.9382	0.4989	-5.2777
21	98.7119	-6.8139	0.1829	-2.1051	-3.0448	1.4321	-4.9104	-1.7247
22	36.6063	-22.5469	12.7133	-9.5478	-1.0243	2.7423	-0.2846	-1.3544
23	81.9698	0.2624	-15.5133	8.4417	-4.8736	-3.3042	3.7077	-6.0821
24	134.7332	-13.6667	0.5667	-3.9055	-1.1887	2.7291	-6.2516	-6.2712
25	88.2658	3.0987	3.2503	-1.7159	-11.4151	3.5226	-3.9754	-17.7235

Table 3. Bayesian hierarchical model parameter estimates (using mean of MCMC sample from posterior distribution) for factors affecting counts of hauled out harbor seals in Prince William Sound.

Location i	β_{0i}	β_{1i}	β_{2i}	β_{3i}	β_{4i}	β_{5i}	β_{6i}	β_{7i}
1	-0.0823	-0.4845	0.8651	-0.3289	-0.3295	-0.2584	0.2777	-0.1998
2	2.5710	-0.0254	-0.1712	0.0949	-0.4762	0.0984	0.0269	-0.1023
3	3.6510	-0.0028	-0.1325	0.0623	-0.1755	-0.0265	0.0827	-0.0321
4	4.3030	-0.0714	-0.3914	0.0357	-0.0172	-0.0084	0.0156	-0.0436
5	1.4080	-0.1995	0.2666	-0.4178	-0.3772	0.0130	-0.1234	-0.0680
6	2.8670	-0.2135	-0.0443	-0.1294	0.0767	-0.1879	-0.0566	0.0082
7	0.0707	-0.2859	-0.2608	0.0136	-0.0546	-0.1319	-0.0553	-0.0623
8	1.7260	-0.2311	0.2955	-0.2851	-0.2454	-0.3218	0.1107	0.0256
9	2.5830	-0.1133	0.3259	-0.2582	0.2389	-0.0556	-0.0439	-0.0565
10	1.4410	-0.2370	0.5623	-0.0987	0.1029	-0.0507	0.0518	-0.0536
11	-1.0220	-0.3723	0.4793	0.0481	-0.1156	-0.0973	0.0011	0.0450
12	3.6250	-0.0641	-0.2925	0.0338	-0.1270	0.0132	-0.0437	0.0361
13	3.4040	-0.1217	-0.2654	0.0046	0.0138	-0.1963	-0.0270	-0.0336
14	3.6870	-0.0845	-0.0145	0.0187	-0.1415	-0.0070	-0.0096	-0.0327
15	3.6360	-0.1176	-0.1495	-0.0271	-0.1197	0.1115	0.0604	-0.0525
16	4.5530	-0.0925	-0.3511	0.1511	0.1412	-0.1110	0.0379	0.0037
17	3.2440	-0.0882	0.1302	-0.1679	-0.2688	0.0351	-0.0730	-0.0153
18	4.1490	-0.1555	-0.6251	0.0502	-0.2238	0.1031	0.0376	-0.0530
19	3.8420	0.0060	0.2018	-0.0637	0.1219	-0.2329	-0.0267	0.1599
20	4.6090	0.0160	-0.0135	-0.0688	0.0251	-0.0141	0.0072	-0.0768
21	3.5920	-0.0429	0.0056	-0.0367	-0.0644	0.0317	-0.0895	-0.0292
22	2.3310	-0.1905	0.7364	-0.3130	-0.0246	0.0908	-0.0098	-0.0290
23	3.4260	0.0023	-0.4144	0.1472	-0.1068	-0.0708	0.0693	-0.1123
24	3.8220	-0.0709	0.0133	-0.0588	-0.0203	0.0486	-0.0829	-0.0182
25	3.8870	0.0242	0.0957	-0.0359	-0.2248	0.0622	-0.0735	-0.3147

Table 4. Bayesian hierarchical model parameter estimates divided by standard errors (standard deviation of MCMC sample from posterior distribution) for factors affecting counts of hauled out harbor seals in Prince William Sound.

Location i	β_{0i}	β_{1i}	β_{2i}	β_{3i}	β_{4i}	β_{5i}	β_{6i}	β_{7i}
1	-0.4263	-22.3891	6.7010	-4.5234	-4.9970	-4.3686	4.6925	-5.9517
2	37.9483	-2.9206	-4.5874	3.8523	-16.6445	3.4501	1.0945	-5.2978
3	94.4387	-0.4864	-5.7409	3.8956	-9.4814	-1.4446	5.5328	-2.9182
4	154.5063	-19.3207	-24.1605	2.7733	-1.3532	-0.6568	1.4111	-5.9336
5	13.9130	-16.2063	3.1127	-6.3380	-7.3342	0.2442	-2.5538	-3.1323
6	58.6179	-34.0945	-1.2523	-4.0949	2.7987	-6.0418	-2.1447	0.7067
7	0.4299	-14.3165	-2.3731	0.1731	-0.6985	-1.6131	-0.7957	-1.6077
8	20.0698	-21.6386	3.8198	-5.3610	-4.9129	-5.3633	2.3812	1.1545
9	45.6683	-12.6989	6.9503	-7.4409	6.3758	-1.5548	-1.0819	-2.3690
10	17.7879	-20.7713	7.8282	-2.3688	2.3688	-1.1471	1.1250	-2.0135
11	-4.4785	-13.2068	3.1083	0.5945	-1.3292	-1.1219	0.0160	1.0910
12	113.2813	-13.1805	-13.1876	2.0245	-5.8017	0.6193	-1.6448	2.2333
13	91.8263	-21.9517	-10.0568	0.2276	0.5429	-7.1201	-0.8804	-1.6448
14	118.7057	-17.5104	-0.6422	1.2468	-6.6338	-0.3132	-0.3732	-1.8256
15	114.5197	-25.5042	-6.7708	-1.7359	-5.8050	4.9271	2.5188	-2.8496
16	217.7427	-27.1232	-25.0071	14.5709	10.4826	-7.9684	2.4053	0.2738
17	78.3575	-13.1961	4.0498	-7.6562	-10.2244	1.1651	-2.7975	-0.7079
18	157.8767	-39.7089	-33.2323	3.4000	-15.6394	6.9521	2.4579	-3.9559
19	112.5696	0.9416	7.5581	-3.5138	4.9694	-8.5783	-1.0835	7.0972
20	190.9279	3.6685	-0.7946	-5.7565	1.7565	-0.9449	0.4995	-5.3025
21	100.6726	-6.9132	0.2159	-2.1778	-3.0730	1.3961	-4.7885	-1.8059
22	37.5847	-22.8417	12.4771	-9.1094	-0.7028	2.2324	-0.4162	-1.4457
23	82.8136	0.3155	-15.4858	8.3352	-4.9953	-3.2711	3.5748	-6.0021
24	136.5976	-13.7253	0.5875	-3.9703	-1.1665	2.6590	-6.1521	-6.2854
25	88.8254	3.2576	3.3646	-1.8011	-11.5697	3.5464	-3.9363	-17.5908

Table 5. Bayesian hierarchical model parameter estimates and credibility intervals for μ.

	2.5%	Mean	97.5%
μ_0	2.21500	2.84500	3.47300
μ_1	-0.18120	-0.12800	-0.07425
μ_2	-0.12260	0.03396	0.19210
μ_3	-0.13420	-0.06551	0.00006
μ_4	-0.16980	-0.09589	-0.02117
μ_5	-0.10150	-0.04676	0.00755
μ_6	-0.03738	0.00227	0.04240
μ_7	-0.08279	-0.04474	-0.00713

Table 6. Bayesian hierarchical model parameter estimates and credibility intervals for τ.

	2.5%	Mean	97.5%
τ_1	-0.07858	-0.07433	-0.06957
τ_2	-0.09550	-0.07941	-0.06447
τ_3	-0.04457	-0.03495	-0.02509
τ_4	-0.08457	-0.07438	-0.06406
τ_5	-0.03564	-0.02449	-0.01321
τ_6	-0.01816	-0.00752	0.00297
τ_7	-0.04971	-0.04205	-0.03436

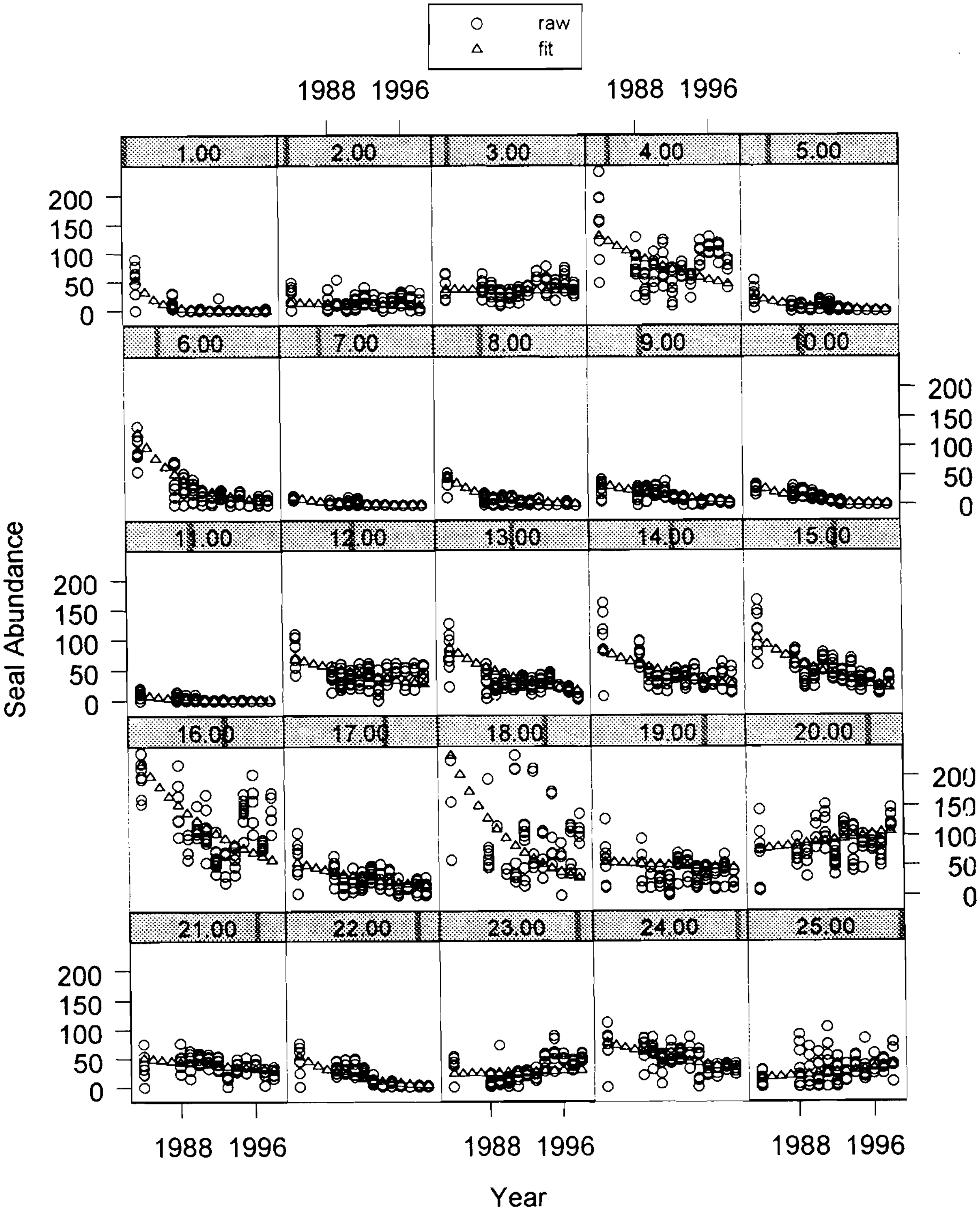

Figure 1. Fitted trends and raw data for 25 harbor seal haulouts in Prince William Sound.

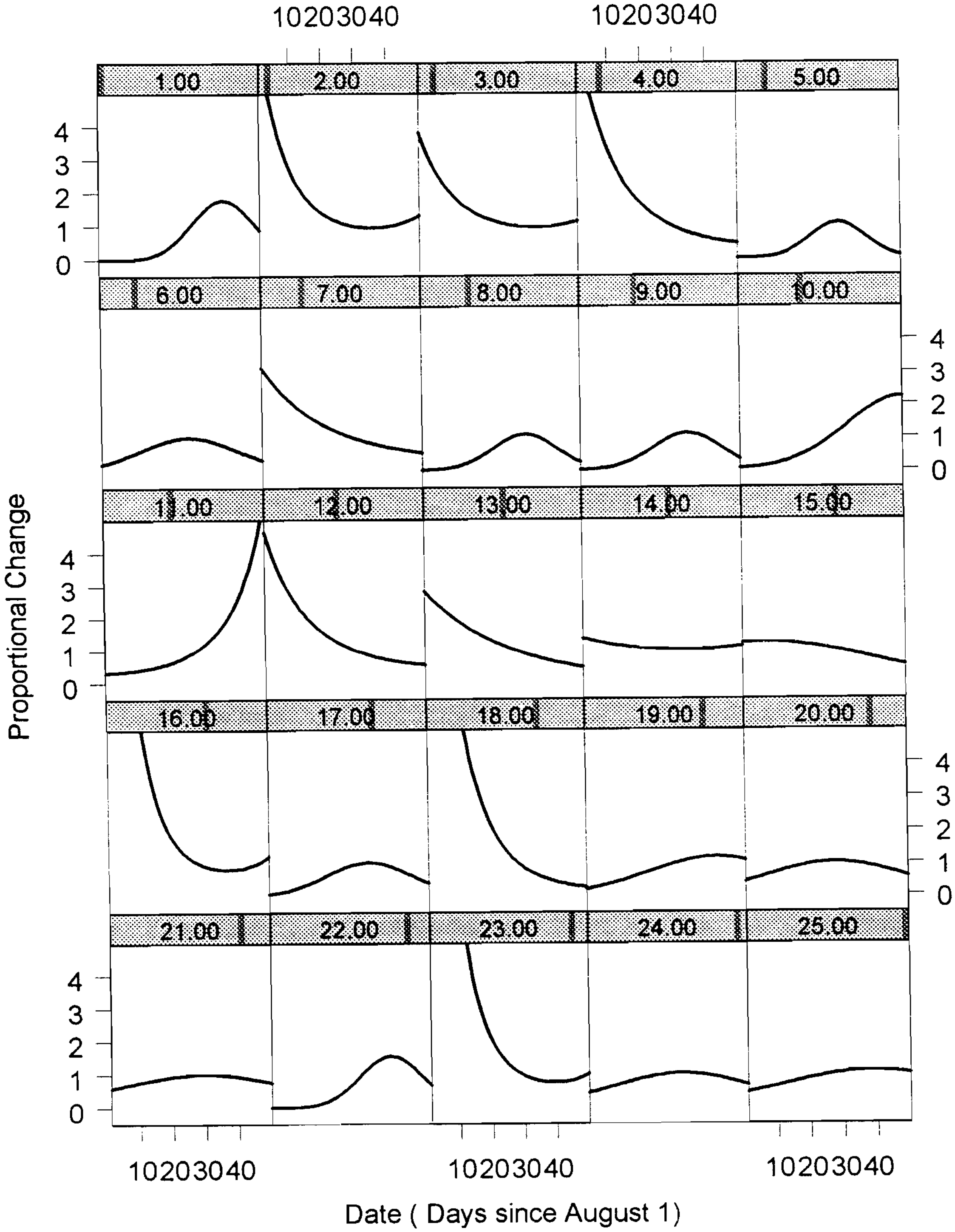

Figure 2. Effects of date on counts for 25 harbor seal haulouts in Prince William Sound.

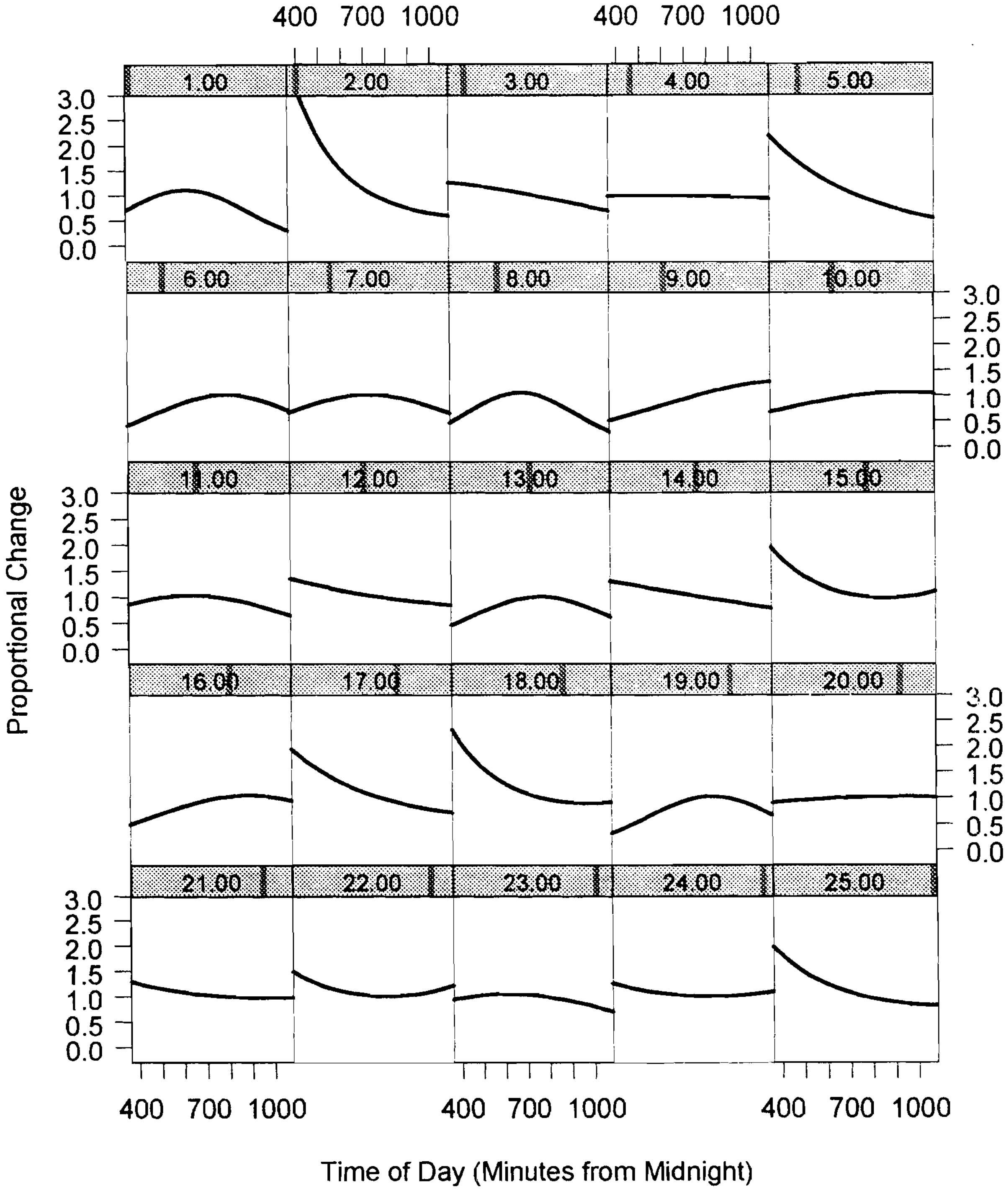

Figure 3. Effects of time of day on counts for 25 harbor seal haulouts in Prince William Sound.

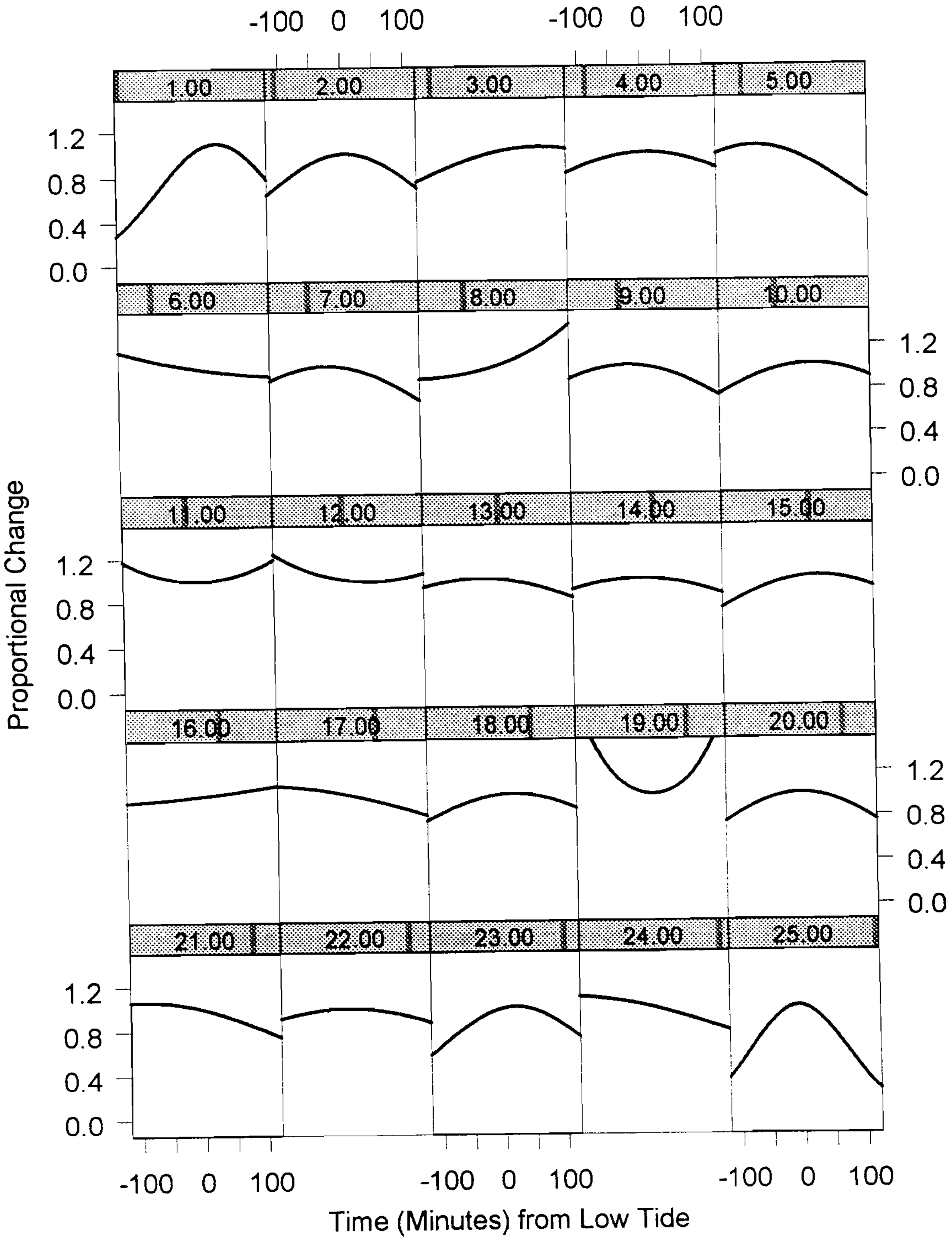

Figure 4. Effects of time relative to low tide on counts for 25 harbor seal haulouts in Prince William Sound.

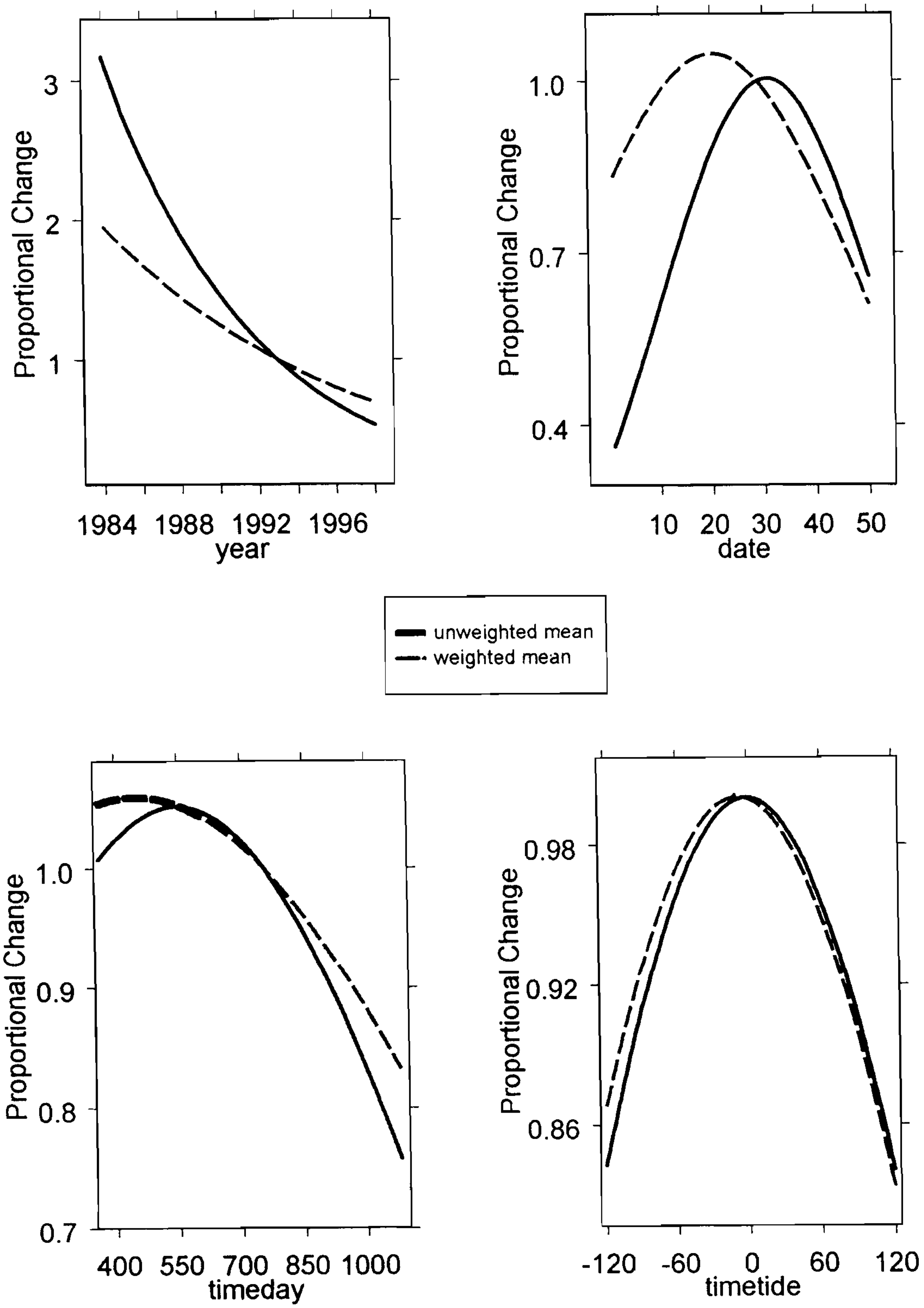

Figure 5. Overall effects in trend, date, time of day, and time relative to low tide for all sites combined. The solid line shows the effect of using μ_p and the dashed line the effect of using τ_r.

CHAPTER FIVE

DIVING BEHAVIOR OF NON-PUP HARBOR SEALS IN PRINCE WILLIAM SOUND, ALASKA, 1993-1996

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OBJECTIVE 8

Determine foraging range and diving behavior of harbor seal pups and juveniles and compare to similar information for other age groups.

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DIVING BEHAVIOR OF NON-PUP HARBOR SEALS IN PRINCE WILLIAM SOUND, ALASKA, 1993-1996

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ABSTRACT

Satellite depth recorders (SDRs) have been deployed on a variety of pinnipeds, providing insights into movements and diving behavior. Unfortunately, individual variability and summing of data into bins have made analyses using standard statistical techniques difficult. We have developed a statistically robust analytical method that accounts for individual variability, temporal autocorrelation, and the binned nature of data. We used this method to analyze the diving behavior of 37 harbor seals, *Phoca vitulina richardsi*, tagged with SDRs in Prince William Sound, Alaska, during 1993-1996. Repeated measures mixed models for effort, focus, and preferred depth bin were created using the MIXED procedure in SAS.

Models indicated that diving effort remained steady throughout winter, then declined from February to July. Preferred depth was deepest during winter and shallowest during May-July. Diving was shallow and focused in Copper River Delta and Cook Inlet and deeper and less focused near Yakutat and southwest of Montague Island, reflecting regional bathymetry. Collinearity between month and region in the preferred depth model suggests that seals migrate to regions of deeper preferred depth in winter, perhaps indicating a seasonal cycle in type or depth of prey. The steady decrease in diving effort during spring and summer indicates that seals gradually increase the proportion of time they spend hauled out as the molt period approaches. However, diving effort increased abruptly in September, making it clear that surveys to estimate population size must be carefully timed.

Diurnal and demographic changes in diving behavior were minor but significant. Diving effort was greatest at night (2100-0300 hrs), and most focused during the day (0900-1500 hrs). Diving was more focused for females than males, and for adults than subadults. These insights into foraging and hauling out behavior have practical management applications for improving surveys and evaluating habitat use by season, region, and depth.

Key words: harbor seal, *Phoca vitulina richardsi*, Prince William Sound, diving behavior, *Exxon Valdez* oil spill, repeated measures mixed models

INTRODUCTION

Harbor seals (*Phoca vitulina richardsi*) are one of the most abundant and widely distributed marine mammals in Prince William Sound (PWS), 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 et al. 1994, 1999). A change in the trophic structure of the ecosystem, and hence the availability of prey, is among the hypothesized causes for this observed decline. 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 the status of other marine resources.

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 some species of seabirds have also declined in the GOA and Bering Sea regions (Byrd and Dragoo 1997). These unanticipated declines have prompted monitoring and assessment of marine mammal, seabird, and fish population trends.

To evaluate the food limitation hypothesis, information is needed not only 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, harbor seal studies funded by the *Exxon Valdez* Oil Spill Trustee Council have included attachment of satellite-linked depth recorders (SDRs) to seals to examine their behavior and habitat use.

Satellite-linked depth recorders (SDRs) have been deployed on a variety of marine mammals, providing insights into both large-scale horizontal movements and diving behavior in these animals (Heide-Jorgensen and Dietz 1995, Norday et al. 1995, Stewart et al. 1996, Merrick and Loughlin 1997, Lowry et al. 1998). However, unlike Time-Depth-Recorders, which record and store information about individual dives, SDRs sum dive information into bins over 6-hr blocks of time. The binned nature of the SDR data, as well as substantial individual variability in diving behavior of the seals, have made SDR data poorly suited to standard analysis techniques. This has often resulted in the application of simple summary statistics to these data and/or in the presentation of individual "stories" for each animal without a suitable means of combining data for a broad cross section of individuals. The inferences about diving behavior which can be drawn from either summary statistics or individual stories are quite limited. Furthermore, while the presentation of individual stories may be adequate for initial tagging efforts when samples sizes are small, it is much less useful for large sample sizes. Temporal autocorrelation in SDR data has also been largely ignored in these summary analyses.

In this paper, we develop a statistically robust method for analyzing SDR data that accounts for individual variability among animals, temporal autocorrelation, and the binned nature of the data. We use this method to analyze the diving behavior of harbor seals in Prince William Sound, Alaska, using a large SDR dataset collected on 37 seals during the years 1993-1996 (Frost et al. 1995, 1996, 1997, 1998). We specifically address patterns in diving behavior due to gender and age of seal, time of day, time of year, and location.

METHODS

Data Collection

Harbor seals in Prince William Sound were captured and outfitted with satellite-linked depth recorders (SDRs) as described previously by Frost et al. (1995, 1996, 1997 and 1998). SDRs stored data about dive depths, durations, and the proportion of time spent at depth in four 6-hr blocks (2100-0300 hr, 0300-0900 hr, 0900-1500 h., and 1500-2100 hr local time). Data were accumulated in bins and analyzed as follows: depths of 4-20 m, 21-50 m, 51-100 m, 101-150 m, 151-200 m, and >200; and durations by 2-min increments up to 18 minutes. These data were transmitted during hours of good satellite coverage, and SDR locations were calculated for satellite passes with sufficient received signals.

Dive data from SDRs were extracted using software provided by the manufacturer (Wildlife Computers, Redmond, WA). 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 daily maximum depth of dive and time at the surface within 6-hr periods.

For this analysis, the diving behavior of seals was analyzed with respect to the gender and age of the seal, month, time of day, and geographical region. Time of day was divided into four periods corresponding to the 6-hr data collection blocks. Location data were assigned to geographical regions. Preliminary analyses using 19 Alaska Department of Fish and Game fish sampling regions indicated that diving behavior was adequately described using eight regions defined as follows: eastern Prince William Sound, northern and western Prince William Sound, central Prince William Sound, southwestern Montague Island, Copper River Delta, Middleton Island, Yakutat, and Cook Inlet (Figure 1).

Hierarchical Analysis

A three tiered analysis scheme was used. Harbor seal SDR data were analyzed for diving effort, diving focus, and preferred depth bin. Diving effort was defined as time spent wet in any 6-hr data collection period. Bin 0 of the time-at-depth data recorded the proportion of time the sensor was dry during each period, so effort was calculated as six hours minus time in Bin 0 for each period. Diving focus was defined as the dominance of one depth bin in the depth data for a given period. D from Simpson's diversity index (Krebs 1989, Simpson 1949, Washington 1984) was used to calculate dominance

$$(D = \Sigma\{[n_i(n_i-1)] / [N(N-1)]\}$$

where n_i = number of dives to depth bin i, and N = total number of dives). The maximum value of focus, D=1, indicated that all dives were to the same depth bin, while D=1/6 indicated that dives were evenly distributed among the 6 depth bins. Preferred depth bin was defined as the depth bin with the maximum number of dives for each period.

The analysis scheme was hierarchical in that the focus data used for analyses were chosen based on effort values, and preferred depth bin data were chosen based on both effort and focus values. A focus value > 1/2 indicated that dives were focused primarily in one depth bin. Since preferred depth bin is only valid when applied to data where a preference was shown, only 'focused' data were used for preferred depth bin analyses. Data with effort < 3 hours could represent the beginning or ending of a diving bout, or sporadic diving which may differ from 'standard' diving behavior. Focus and preferred depth bin were analyzed both for data with effort > 3 hours and all data to account for possible biases involved in analyzing non-standard diving behavior.

Database Creation

Databases, which included data from all seal SDRs, were created for each data type. Erroneous location data were removed from the location database as described in Chapter Two of this report, and in previous reports (Frost et al. 1995, 1996, 1997; Lowry et al. 1998). The databases were imported into S-PLUS (version 3.3, MathSoft Inc.), and all non-statistical data manipulation was conducted using S-PLUS functions.

The effort, focus, and preferred depth bin variables were created as described above. A time series variable was also created which combined the Julian date and time period for each record (time series = Julian date + time period/4). In cases where data from one seal spanned two years, the time series values in the second year were in sequence with those of the first year (e.g., 31 December 1995 period 3 = 365.75, 1 January 1996 period 2 = 366.5).

Statistical Analysis

Repeated measures mixed models for effort, focus, and preferred depth bin were created using the MIXED procedure in SAS (version 6.12, SAS Institute Inc.). Random subsets of 100 records for each seal were taken from the appropriate database for each analysis. For seals with less than 100 records, all data were included in analyses. Subsetting the data drastically reduced computation time, and also balanced the impact on the model of seals with large or small databases.

Since the repeated measures analysis (which accounted for temporal autocorrelation in the data) was more computation-intensive, the best model for each analysis was first determined using forward stepwise procedures with seal as a random effect but without repeated measures analysis. Fixed effects (sex, age, month, period, and region) were added singly to each model, using Akaike's Information and Schwarz's Bayesian Criteria (Carlin and Louis 1996) to determine the order of entry into the model.

Models with the maximum number of significant fixed effects were chosen for further analysis by including repeated measures within the MIXED procedure. Specifically, a spatial spherical autocorrelation model was used with time series and a column of ones as the dimensions and seal as the subject. In several cases, parameters which had been significant in the mixed model were no longer significant in the repeated measures mixed model. In these cases, stepwise reverse procedures were used to determine the best models.

RESULTS

Statistical analyses of effort, focus, and preferred depth bin were conducted on data from 37 seals (24 females, 13 males, 18 adults, and 19 subadults) which were captured between 1993 and 1996 (Table 1). All but four were captured and tagged in the central PWS region. Two were tagged in eastern PWS and one in northern PWS.

Effort

The original diving effort database had 4,995 records, and the 100-record-per-seal subset contained 2,808 records. Month, region, and time period were significant fixed effects in the repeated measures mixed model for diving effort (Table 2). Sex of the seal, and whether it was an adult or subadult were not significant. The model indicated that diving effort remained steady throughout the fall and winter months, then declined from February to July (Figure 2a). Seals spent over 90% of their time diving during September through February, compared to 68% in June and 61% in July. Southwestern Montague Island and Cook Inlet were regions of greater diving effort than the other six regions (Figure 2b). The model indicated that seals in these two regions spent more than 90% of their time diving, compared to 75% or less in the other six regions. Diving effort increased from 0300-0900 in the morning to a peak at 2100-0300 at night (Figure 2c).

Focus

The focus analysis was conducted on two databases. One database was created without regard to effort (n=3,876, 100-record-seal subset=2,486), and one included only records with effort > 3 hr (n=3,095, 100-record-seal subset=2,102). The repeated measures mixed models created for both analyses were similar (Table 3). Using the model with the most data (any effort) indicated that seal diving was most focused during midday (0900-1500) (Figure 3a). Seal diving was most focused in Copper River Delta and Cook Inlet (both very shallow regions) and least focused at Yakutat and southwestern Montague Island (Figure 3b). Female diving was more focused than male diving, and adult diving more focused than subadult diving (Figure 3c).

Preferred depth bin

The preferred depth bin analysis was also conducted on two databases: an 'any effort' database (n=2,958; 100-record-per-seal subset=2,090), and an 'effort > 3 hr' database (n=2,166; 100-record-per-seal subset=1,690). Month and region were significant fixed effects in the repeated measures mixed model using data with any effort. However, collinearity between month and region, combined with lower sample size, resulted in month and region not being significant together in the model using only data with effort > 3 hr. The general trends in parameter estimates for regions were similar between the two models (Table 3). Using the 'any effort' model, since it overcame collinearity problems, indicated that preferred depth bin was deepest during February and shallowest during May-July (Figure 4a). Diving was deeper off southwestern Montague Island and shallower in Copper River Delta than in the other six regions (Figure 4b).

DISCUSSION

The diving behavior of harbor seals in Prince William Sound changes seasonally and by region, with additional minor, but significant, changes due to time of day. Seasonally, seals show an approximately linear decrease in diving effort from February to July (Figure 2a) and a preference for dives to deeper depth bins in the winter than the summer (Figure 4a). The steady decline in diving effort suggests that seals gradually increase the proportion of time they spend hauled out as the onset of molt approaches in late June to August. The abrupt increase in diving effort between July and September (Figure 2a) makes it clear that the timing of surveys used to estimate population size in these animals is crucial. This satellite tagging data suggests that surveys in September should probably be avoided, even when counts are adjusted to account for survey variables such as date (see Chapters 1 and 4). Seals spend 106 minutes less time in the water per 6 hour period in July than September (Figure 2a), which is reflected in models which include the effect of survey date on number of seals observed (Chapter 1, Frost et al. 1999). The lack of evidence for a secondary peak in haul-out behavior during pupping is likely a result of the simplicity of our model, which did not include interactions between month and age and gender of seals. We expect that a model including such interactions would show a secondary minimum in diving effort, or secondary peak in haul-out behavior, for adult females during pupping. Such a model of the seasonal haul-out behavior of different demographic classes may be very useful in evaluating population surveys.

Seasonal changes in the preferred diving depth of harbor seals may indicate seasonal variation in the depth and/or distribution of preferred prey, or in the choice of prey. The collinearity found between month and region in the statistical model for preferred depth suggests that seals were distributed differently among regions seasonally. It is possible that the deeper diving during winter was a by-product of movements to offshore areas of the Gulf of Alaska, which were also deeper. Deeper preferred depth of diving was not directly responsible for greater effort spent diving, as might be expected. Although effort was consistently high from September through February, the high prevalence of deep dives occurred only in January-March.

Seasonal differences in effort and depth were not reflected in diving focus, which showed no significant seasonal change. This suggests that, although seals do focus their effort within different depth bins seasonally, the narrowness of diving focus does not vary throughout the year. This makes sense if one assumes that seals target different prey living at different depths throughout the year. For example, focus might be similarly narrow for seals feeding either on herring (*Clupea harengus*) in nearshore spawning concentrations or in offshore overwintering areas, but the actual depth where feeding occurred would be quite different.

Differences in diving focus of seals between regions seem to reflect bathymetry of the regions. Seal diving was less focused in regions which are characterized predominantly by deep water, such as southwestern Montague Island. Conversely, in regions characterized by shallow water, such as Copper River Delta, seal diving was more focused. When diving in shallow water, a seal can only choose from one or two depth bins, thus the focus variable is constrained to be greater than 1/2. In deep water however, a seal can choose from all six depth bins, and the focus variable can range as low as 1/6. It should be noted that the intercept for the diving focus model is 0.70, and the minimum diving focus predicted from the model is 0.46 (Table 1, southwestern

Montague Island). Thus, even in regions where seals could use all 6 depth bins, the seals tend to focus their diving effort within one or two depth bins.

Regional differences in preferred depth also seem to reflect bathymetry, with the two shallowest regions (Copper River Delta and Cook Inlet) having the shallowest preferred depths. As mentioned above, the collinearity between month and region in the statistical model for preferred depth suggests that seals tend to migrate to regions of deeper preferred depth in the winter.

Harbor seal diving behavior was significantly linked to time of day, as reflected in significant changes in diving effort and focus between the four 6-hour time periods. The increase in diving effort from the 0300-0900 time period to 2100-0300 indicates that harbor seals were more active in the middle of the night. Similar nocturnal foraging behavior has been observed for harbor seals in other areas (Thompson et al. 1989). This could represent foraging on diel migrating prey, which are more accessible at night. Higher diving focus at the mid-night and mid-day periods may also reflect seals foraging on diel migrating prey, which are shallow at mid-night and concentrated at depth at mid-day. The lack of a shift in preferred depth by period, as would be expected if seals were foraging on vertically migrating prey, may be a result of the imprecision of analyzing depth use by bins. Also, it is likely that seals in different regions are foraging differently. For example, diel migrating prey would only be present in regions with deep water. Thus, statistical models that include interactions between region and period may provide stronger evidence of harbor seals foraging on diel migrating prey in some regions.

Harbor seal age and gender were only significant in the diving focus model. However, this result may be confounded by the unequal distribution of age and sex categories among regions. Most of the adult females included in this study were both tagged and remained resident in the very shallow Port Chalmers region. These adult females only had access to one depth bin, thus their focus values were all 1. The presence of other seals within the same region, but not in Port Chalmers could have weakened the appearance of a regional effect in the statistical model and resulted in significant estimates for higher focus in adults and females. It should be noted that, although our models indicated no general demographic behavioral differences, there may be gender or age-specific differences in certain months, regions, or periods. As we suggested earlier, the use of models with interactions between gender, age and other factors may provide useful, e.g., in determining whether there is a secondary peak in adult female haulout use during pupping.

The technique we have developed here provides a statistically robust method of analyzing the relatively intractable histogram data provided by SDRs. This method accounts not only for the random effect of individual seal behavior, but also corrects for temporal autocorrelation in the data. As discussed above, the parameter estimates resulting from our statistical models provide insights into foraging and haul-out behavior of SDR-tagged animals. These insights will be useful in managing harbor seal stocks, both in terms of improving surveys, as well as in determining the seasonal and regional use of different depths by these seals. We intend to extend the work presented here by including in the analysis SDR data from harbor seals tagged in Southeast Alaska and the Kodiak Island area. We will specifically focus our attention on behavioral differences between seals in these geographically distant regions. In the future, more complex models, which include interactions between factors, may be created to address specific questions raised in this analysis. Finally, this technique can be used to analyze SDR data from other species for which these data exist, allowing scientists to draw comparisons between species.

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Table 1. Harbor seals tagged with satellite-linked depth recorders in Prince William Sound, 1993-1996.

Specimen Number	Capture Date	Capture Location	Sex	Age Class	Standard Length (cm)	Axillary Girth (cm)	Weight (kg)
93-7	9/15/93	Seal Island	F	Adult	122	118	84.1
93-8	9/15/93	Seal Island	M	Adult	139	91	65.0
93-9	9/15/93	Seal Island	M	Subadult	112	96	47.7
93-12	9/18/93	Channel Island	M	Adult	144	104	81.8
94-1	9/18/94	Channel Island	F	Subadult	102	71	27.9
94-2	9/18/94	Channel Island	M	Adult	121	98	56.9
94-3	9/18/94	Channel Island	M	Adult	143	95	62.4
94-4	9/19/94	Gravina Island	M	Subadult	121	78	36.1
94-5	9/22/94	Port Chalmers	F	Adult	141	104	72.6
94-6	9/22/94	Port Chalmers	F	Adult	141	113	71.6
94-7	9/22/94	Port Chalmers	F	Subadult	119	85	40.5
94-8	9/22/94	Port Chalmers	F	Adult	129	102	55.4
95-1	5/9/95	Dutch Group	M	Subadult	96	81	33.1
95-2	5/11/95	Olsen Bay	F	Subadult	114	84	38.0
95-3	5/11/95	Port Chalmers	F	Adult	134	105	90.0
95-4	5/12/95	Stockdale Harbor	M	Adult	147	101	80.5
95-5	5/12/95	Stockdale Harbor	F	Subadult	109	91	42.8
95-6	5/14/95	Port Chalmers	F	Adult	135	111	105.0
95-7	9/25/95	Gravina Island	F	Subadult	105	82	36.6
95-9	9/26/95	Port Chalmers	F	Adult	125	102	69.5
95-10	9/26/95	Port Chalmers	F	Adult	136	105	77.1
95-11	9/26/95	Little Green Island	M	Subadult	120	90	48.4
95-12	9/26/95	Little Green Island	F	Adult	129	94	61.2
95-13	9/27/95	Port Chalmers	F	Subadult	127	83	41.8
96-1	4/28/96	Little Green Island	F	Subadult	109	85	39.2
96-2	4/28/96	Little Green Island	F	Subadult	112	89	38.0
96-3	4/30/96	Applegate Rocks	F	Subadult	109	76	31.9
96-4	4/30/96	Seal Island	M	Subadult	113	84	38.7

Table 1. Continued.

Specimen Number	Capture Date	Capture Location	Sex	Age Class	Standard Length (cm)	Axillary Girth (cm)	Weight (kg)
96-5	4/30/96	Port Chalmers	F	Adult	143	112	84.2
96-6	4/30/96	Port Chalmers	F	Adult	138	117	93.8
96-7	9/26/96	Channel Island	F	Subadult	113	83	43.5
96-9	9/27/96	Port Chalmers	F	Adult	142	115	101.7
96-10	9/27/96	Stockdale Harbor	M	Subadult	125	93	52.9
96-11	9/27/96	Channel Island	M	Subadult	114	95	47.7
96-12	9/27/96	Channel Island	M	Subadult	112	92	42.3
96-13	9/27/96	Channel Island	F	Adult	136	102	70.5
96-14	9/28/96	Applegate Rocks	F	Subadult	124	92	47.6

Table 2. Parameter estimates for diving effort model for harbor seals in Prince William Sound.

Fixed Effect	Parameter Estimate (minutes)	Standard Error of Estimate
INTERCEPT	329.4722	38.8212
MONTH 1	-7.0820	11.8974
MONTH 2	20.7241	13.1850
MONTH 3	-4.8978	15.5197
MONTH 4	-18.9186	15.3343
MONTH 5	-47.7220	12.7974
MONTH 6	-83.7467	13.4431
MONTH 7	-110.8520	18.3356
MONTH 9	-4.8005	14.3759
MONTH 10	4.8748	10.8612
MONTH 11	2.2443	10.8902
MONTH 12	0	
REGION 1	-68.3053	41.8067
REGION 2	-83.2827	40.2192
REGION 3	-58.7430	38.2089
REGION 4	17.4823	43.1501
REGION 5	-74.1749	40.4026
REGION 6	-63.0720	39.3788
REGION 7	-90.8955	44.9668
REGION 8	0	
PERIOD 0	29.8413	8.4615
PERIOD 1	-26.8566	4.9349
PERIOD 2	-11.7250	4.9810
PERIOD 3	0	

Covariance Parameter	Parameter Estimate
Seal (random effect)	779.8261
Sill-Nugget (repeated measures)	1401.7847
Range in days (repeated measures)	14.3606
Nugget (repeated measures)	9818.4923

Table 3. Parameter estimates for diving focus models for harbor seals in Prince William Sound.

	Effort > 3		Any Effort	
Fixed Effect	Estimate	Standard Error	Estimate	Standard Error
INTERCEPT	0.64888	0.11886	0.70150	0.11505
PERIOD 0	0.03524	0.01636	0.02817	0.01666
PERIOD 1	0.02703	0.01127	0.00535	0.01085
PERIOD 2	0.07007	0.01109	0.06436	0.01109
PERIOD 3	0		0	
REGION 1	-0.11841	0.12618	-0.15812	0.12432
REGION 2	-0.14028	0.11739	-0.14279	0.11380
REGION 3	-0.08326	0.11310	-0.10698	0.11034
REGION 4	-0.22820	0.12196	-0.23646	0.11953
REGION 5	0.02210	0.11869	0.01221	0.11587
REGION 6	-0.07751	0.11564	-0.08259	0.11306
REGION 7	-0.16981	0.14134	-0.22790	0.13487
REGION 8	0		0	
SEX - F	0.09914	0.04625	0.11143	0.04171
SEX - M	0		0	
AGE - AD	0.10418	0.04556	0.08217	0.04142
AGE - SUB	0		0	

Covariance Parameters	ParameterEstimate (effort > 3)	ParameterEstimate (any effort)
Seal (random effect)	0.01423	0.01117
Sill-nugget	0.00099	0.00979
Range	25.94091	26.78786
Nugget	0.03523	0.04073

Table 4. Parameter estimates for preferred depth bin diving model for harbor seals in Prince William Sound.

	Effort > 3		Any Effort	
Fixed Effect	Estimate	Standard Error	Estimate	Standard Error
INTERCEPT	1.18809	0.42296	0.86969	0.37821
REGION	0.04948	0.47144	0.50618	0.40984
REGION	0.34662	0.44456	0.48125	0.38605
REGION	0.23084	0.42529	0.52098	0.37256
REGION	0.95112	0.45464	1.17501	0.39766
REGION	-0.30275	0.44315	-0.19258	0.38824
REGION	0.15196	0.43138	0.51674	0.37741
REGION	0.77219	0.55599	0.84345	0.46317
REGION	0		0	
MONTH			0.18108	0.11123
MONTH			0.33153	0.12720
MONTH			0.22291	0.13902
MONTH			-0.01345	0.14123
MONTH			-0.19519	0.12146
MONTH			-0.17287	0.12670
MONTH			-0.14387	0.16768
MONTH			0.08583	0.12848
MONTH			-0.04398	0.10286
MONTH			-0.00923	0.10154
MONTH			0	

Covariance Parameter	ParameterEstimate (effort > 3)	ParameterEstimate (any effort)
Seal (random effect)	0.11626044	0.07417330
Sill-nugget	0.30604	0.23335
Range	15.49226	16.36637
Nugget	0.19115	0.20269

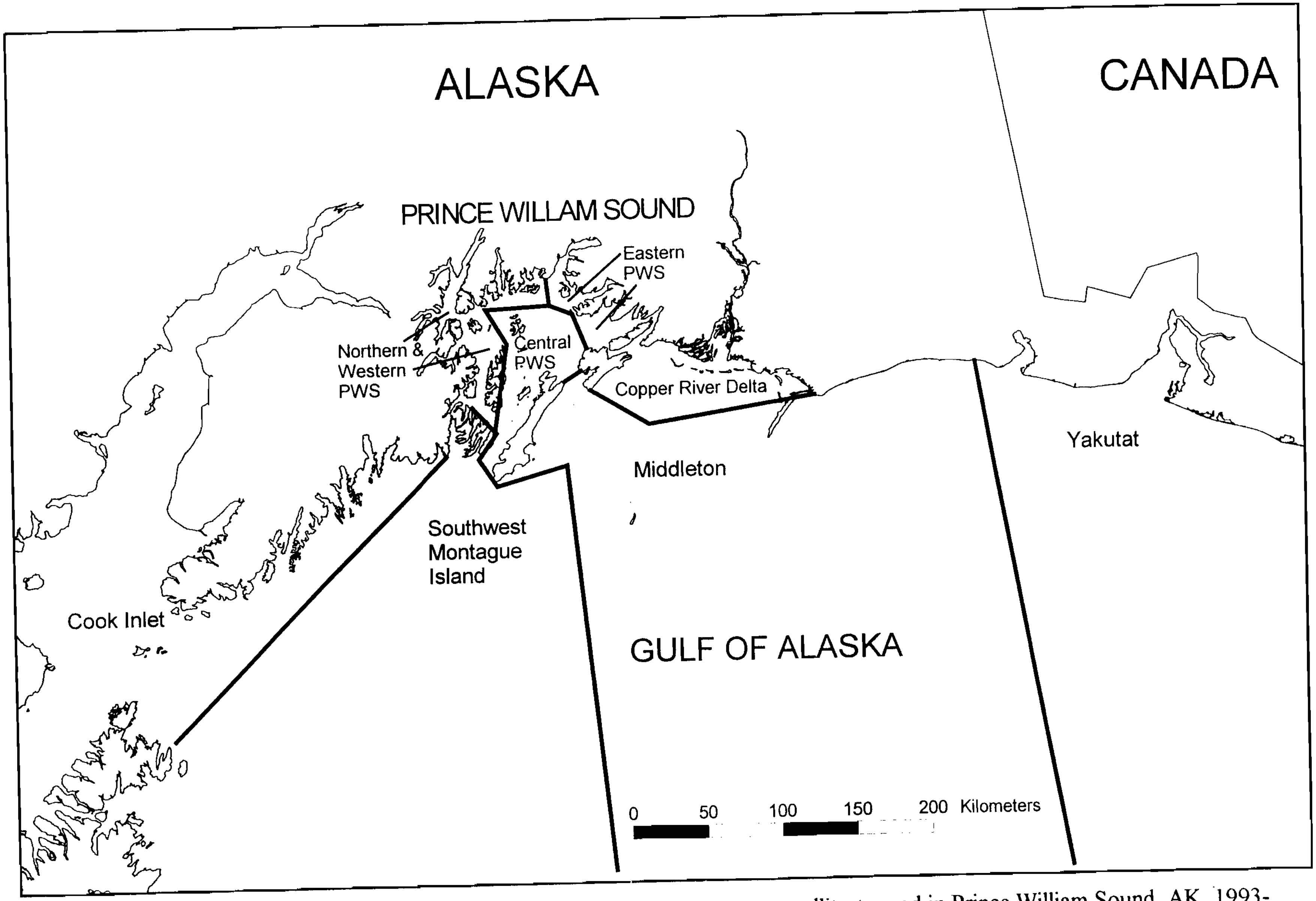

Figure 1. Regions used for analysis of diving date from harbor seals that were satellite-tagged in Prince William Sound, AK, 1993-1996.

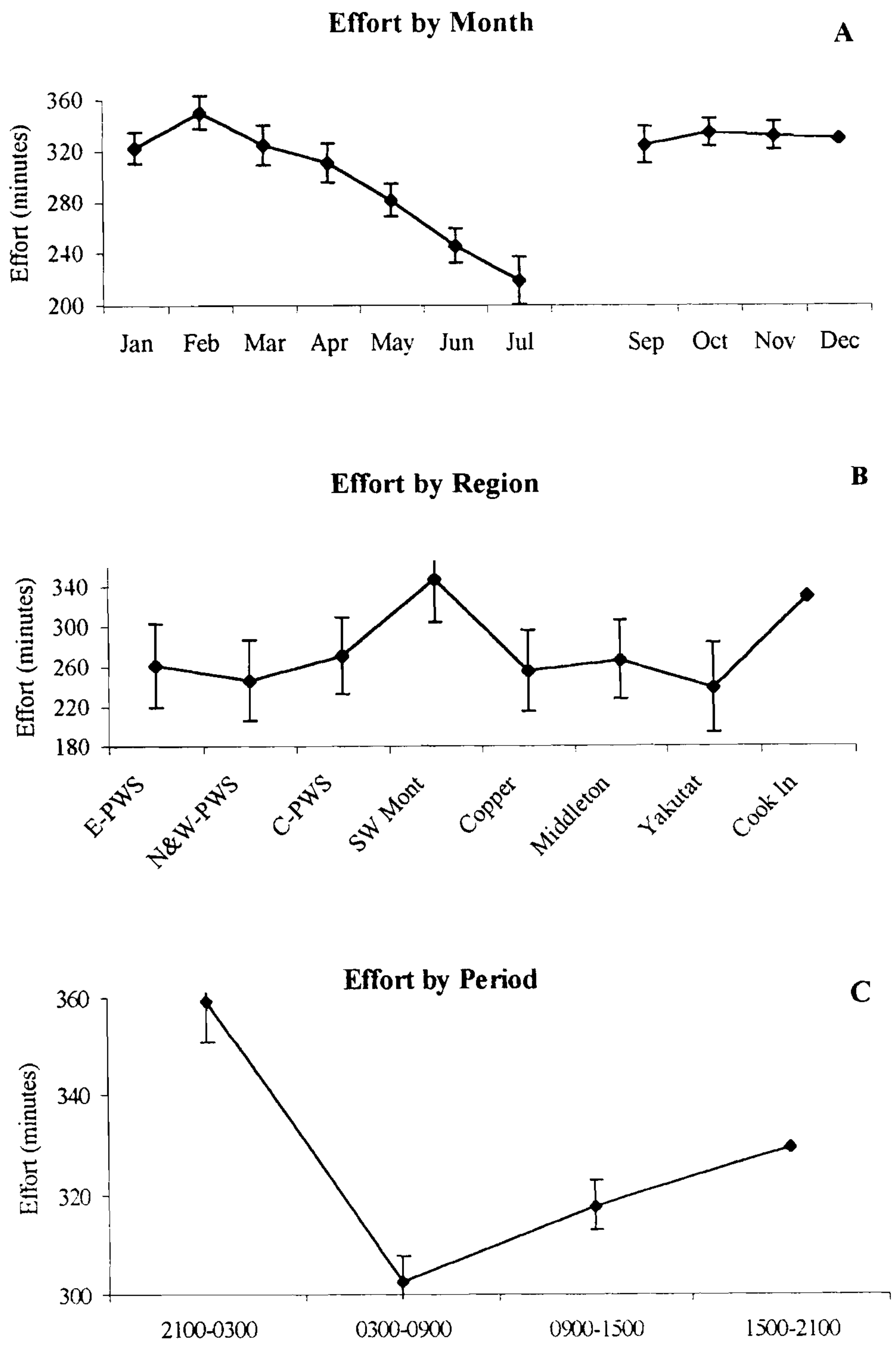

Figure 2. Modeled estimates of diving effort: A – month, B – region, C – period.

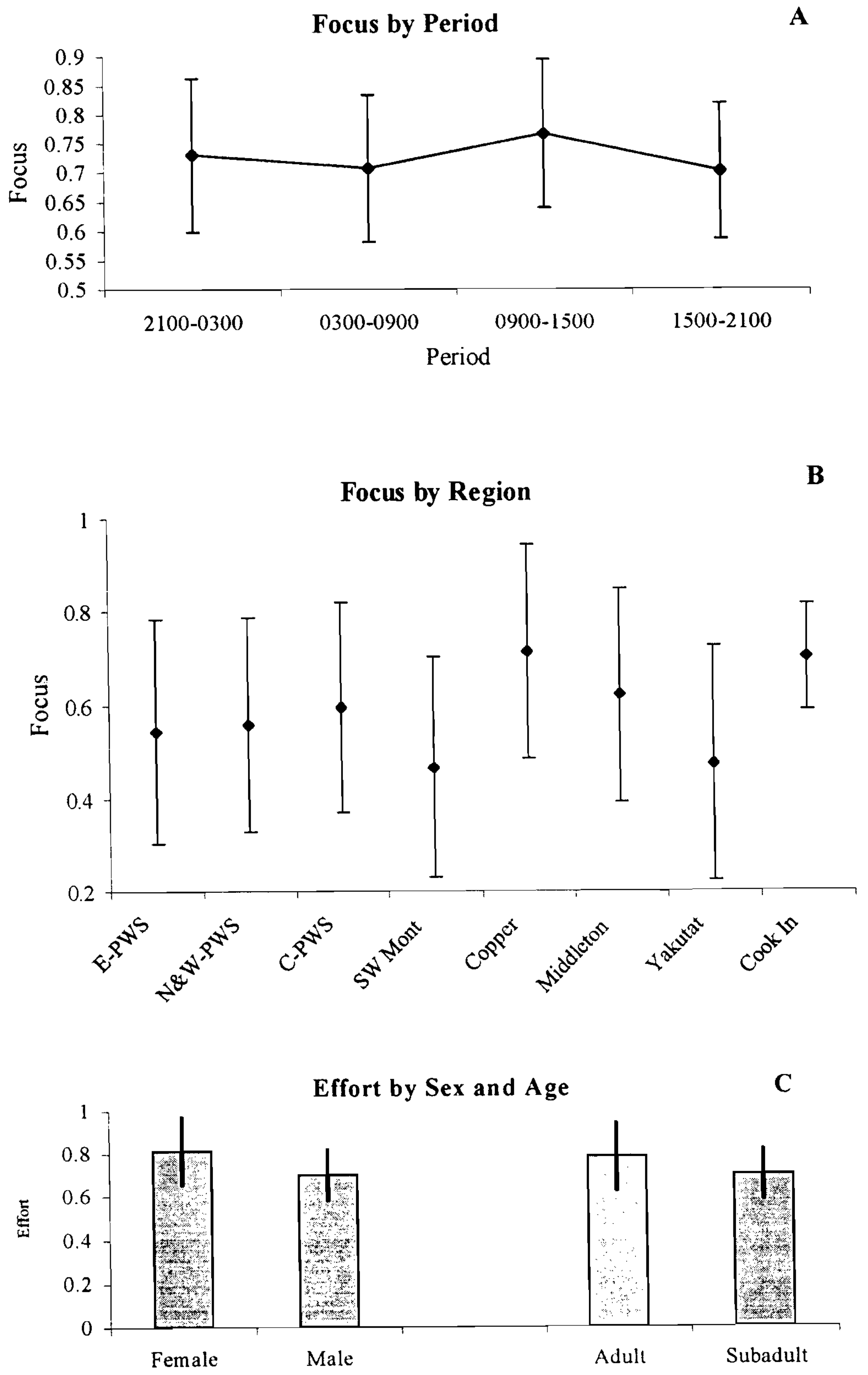

Figure 3. Modeled estimates of diving focus: A – period, B – region, C – sex and age.

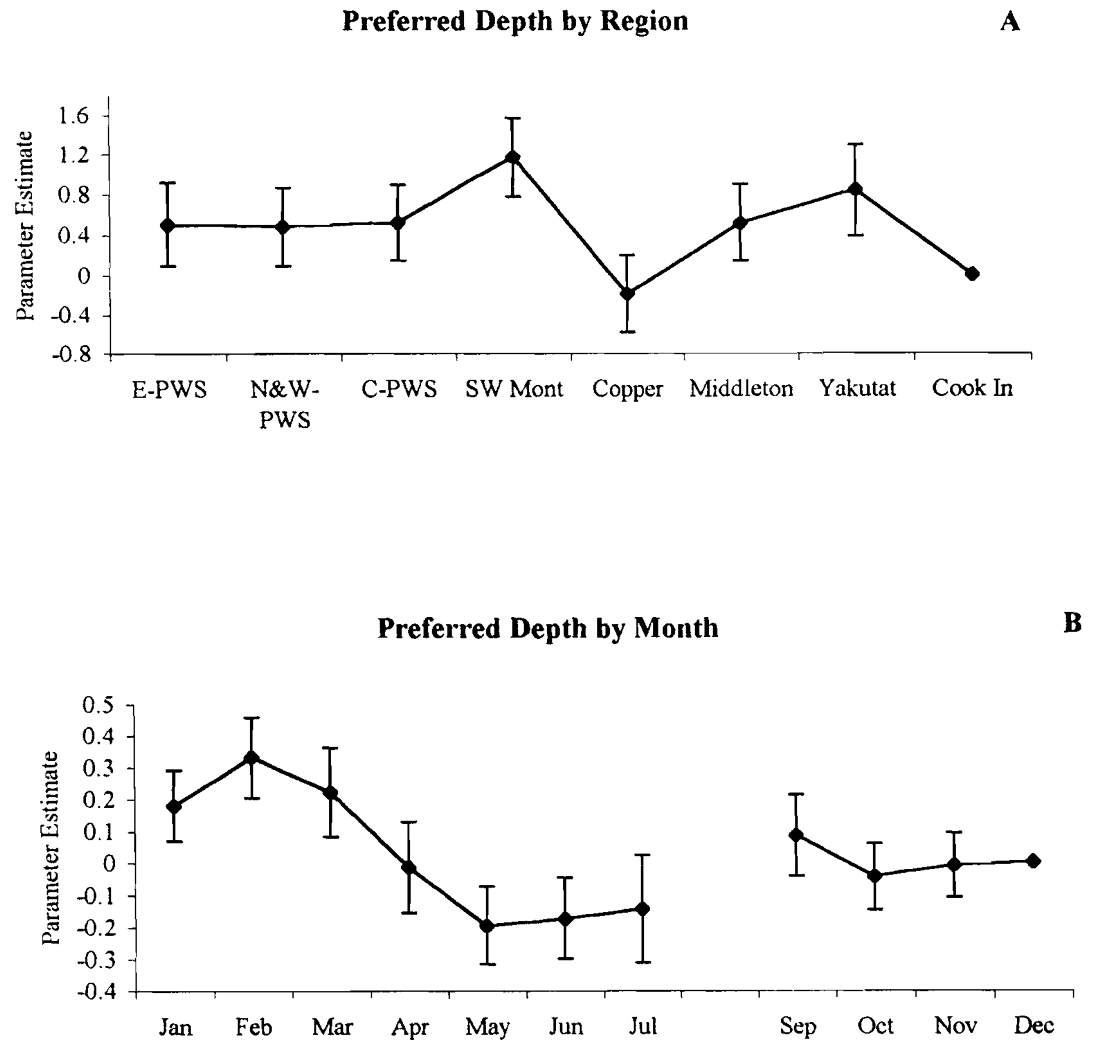

Figure 4. Modeled estimates of preferred diving depth: A – region, B – month. Parameter estimates for this analysis are in units of depth bins where bins are numbered from 0 (4-20 m) to 5 (>200 m).