Exxon Valdez Oil Spill
Restoration Project Annual Report

Isotope Ratio Studies of Marine Mammals in Prince William Sound

Restoration Project 97170
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 report.

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Study History: This project originated as part of the Sound Ecosystem Assessment program conducted by the University of Alaska and the Prince William Sound Science Center. In cooperation with K. Frost of the Alaska Department of Fish and Game, we began a stable isotope study of harbor seals and potential prey species in Prince William Sound (Restoration Project 95170). T. Kline, then of the University of Alaska Fairbanks, was a co-investigator, but upon his taking a position with the Prince William Sound Science Center, the project was split into two parts. Kline collected, as needed, data on lower trophic levels, while this project focused on harbor seals and prey species. In FY96, this project (Restoration Project 96170) was separated completely, although we are still responsible for all of the stable isotope analyses run for the Prince William Sound Science Center and the University of Alaska Fairbanks. Other stable isotope ratio users are accommodated as required.

Abstract: This project continues to consist of two components: (1) provision of analytical services for the stable isotope ratio investigations associated with *Exxon Valdez* oil spill projects, and (2) an investigation of food web relationships and trophic interactions of harbor seals and other top consumers in Prince William Sound (PWS). Through the use of harbor seal tissues collected from Native-harvested animals and tagging programs, seasonal and migrational information has been obtained with regard to prey utilization and trophic status at differing locations within PWS and the adjacent Gulf of Alaska (GOA). Preliminary results indicate that within PWS, harbor seals fall at the top of food chains based on locally derived productivity. Isotope ratios along whiskers grown over the past year indicate, however, that some individuals migrate into areas (presumably in the GOA) wherein the food web structure has different carbon and nitrogen isotope ratios. Isotope ratios indicate that offshore primary productivity is lower than in PWS and may reflect long-term declines in carrying capacity observed in the western GOA and Bering Sea. Findings from experiments with captive seals to determine whisker growth rates indicate faster whisker growth rates in spring following pupping and molting and slower growth in the winter.

Key Words: *Exxon Valdez* oil spill, food webs, harbor seals, $\delta^{13}C$, $\delta^{15}N$, isotope ratios, *Phoca vitulina*, Prince William Sound.

Project Data: *Description of data* - Data consist of carbon and nitrogen stable isotope ratios of zooplankton, forage fishes and harbor seals from Prince William Sound and selected areas of the Gulf of Alaska. *Format* - spreadsheets and tabular format in Corel QuattroPro and Microsoft Excel. *Custodian* - Dr. Donald M. Schell, P.O. Box 757220, Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, Alaska 99775-7220, (907) 474-7978, (907) 474-5863 (fax), ffdms1@aurora.alaska.edu

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EXECUTIVE SUMMARY

This study focused on the food webs supporting harbor seals in Prince William Sound; its integrating methodology was the use of natural stable isotope abundances as tracers of carbon and nitrogen transfers through the food webs. The goal of the study was to determine if declines in populations of harbor seals resulted from oil-spill-related effects or from shifts in ecosystem variables in response to external forcing. During the past three years, vibrissae (whiskers) and other tissues were collected from harbor seals within Prince William Sound and from the surrounding Gulf of Alaska. Samples were obtained from recently taken animals and from specimens archived at the Alaska Department of Fish and Game and the University of Alaska Museum. One or two long vibrissae were cut or pulled from live animals, and harvested or dead animals had all available vibrissae removed for analysis. To date, vibrissae from 167 seals have been sampled and analyzed. The data from these vibrissae revealed a temporal record allowing comparisons of interannual changes in feeding. Samples from different organ tissues, e.g., muscle and blubber, were also taken from 53 seals. A variety of tissues from a single animal were analyzed to determine isotopic fractionation among the tissues. This allowed normalization of isotope data to a single tissue type (muscle) when samples of only a different type were available.

To enable estimation of the time represented by the growth of a whisker, a captive seal was infused with ^{13}C- and ^{15}N-labeled glycine in January 1996. A repeat infusion occurred in June 1996 on two seals, and a whisker was clipped from each on 29 August 1996, for analysis. The second label was not visible in August, indicating the whisker had grown during the early spring and ceased growth by the second infusion. One wild seal tagged in fall 1994 was recaptured in spring 1995 and whiskers collected at both times were analyzed. This revealed that whiskers had grown only about 2 cm in seven months. The marked contrast between these two results implies that whisker growth rates in harbor seals are highly seasonal, and that detailed marking will be required to accurately determine growth rates in specific seasons. A program of periodic oral dosing of singly- versus doubly-labeled isotope tracers is now underway at Mystic MarineLife Aquarium, Mystic, Connecticut, on two new harbor seals.

Carbon isotope ratios are used as conservative tracers of energy supply between trophic levels (phytoplankton to zooplankton to fishes to top consumers). To establish the required baseline information, we have collected potential prey species of fishes and other organisms from Prince William Sound and the adjacent Gulf of Alaska. These data provided isotopic links to interpret the trophic dynamics of the seals.

Our research findings include a number of interesting points:

Harbor seals tend to have a strong site fidelity and do not migrate extensively, though some have been tracked over many kilometers within a region. Most seals have relatively constant isotope ratios, implying a consistency in location and type of diet. Some seals, however, do show large differences between enriched and depleted values, implying major seasonal shifts in diet type, or movement to a feeding location with different isotope ratios. Observed shifts in the nitrogen

isotope ratios may reflect seasonal changes in the trophic status of prey available within a given region.

Samples of zooplankton collected by cooperating investigators reveal that primary productivity rates are lower in offshore waters, as indicated by depletions in both $\delta^{13}C$ and $\delta^{15}N$. These low values provide a distinctive indicator visible in vibrissae of seals that feed in pelagic regions or on prey that have emigrated from offshore areas. Samples of fatty acids from these seals have been analyzed by S. Iverson and K. Frost in a collaborating study and have been found to be very different among regions. This supports the hypothesis that seals in differing parts of the Sound have different food web structures.

Archived samples from harbor seals have been analyzed to determine if the trophic structure of the food webs has changed between the period prior to the decline in seal populations and current years. In order to detect changes in trophic status over several decades, bone collagen was extracted and analyzed from 55 seals. Similar $\delta^{15}N$ values were observed in samples from 1950-1996, but $\delta^{13}C$ values showed a general decline, which is indicative either of prey derived from offshore areas, or a general decrease in primary productivity in Prince William Sound and the surrounding Gulf of Alaska.

A conceptual model of harbor seal feeding has been constructed based on the known isotope ratios in lower trophic levels and fishes. Predicted isotope ratios in seals, based on these food sources, match observed $\delta^{15}N$ values closely, but the measured $\delta^{13}C$ values are higher than predicted. We hypothesize that benthos, which are usually enriched relative to water column species, are more important than previously believed in the food supply to these seals.

INTRODUCTION

This annual report describes the preliminary results of the ongoing study of the food webs supporting harbor seals in Prince William Sound. This project also contributes to the Sound Ecosystem Assessment (SEA) program being conducted by the Prince William Sound Science Center and the Institute of Marine Science, University of Alaska Fairbanks, to describe the food chains supporting important commercial fish species that appear to have been impacted by the *Exxon Valdez* oil spill. In addition, it contributes to studies by Alaska Department of Fish and Game (ADFG) personnel to determine the reasons for the decline of harbor seal and Steller sea lion populations in Prince William Sound (Pitcher 1990, Alaska Sea Grant 1993, Lowry et al. 1994, Small 1996). The project also seeks to better describe the trophic interactions and trophic status of marine mammals, birds and their prey species. The integrating methodology for this wide range of tasks is the use of stable isotope ratios as natural tracers of carbon and nitrogen transfers through the food webs.

Carbon isotope ratios serve as conservative tracers of energy supply among trophic levels (phytoplankton to zooplankton to fishes to top consumers) (DeNiro and Epstein 1978, Fry and Sherr 1984). Pinnipeds, cetaceans, birds, etc. acquire isotope ratios in proportion to the amount of food derived from each differing source. This, in turn, is reflected in the composition of body tissues and as a temporal record in keratinous tissues (claws, feathers, baleen, whiskers) when multiple sources of food are consumed over time and space (Schell and Saupe 1993). This allows the discerning of important habitats and food resources in animals that seasonally migrate or undergo periods of hyper- and hypotrophy.

Nitrogen isotope ratios reflect both the food sources and the trophic status of that animal. As nitrogen in food is consumed and assimilated by a consumer, the heavy isotope is enriched by approximately 3‰ with an accompanying loss of the lighter isotope through excretion (DeNiro and Epstein 1981, Minigawa and Wada 1984). The enrichment occurs with each trophic step and thus allows the construction of conceptual models and food webs and the assignment of trophic status to species for which dietary data are sparse. The data obtained from these measurements are unique in that they trace materials actually assimilated and thus can be used for more accurate ecosystem modeling.

It can be postulated that the natural stable isotope abundances of PWS biota will shift because of changes in trophic level, food web structure, and primary productivity in the context of the SEA hypotheses, thus providing an independent tool to verify, quantify and model ecosystem processes. The tracer nature of the approach will enable the integration of ecosystem components. It will enable us to monitor both "top down" (predation) and "bottom-up" (food supply) controls on herring and salmon production.

The project is composed of three elements:

1. A research component on marine mammals focuses on the trophic energetics and ecosystem dynamics of harbor seals, conducted by Dr. Schell, PI, in cooperation with ADFG personnel working as part of the marine mammal program. A smaller additional effort using captive animals to determine vibrissae growth rates is also currently under way.

2. A research effort closely tied to the study focuses on lower trophic levels having direct application to the testing of hypotheses regarding fisheries resources. This work is being conducted by Dr. T. Kline of the Prince William Sound Science Center.

3. As the major isotope ratio analysis facility, we have provided analytical services for carbon and nitrogen isotope ratios to other PIs involved with spill-related studies and assisted with the interpretation of the acquired data. This task has required approximately 10-20% of the analytical and research effort and is continuing.

OBJECTIVES

The objectives of our section of the isotope study continue to include:

1. Collect and analyze samples of harbor seal vibrissae through continued cooperative work with the Alaska Department of Fish and Game in Prince William Sound.

2. Collect and analyze samples of harbor seal prey species including forage fishes, salmon and herring in the vicinity of major haul-outs and high population densities. Samples of seal tissues are collected from Native hunters. These samples are obtained with the assistance of ADFG personnel monitoring harvests and through the efforts of T. Kline.

3. Perform stable isotope ratio analyses on tissues and organisms collected during the sampling program. Through the use of **carbon** isotope data on taxa collected over geographical regions, the presence/absence of **isotopic gradients** useful in sorting out habitat dependencies will be determined.

4. Assist other research programs in the Prince William Sound ecosystem study by conducting stable isotope ratio analyses on samples provided by aiding in the interpretation of results. This effort will require approximately 20% of the analytical and research effort.

5. Through the use of **nitrogen** isotope ratios in collected taxa, assign **trophic status** to species in each region. Compare trophic status with predictive models based on conceptual food webs.

6. Determine temporal changes in harbor seal trophic status and food dependencies by comparing isotope ratios along the lengths of vibrissae with prey availability and their isotope ratios. Through the use of captive animals, establish the relationships between whisker growth rate and temporal/metabolic changes.

7. Compare the isotope-ratio-derived food web models to predictions by the "Lake-River" hypothesis, and others being tested by the SEA project, as an independent means of validation.

METHODS

The analytical methods for stable isotope analysis are described in detail in the initial annual report by T. Kline. Sampling of tissues for stable isotope analysis has been described for both bulk tissues (muscle, blubber) and temporally variable tissues (whiskers) (Schell et al. 1989; Michener and Schell 1994). This report includes only the pertinent sampling protocols and a synopsis of the analytical methods.

Forage Fishes

Lower trophic level organisms within Prince William Sound were obtained by T. Kline and analyzed within the scope of this project. Stable isotope ratios for these species were used to construct food webs for harbor seal foraging within the Sound. Samples of a few additional forage fishes from areas of harbor seal haul-outs were provided by ADFG personnel and combined with other lower trophic level organisms to assist in assigning trophic status. National Marine Fisheries Service (NMFS) personnel provided forage species from inshore and offshore waters in southeast Alaska. Isotopic values for these species were used to indicate if species originating in food webs in southeast waters are being transported via the Alaska Coastal Current into the Sound and once there, being utilized as food by seals. Pelagic and benthic species were sampled during shellfish surveys conducted by ADFG personnel in the western Gulf of Alaska. During the NMFS 1996 Gulf of Alaska survey, pollock, capelin and sandlance were collected from Gulf of Alaska waters outside Prince William Sound at depths between 50 and 140 m. These prey are being used as indicators of regional isotopic differences. These isotopic regions are used to help isolate areas of foraging by seals traveling outside Prince William Sound.

A 1996 scientific cruise conducted by the Canadian Pacific Biological Station provided us with additional zooplankton samples collected within and outside Prince William Sound. These samples were used to determine the range of the isotopic gradient between the Sound and locations in the Gulf of Alaska. These regional isotopic differences are exhibited in higher-order consumers due to trophic transfers in food webs. Data collected by Schell et al. (in press) and Kline (1997) have shown that these regional differences exist throughout the Bering Sea and between Prince William Sound and the Gulf of Alaska.

A few grams of lateral muscle (fish) or mantle (cephalopods) tissue were extracted from several individuals of each available species at a sampling site. The tissues were frozen at -17° C and transported to the stable isotope facility for analysis. Subsamples of the frozen tissues were dried at 60°C, ground for homogeneity and prepared for mass spectroscopy.

Pinnipeds

Harbor seal tissues were collected with the assistance of ADFG personnel and Native subsistence hunters. Stable isotope values for muscle tissue were assumed to be representative of the values for a whole animal.

During the past four years, vibrissae from harbor seals were collected within Prince William Sound and from the surrounding Gulf of Alaska. One to two long vibrissae were cut or pulled from live animals, while harvested or dead animals had all their vibrissae removed for analysis. When possible, samples from different organ tissues, e.g., muscle and blubber, were collected from each animal and analyzed to identify the isotope fractionation that occurs among different tissues.

Vibrissae and tissues from two hundred seventy-five harbor seals have been analyzed for stable isotope ratios. Tissues were dried at 60°C, ground for homogeneity and prepared for mass spectroscopy. Vibrissae were scrubbed with steel wool to remove any debris and segmented from base to tip in 2.5 mm segments. Every second segment beyond the base was analyzed for carbon and nitrogen isotope ratios and the reserved segments were archived for future reference.

Tissues from Prince William Sound, southeast Alaska and Kodiak harbor seals have been provided by ADFG personnel working as part of the marine mammal monitoring effort. The ADFG researchers have provided archived harbor seal tissues, dating from 1975, for stable isotope comparisons. These comparisons were essential in determining if a dietary shift in harbor seals occurred during the past two decades (i.e., since the "regime shift"). Harbor seal, Steller sea lion and northern fur seal bones archived at the University of Alaska Museum and the Kodiak Historical Society were sampled from animals dating from 1950 through 1996. Collagen was extracted from bone samples (free of humus and tissues) from a total of fifty-five harbor seals, twenty-eight Steller sea lions and fourteen northern fur seals from various regions of the Gulf of Alaska and Bering Sea. Bone collagen was extracted using the methods described in Matheus (1997). The stable isotope ratios of these tissues were used for comparison and contrast with the stable isotope ratios of present samples (Schoeninger and DeNiro 1984). Because they are based on seal tissues from multiple regions prior to the population decline (pre-1970), any significant changes in these ratios may be an indication of trophic changes or fluctuations in ecosystem productivity during the past several decades.

Analytical Techniques

The samples obtained were dried and powdered for homogeneity and the isotope ratios of carbon and nitrogen determined with a Europa 20/20 mass spectrometer system. The sample was combusted at high temperature and the nitrogen and carbon dioxide gases separated and purified by gas chromatography. These gases were transferred into the mass spectrometer by capillary action and the isotope ratios determined. Results are reported in the standard $\delta^{13}C$ and $\delta^{15}N$ notation.

Captive Animal Studies

Vibrissae growth rate studies were initiated with captive harbor seals to determine if growth rates fluctuate with season, age and, ultimately, diet. In January 1996 an adult harbor seal at Mystic MarineLife Aquarium in Connecticut was administered 4 ml (100mg/ml) of doubly-labeled glycine ($\delta^{13}C$ and $\delta^{15}N$) over a two-day period. The sudden increase in ^{13}C and ^{15}N, which was expected to be incorporated by the vibrissae, created a marked peak in these values corresponding to the time of infusion. Subsequently, another dose was administered in June 1996, and on 29 August, a whisker was clipped. The seal at this time was moved from Mystic MarineLife Aquarium to an aquarium in Virginia where another whisker was clipped on 5 November. The initial results from this experiment revealed a much faster growth rate than expected and the experiments were redesigned to account for the rate. Oral administration of singly-labeled amino acid was initiated on two new harbor seals in May 1997 and continues.

A second type of growth rate experiment was conducted simultaneously at the Vancouver Aquarium in British Columbia, Canada, on subadult Steller sea lions. Vibrissae were cut from the muzzles of the six animals periodically over three years. The vibrissae were analyzed for their stable isotopes and all the whiskers from each animal were plotted together. Overlap in growth from one vibrissae to the next was measured from an inflection point obvious on at least two separate segments. The date of each cutting was known and the growth rate calculated.

PRELIMINARY RESULTS

Isotope Ratio Variations in Harbor Seals

To date, vibrissae and tissue samples have been collected and analyzed from 275 harbor seals. Additionally, vibrissae have been collected from 143 harbor seals in Prince William Sound; these require subset analyses. Analyzed vibrissae from harbor seals are listed in Table 1 with the range, mean, and maximum and minimum stable isotope ratios. These represent the $\delta^{13}C$ and $\delta^{15}N$ values at 2.5 mm intervals along the lengths of the vibrissae. Vibrissae were collected during the ADFG seal surveys in Prince William Sound and body tissues were collected by Native subsistence hunters in cooperation with ADFG.

Based on the combined use of averaged $\delta^{13}C$ and $\delta^{15}N$ values from vibrissae, Hotelling's T-test was able to detect regional differences in the harbor seals. Seals in southeast Alaska and Prince William Sound were significantly different by region $F_{4,98} = 6595.92$, $p \leq 0.001$. Harbor seals in southeast Alaska and Kodiak were significantly different by region $F_{4,62} = 5648.64$, $p \leq 0.001$. Harbor seals in Prince William Sound and Kodiak were significantly different by region, $F_{4,92} = 12555.49$, $p \leq 0.001$. Southeast Alaska seals, all from Frederick Sound, had a mean $\delta^{13}C = -18.05 \pm 0.22‰$ and a mean $\delta^{15}N = 16.24 \pm 0.15‰$. Prince William Sound seals had a mean $\delta^{13}C = -17.85 \pm 0.16‰$ and a mean $\delta^{15}N = 16.97 \pm 0.17‰$. Kodiak seals, from the east and west side of the island, had a mean $\delta^{13}C = -16.51 \pm 0.24‰$ and a mean $\delta^{15}N = 17.29 \pm 0.17‰$ (SYSTAT 1997). Both the ^{13}C and ^{15}N isotopes of harbor seals are increasingly enriched from southeast Alaska westward to Kodiak. This enrichment may be the result of more nutrient-rich water in the western portion of the Gulf, allowing for larger, faster-growing phytoplankton near shore. More nutrients may be transported by the Alaska Coastal Current as it travels westward along the gulf coast of Alaska; the increased amount of nutrients would be available for western phytoplankton communities. These phytoplankton would have more enriched stable isotope ratios and these values would be incorporated and transferred through the food web so all organisms would reflect a greater enrichment (France and Peters 1997).

Seals from eleven sites were sampled in Prince William Sound at the locations shown in Figure 1. The $\delta^{13}C$ and $\delta^{15}N$ values were averaged from the vibrissae for each seal and their values used for statistical analysis. Nine of the eleven sites are in close proximity to one another and were grouped for MANOVA analysis. The two remaining locations in northeastern PWS were grouped together for analysis. Adult and subadult harbor seals from the nine areas in southern

PWS were significantly different by area $F_{16,1896} = 19.11$, $p \leq 0.001$; sex $F_{2,955} = 11.05$, $p \leq 0.001$ and age $F_{4,1908} = 45{,}953$, $p \leq 0.001$. The two areas in northeastern PWS were significantly different from each other $F_{2,86} = 11.79$, $p \leq 0.001$. There is a significant difference in age $F_{4,170} = 9.43$, $p \leq 0.001$ but not between sexes (SYSTAT 1997). Further analyses are being conducted individually for each of the eleven sampling areas. The stable isotope differences observed in seals from different locations appeared to agree with some of the location differences defined by the fatty-acid analysis and tagging studies (Frost and Lowry 1997, Iverson et al. 1997).

Stable isotope ratios within harbor seal vibrissae do not appear to oscillate with any regular periodicity, although some seals do show large changes between enriched and depleted values. Harbor seals sampled in PWS in 1993 had relatively constant $\delta^{13}C$ values and some minor fluctuations (<2‰) in $\delta^{15}N$ values which likely correspond to seasonal changes in prey type. The periodicity of the fluctuations in the nine seals does not appear regular. Six of ten seals sampled from southern PWS in the spring of 1994 had large fluctuations, as great as 5.5‰, occurring concurrently in $\delta^{13}C$ and $\delta^{15}N$. Two-thirds of the seals sampled in September 1994 had oscillations larger than 1‰ occurring simultaneously in $\delta^{13}C$ and $\delta^{15}N$ in at least one location along the length of the whisker. All but two seals analyzed in spring 1995 also had simultaneous fluctuations larger than 1‰ in $\delta^{13}C$ and $\delta^{15}N$ in at least one location along the length of the whisker (Table 1).

Table 1. Stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope ratios in vibrissae of harbor seals from Prince William Sound, Kodiak and southeast Alaska. Age designation refers to adult (A), subadult (SA) and pup (P) seals.

Harbor Seal	**Sample Date**	**Sex**	**Age**	**Range ^{13}C**	**^{13}C**	**Max./Min. ^{13}C**	**Range ^{15}N**	**^{15}N**	**Max./Min. ^{15}N**
Harbor Seals - southeast Alaska, Gulf of Alaska									
HSA1SE	5 April 1993	F	P	-14.4 to -13.3	-13.8	-13.4 / -14.2	15.6 to 18.2	17.5	18.1 / 17.2
HSA2SE	5 April 1993	M	A	-17.6 to -14.1	-16.8	-14.1 / -17.1	14.4 to 18.5	15.3	16.1 / 14.5
HSA3SE	8 April 1993	M	A	-13.6 to -13.1	-13.3		17.4 to 18.1	17.8	
HSA4SE	9 April 1993	M	SA	-17.0 to -13.4	-14.7	-13.6 / -16.7	14.5 to 17.8	16.6	17.4 / 16.1
HSA5SE	9 April 1993	F	P	-14.6 to -13.9	-14.3		14.0 to 15.7	14.5	
HSA6SE	9 April 1993	F	SA	-14.2 to -13.5	-13.9		14.7 to 16.3	15.5	
HSA7SE	9 April 1993	M	A	-14.1 to -12.4	-13.4	-12.5 / -14.0	16.9 to 17.5	17.1	17.5 / 16.9
HSA8SE	9 April 1993	M	P	-14.1 to -13.0	-13.6	-13.0 / -13.8	14.1 to 17.9	16.9	18.0 / 15.3
HSA9SE	9 April 1993	F	A	-16.9 to -13.5	-15.4	-13.6 / -15.5	13.1 to 17.0	14.6	16.9 / 13.1
HSA10SE	Sept. 1993			-17.8 to -14.5	-16.8	-14.5 / -17.6	14.5 to 17.0	15.6	16.9 / 15.4
HSA11SE	Sept. 1993			-14.1 to -13.5	-13.7		17.8 to 18.6	18.2	
HSA12SE	Sept. 1993			-14.5 to -14.1	-14.3		15.1 to 16.1	15.4	
HSA13SE	Sept. 1993			-14.5 to -14.0	-14.2		15.5 to 17.2	16.1	
HSA14SE	Sept. 1993			-14.4 to -14.1	-14.2		14.9 to 15.4	15.2	
HSA15SE	Sept. 1993	M	A	-16.2 to -13.6	-14.3	-13.7 / -16.2	14.4 to 16.4	15.4	16.4 / 14.4
HSA16SE	Sept. 1993	M	A	-16.8 to -14.8	-16.1	-15.0 / -16.9	14.0 to 15.3	14.5	15.3 / 14.3
HSA17SE	Sept. 1993	M	SA	-17.8 to -14.0	-15.4	-14.1 / -17.6	13.5 to 16.0	14.8	15.8 / 13.7
HSA18SE	Sept. 1993	M	A	-14.3 to -12.9	-13.3	-13.1 / -14.2	16.5 to 17.9	17.2	17.8 / 16.5
HSA19SE	Sept. 1993	F	A	-14.6 to -14.0	-14.2		15.0 to 17.1	15.9	
HSA20SE	Sept. 1993	M	A	-14.5 to -13.5	-13.8	-13.5 / -14.5	14.6 to 16.0	15.3	16.0 / 14.6
HSB1SE	17 Aug. 1994	M	A	-18.0 to -14.6	-16.8	-14.6 / -18.0	14.2 to 16.9	14.9	16.9 / 14.2
HSB2SE	19 Aug. 1994	M	A	-18.1 to -14.8	-17.1	-14.8 / -18.0	13.7 to 16.2	14.5	16.2 / 13.8
HSB3SE	19 Aug. 1994	M	A	-17.7 to -16.0	-17.2	-16.0 / -17.7	13.8 to 15.8	14.6	15.8 / 13.8
HSB4SE	23 Aug. 1994	M	SA	-15.2 to -14.7	-14.8		15.6 to 16.6	16.1	

HSB5SE	23 Aug. 1994	F	A	-15.0 to -14.6	-14.8		15.9 to 17.2	16.4	
HSB6SE	23 Aug. 1994	F	A	-15.7 to -14.4	-14.9	-14.5 / -15.6	14.8 to 16.1	15.4	16.0 / 15.0
HSB7SE	19 Aug. 1994	F	A	-17.9 to -14.2	-17.1	-14.2 / -17.7	13.7 to 15.8	14.4	15.8 / 13.8
HSB8SE	24 Aug. 1994	F	SA	-15.9 to -14.6	-15.1	-14.8 / -15.7	15.0 to 16.2	15.6	16.2 / 15.3
HSB9SE	13 Sept. 1994	M	A	-16.1 to -13.5	-14.3	-13.7 / -16.1	15.3 to 17.3	16.6	17.3 /15.3
HSB10SE	13 Sept. 1994	F	A	-16.2 to -14.0	-14.9	-14.0 / -16.2	14.8 to 16.2	15.7	16.0 / 14.8
HSB11SE	13 Sept. 1994	M	A	-17.6 to -13.8	-15.5	-13.8 / -17.5	14.4 to 17.8	15.9	17.7 / 14.4
HSB12SE	13 Sept. 1994	M	A	-17.5 to -13.9	-15.0	-14.0 / -17.4	14.3 to 16.3	15.5	16.3 / 14.3
HSB13SE	13 Sept. 1994	F	SA	-17.7 to -16.3	-17.0	-16.3 / -17.5	13.8 to 15.6	14.4	15.5 / 13.9
HSB14SE	13 Sept. 1994	F	P	-14.8 to -14.1	-14.4		15.2 to 15.9	15.7	
HSB15SE	13 Sept. 1994	M	A	-17.3 to -14.3	-15.3	-14.4 / -16.9	14.0 to 17.6	15.8	17.6 / 14.0
HSB16SE	13 Sept. 1994	F	A	-17.6 to -15.3	-16.8	-15.3 / -17.6	14.5 to 15.9	15.0	15.9 / 14.5
HSB17SE	13 Sept. 1994	M	A	-17.1 to -13.9	-14.8	-14.0 / -17.1	14.7 to 17.7	16.7	17.7 / 14.7
HSC1SE	19 April 1995	M	A	-15.8 to -13.3	-14.1	-13.3 / -15.8	14.9 to 17.5	16.3	17.5 / 14.9
HSC2SE	19 April 1995	M	A	-17.2 to -14.1	-15.3	-14.1 / -17.2	14.7 to 18.0	16.5	18.0 / 14.7
HSC3SE	19 April 1995	F	A	-16.5 to -13.9	-14.8	-14.1 / -16.5	14.8 to 16.2	15.7	16.2 / 14.9
HSC4SE	19 April 1995	F	SA	-15.6 to -14.1	-14.6	-14.1 / -15.6	14.5 to 15.8	15.1	15.8 / 14.6
HSC5SE	19 April 1995	M	A	-17.7 to -16.4	-17.1	-16.4 / -17.7	14.5 to 16.1	15.2	16.0 / 14.5
HSC6SE	19 April 1995	M	A	-17.8 to -13.9	-16.0	-14.0 / -17.8	14.8 to 17.9	15.9	17.9 / 14.9
HSC7SE	19 April 1995	F	SA	-15.1 to -14.0	-14.3	-14.0 / -15.1	14.7 to 16.3	15.5	16.1 / 15.0
HSC8SE	19 April 1995	M	A	-17.8 to -13.8	-16.7	-13.8 / -17.8	14.3 to 16.6	15.2	16.4 / 14.3
HSC9SE	19 April 1995	F	SA	-15.2 to -13.8	-14.3	-13.8 / -15.2	14.7 to 15.3	15.0	15.3 / 14.7
HSC10SE	19 April 1995	M	A	-17.2 to -13.4	-14.5	-13.4 / -17.2	14.3 to 18.6	16.7	18.6 / 14.3
HSC11SE	20 April 1995	M	A	-17.4 to -14.4	-15.7	-14.6 / -17.4	14.4 to 18.4	16.2	17.8 / 14.9
HSC12SE	20 April 1995	M	A	-14.1 to -13.2	-13.8		17.8 to 19.1	18.2	
HSC13SE	20 April 1995	M	A	-18.1 to -13.9	-15.9	-14.0 / -18.1	14.7 to 17.7	16.3	17.6 / 15.4
HSC14SE	20 April 1995	M	SA	-14.1 to -13.2	-13.6		16.2 to 17.5	16.9	
HSC15SE	21 April 1995	M	A	-17.3 to -13.4	-14.8	-13.4 / -17.3	16.4 to 17.6	17.1	17.3 / 16.4
HSC16SE	21 April 1995	M	A	-17.0 to -13.4	-14.9	-13.4 / -17.0	15.1 to 16.0	15.6	16.0 / 15.1
HSC17SE	21 April 1995	F	A	-18.1 to -13.5	-16.4	-13.5 / -18.0	14.2 to 17.0	15.2	17.0 / 14.2
HSC18SE	21 April 1995	M	A	-14.9 to -14.2	-14.6		17.6 to 18.1	17.8	

HSC19SE	21 April 1995	F	A	-17.9 to -14.3	-15.4	-14.5 / -17.8	14.2 to 15.5	14.7	15.3 / 14.3
HSC20SE	21 Sept. 1995	M	A	-14.9 to -14.0	-14.3		15.5 to 17.1	16.6	
HSC21SE	21 Sept. 1995	M	A	-16.1 to -14.0	-14.6	-14.0 / -16.1	14.9 to 16.6	16.2	16.7 / 14.9
HSC22SE	21 Sept. 1995	F	A	-14.4 to -14.2	-14.3		16.7 to 17.0	16.8	
HSC23SE	21 Sept. 1995	M	A	-16.0 to -14.0	-14.6	-14.1 / -16.0	14.9 to 17.2	16.5	17.2 / 14.9
HSC24SE	22 Sept. 1995	F	SA	-15.7 to -14.4	-14.7	-14.4 / -15.7	15.0 to 15.8	15.3	15.8 / 15.0
HSC25SE	22 Sept. 1995	F	A	-14.6 to -14.1	-14.3		15.7 to 16.9	16.2	
HSC26SE	22 Sept. 1995	M	A	-17.4 to -15.6	-16.6	-15.8 / -17.3	14.3 to 15.5	14.8	15.4 / 14.4
HSC27SE	22 Sept. 1995	M	A	-14.5 to -13.7	-14.0		15.6 to 16.5	16.0	
HSC28SE	22 Sept. 1995	F	P	-15.0 to -13.6	-14.1	-13.7 / -14.9	16.3 to 18.3	17.3	18.3 / 16.3
Harbor Seals - Prince William Sound									
HSA1PWS	7 May 1993	M	A	-14.8 to -13.9	-14.5		18.1 to 19.5	18.8	
HSA2PWS	7 May 1993	F	SA	-16.2 to -14.8	-15.4	-15.0 / -16.2	15.3 to 19.0	17.7	19.0 / 15.3
HSA3PWS	7 May 1993	M	A	-15.8 to -14.8	-15.2		17.3 to 17.9	17.5	
HSA4PWS	7 May 1993	M	A	-16.5 to -15.0	-15.9	-15.0 / -16.4	15.8 to 17.9	16.7	17.8 / 15.9
HSA5PWS	7 May 1993	F	SA	-16.0 to -15.4	-15.8	-17.0 / -17.9	15.8 to 18.8	17.1	15.8 / 14.2
HSA6PWS	8 May 1993	F	SA	-16.4 to -15.0	-15.9		15.4 to 16.7	16.1	
HSA7PWS	8 May 1993	F	A	-16.4 to -15.2	-15.7		15.8 to 16.7	16.2	
HSA8PWS	8 May 1993	M	SA	-15.7 to -15.2	-15.4		15.5 to 17.9	16.4	
HSA9PWS	8 May 1993	M	A	-15.3 to -14.7	-15.0		16.9 to 18.7	17.5	
HSA10PWS	8 May 1993	M	SA	-15.6 to -15.1	-15.3		18.1 to 19.2	18.6	
HSA11PWS	9 May 1993	M	A	-15.1 to -14.7	-14.9		16.3 to 17.9	16.8	
HSA12PWS	9 May 1993	M	SA	-15.2 to -14.2	-14.6		16.1 to 19.3	18.5	
HSA13PWS	9 May 1993	F	SA	-16.3 to -16.0	-16.1		15.8 to 17.1	16.4	
HSB1PWS	26 April 1994	F	SA	-17.1 to -15.7	-16.4		14.7 to 16.7	15.8	
HSB2PWS	27 April 1994	M	SA	-16.6 to -15.7	-16.2		15.2 to 17.3	16.1	
HSB3PWS	27 April 1994	F	A	-16.5 to -12.6	-14.6	-12.6 / -16.3	13.4 to 18.0	16.0	17.8 / 13.8
HSB4PWS	27 April 1994	M	SA	-16.2 to -15.3	-16.1		15.8 to 16.6	16.1	
HSB5PWS	27 April 1994	M	A	-17.9 to -17.0	-17.5		14.0 to 15.9	14.9	
HSB6PWS	28 April 1994	M	A	-17.6 to -15.8	-16.6	-16.0 / -17.5	13.3 to 16.2	15.0	15.8 / 13.5

HSB7PWS	28 April 1994	F	A	-17.8 to -12.5	-15.2	-12.7 / -17.6	13.7 to 17.4	15.6	17.1 / 13.7
HSB8PWS	28 April 1994	M	SA	-17.7 to -15.5	-16.3	-15.6 / -17.6	13.7 to 16.9	15.6	16.7 / 13.9
HSB9PWS	28 April 1994	M	SA	-18.1 to -16.4	-17.1	-16.5 / -18.0	13.6 to 16.8	15.4	16.7 / 13.8
HSB10PWS	28 April 1994	M	A	-17.7 to -14.5	-15.8	-14.8 / -17.7	15.2 to 17.8	16.2	17.4 / 13.8
HSB11PWS	18 Sept. 1994	F	A	-17.9 to -16.3	-17.1	-16.6 / -17.6	14.7 to 17.1	15.4	17.0 / 14.7
HSB12PWS	18 Sept. 1994	F	SA	-16.9 to -15.8	-16.2		16.1 to 17.2	16.7	
HSB13PWS	18 Sept. 1994	M	SA	-16.8 to -15.8	-16.1		15.5 to 16.1	15.8	
HSB14PWS	18 Sept. 1994	M	A	-17.2 to -16.1	-16.6	-16.2 / -17.1	14.8 to 16.1	15.4	16.0 / 14.8
HSB15PWS	18 Sept. 1994	F	SA	-17.0 to -13.2	-15.2	-13.6 / -16.6	15.8 to 18.9	17.7	18.8 / 15.9
HSB17PWS	18 Sept. 1994	M	SA	-16.6 to -15.5	-15.9		15.5 to 16.3	15.9	
HSB18PWS	18 Sept. 1994	M	SA	-16.6 to -16.1	-16.3		15.6 to 17.0	16.2	
HSB19PWS	18 Sept. 1994	M	SA	-16.8 to -16.2	-16.4		15.5 to 16.5	16.0	
HSB20PWS	18 Sept. 1994	F	SA	-16.5 to -15.8	-16.1		16.1 to 17.2	16.7	
HSB21PWS	18 Sept. 1994	M	SA	-17.0 to -14.5	-15.8	-13.5 / -18.2	15.6 to 17.1	16.4	17.1 / 15.6
HSB22PWS	18 Sept. 1994	M	SA	-18.2 to -13.5	-15.1	-13.5 / -18.2	15.4 to 19.2	17.5	19.1 / 15.5
HSB23PWS	18 Sept. 1994	M	A	-17.9 to -16.2	-17.6	-16.4 / -17.8	14.0 to 15.4	14.4	15.3 / 14.3
HSB24PWS	19 Sept. 1994	F	A	-16.1 to -15.6	-15.9		15.6 to 16.8	16.3	
HSB25PWS	19 Sept. 1994	F	P	-17.5 to -14.2	-15.1	-14.3 / -17.3	16.6 to 17.9	17.1	17.3 / 16.2
HSB26PWS	19 Sept. 1994	M	SA	-16.5 to -16.0	-16.3		15.0 to 16.6	15.5	
HSB27PWS	22 Sept. 1994	F	A	-17.3 to -13.9	-15.4	-14.1 / -17.3	14.9 to 17.5	16.4	17.4 / 14.9
HSB28PWS	22 Sept. 1994	M	A	-17.5 to -15.6	-16.4	-15.7 / -17.3	14.6 to 16.4	15.7	16.4 / 14.7
HSB29PWS	22 Sept. 1994	M	P	-16.7 to -15.2	-15.9	-15.2 / -16.5	17.5 to 19.2	18.4	19.0 / 17.5
HSB30PWS	22 Sept. 1994	F	A	-17.8 to -15.2	-16.9	-15.6 / -17.6	14.5 to 16.8	15.2	16.5 / 14.7
HSB31PWS	22 Sept. 1994	F	SA	-17.7 to -16.1	-16.8	-16.1 / -17.6	14.6 to 16.7	15.7	16.5 / 14.5
HSB32PWS	22 Sept. 1994	F	A	-17.8 to -13.8	-16.1	-14.0 / -17.9	14.3 to 17.1	15.5	17.0 / 14.4
HSB33PWS	22 Sept. 1994	F	SA	-17.8 to -14.3	-16.4	-14.3 / -17.5	14.7 to 16.6	15.9	16.4 / 14.8
HSB34PWS	22 Sept. 1994	M	A	-17.2 to -14.4	-15.3	-14.4 / -17.0	14.7 to 17.2	16.0	17.0 / 14.9
HSB35PWS	22 Sept. 1994	F	A	-18.1 to -15.6	-16.8	-15.6 / -18.0	15.0 to 17.4	15.9	17.4 / 15.1
HSB36PWS	22 Sept. 1994	M	A	-17.9 to -16.8	-17.6	-16.9 / -17.9	14.5 to 16.2	15.1	16.2 / 14.5
TAHS1PWS	27 Sept. 1994	F	SA	-18.1 to -16.7	-17.5	-16.8 / -18.0	14.4 to 17.8	15.8	17.8 / 14.9

TAHS3PWS	29 Sept. 1994	F	A	-17.5 to -15.5	-17.0	-15.6 / -17.4	14.3 to 17.1	14.9	17.1 / 14.7
TAHS4PWS	30 Sept. 1994	M	A	-16.4 to -16.1	-15.6		16.1 to 18.7	17.3	
TAHS5PWS	30 Sept. 1994	M	A	-17.9 to -15.7	-16.4	-15.8 / -17.7	14.4 to 16.1	15.6	16.2 / 14.5
TAHS6PWS	1 Oct. 1994	F	P	-17.8 to -16.1	-16.5	-15.5 / -17.7	16.0 to 18.3	16.8	17.5 / 14.5
TAHS7PWS	1 Oct. 1994	M	P	-17.8 to -14.9	-15.7	-15.3 / -17.4	14.3 to 19.8	17.5	19.5 / 14.8
HSC1PWS	9 May 1995	M	SA	-17.3 to -15.5	-16.1	-15.5 / -16.9	15.3 to 17.6	16.3	17.3 / 15.4
HSC2PWS	9 May 1995	M	SA	-17.5 to -13.4	-14.9	-13.5 / -17.5	14.6 to 20.0	17.9	19.9 / 14.6
HSC3PWS	9 May 1995	M	SA	-16.3 to -15.0	-15.4	-15.0 / -15.9	16.4 to 19.5	18.4	19.5 / 16.4
HSC4PWS	9 May 1995	M	SA	-17.5 to -16.1	-16.6	-16.4 / -17.4	14.1 to 17.2	15.8	16.4 / 14.5
HSC5PWS	9 May 1995	M	SA	-17.5 to -15.6	-16.2	-15.6 / -17.5	14.6 to 16.9	15.8	16.9 / 14.8
HSC6PWS	11 May 1995	F	SA	-17.2 to -15.4	-16.2	-15.5 / -17.0	15.3 to 16.8	16.1	16.8 / 15.3
HSC7PWS	11 May 1995	M	SA	-17.6 to -15.1	-16.2	-15.2 / -17.5	14.2 to 16.9	15.7	16.8 / 14.3
HSC8PWS	11 May 1995	F	A	-17.8 to -14.3	-16.4	-14.4 / -17.8	14.1 to 16.8	15.3	16.6 / 14.4
HSC9PWS	11 May 1995	F	SA	-18.0 to -15.1	-15.9	-15.2 / -17.9	16.5 to 18.8	17.8	18.6 / 16.5
HSC10PWS	11 May 1995	M	SA	-17.2 to -12.8	-14.1	-12.9 / -17.1	16.0 to 18.9	17.9	18.7 / 16.1
HSC11PWS	11 May 1995	F	SA	-15.0 to -13.7	-14.3		16.7 to 17.3	17.0	
HSC12PWS	11 May 1995	M	A	-16.5 to -16.0	-16.1		15.6 to 16.9	16.2	
HSC13PWS	12 May 1995	F	SA	-17.1 to -15.0	-16.4	-15.0 / -17.0	15.6 to 17.0	16.1	16.7 / 15.8
HSC14PWS	12 May 1995	M	A	-16.5 to -15.0	-15.5	-15.0 / -16.5	16.7 to 18.1	17.7	18.0 / 16.7
HSC15PWS	12 May 1995	M	A	-17.7 to -15.6	-16.3	-16.0 / -17.7	14.9 to 16.9	16.2	16.8 / 14.9
HSC16PWS	12 May 1995	M	A	-17.4 to -16.0	-16.5	-16.1 / -17.3	14.6 to 16.3	15.7	16.3 / 14.6
HSC17PWS	12 May 1995	F	SA	-17.3 to -16.0	-16.5	-16.3 / -17.3	15.0 to 16.5	15.7	16.3 / 15.1
HSC18PWS	12 May 1995	M	SA	-17.4 to -16.1	-16.5	-16.2 / -17.5	15.0 to 16.7	15.9	16.6 / 15.0
HSC19PWS	12 May 1995	F	SA	-17.0 to -15.4	-15.9	-15.6 / -17.0	15.6 to 16.7	15.9	16.7 / 15.6

HSC20PWS	13 May 1995	F	A	-16.8 to -13.3	-15.1	-13.5 / -16.7	15.5 to 17.3	16.3	17.2 / 15.5
HSC21PWS	13 May 1995	F	SA	-17.5 to -14.8	-16.0	-14.8 / -17.4	15.7 to 18.5	17.5	18.4 / 15.8
HSC22PWS	13 May 1995	M	SA	-17.9 to -15.8	-16.2	-15.8 / -17.9	16.1 to 18.7	17.5	18.7 / 16.2
Harbor Seals - Kodiak, Gulf of Alaska									
HSA1KO	22 April 1993	F	A	-14.4 to -13.3	-13.8		15.6 to 16.2	16.0	
HSA2KO	24 April 1993	F	A	-14.6 to -13.3	-14.0		16.7 to 17.2	16.9	
HSA4KO	26 April 1993	F	SA	-15.0 to -14.0	-14.5		16.1 to 17.4	17.0	
HSA5KO	2 Oct. 1993	F	A	-14.3 to -13.8	-14.0		16.3 to 17.3	16.9	
HSB1KO	5 Oct. 1994	M	A	-15.1 to -13.5	-14.2		16.9 to 18.3	17.8	
HSB2KO	5 Oct. 1994	M	A	-15.5 to -14.1	-14.7		16.7 to 18.0	17.3	
HSB3KO	5 Oct. 1994	M	A	-14.4 to -12.8	-13.8		18.0 to 19.1	18.4	
HSB4KO	6 Oct. 1994	F	SA	-15.3 to -14.3	-14.8		15.5 to 18.8	17.2	
HSB5KO	6 Oct. 1994	F	P	-14.2 to -13.6	-13.7		17.7 to 18.9	18.3	
HSB6KO	6 Oct. 1994	M	SA	-17.9 to -13.8	-14.7	-13.8 / -15.9	15.4 to 18.1	17.6	18.1 / 16.2
HSB7KO	7 Oct. 1994	M	A	-15.6 to -14.3	-14.7		16.5 to 17.7	17.4	
HSB8KO	8 Oct. 1994	M	SA	-17.5 to -15.3	-16.0	-15.5 / -17.2	14.5 to 16.9	15.8	16.7 / 14.7
HSB9KO	8 Oct. 1994	F	SA	-16.5 to -15.7	-16.0		15.5 to 17.4	16.4	
HSB10KO	8 Oct. 1994	M	SA	-14.1 to -13.0	-13.7	-13.0 / -14.1	17.1 to 18.9	18.0	18.8 / 17.1
HSC1KO	29 Mar. 1995	M	A	-15.9 to -14.7	-15.2		15.7 to 16.6	16.1	
HSC2KO	29 Mar. 1995	F	SA	-15.7 to -15.0	-15.3		15.5 to 17.4	16.1	
HSC3KO	29 Mar. 1995	F	A	-17.3 to -14.9	-15.8	-15.1 / -16.6	14.3 to 16.5	15.5	16.2 / 14.9
HSC4KO	29 Mar. 1995	M	SA	-16.3 to -13.1	-13.9	-13.4 / -16.3	15.7 to 18.5	17.4	17.6 / 15.7
HSC5KO	29 Mar. 1995	F	SA	-16.4 to -15.4	-15.8	-15.5 / -16.5	15.0 to 16.5	15.7	15.9 / 15.0
HSC6KO	29 Mar. 1995	M	SA	-17.2 to -16.7	-17.0		15.6 to 16.2	15.8	
HSC9KO	9 Oct. 1995	F	SA	-16.4 to -14.6	-15.1	-14.7 / -16.2	14.9 to 16.6	15.6	16.5 / 14.9
HSC10KO	9 Oct. 1995	M	P	-15.3 to -13.8	-14.8	-13.8 / -15.3	16.5 to 20.0	18.1	20.0 / 16.5

HSC11KO	9 Oct. 1995	M	A	-17.1 to -13.9	-15.3	-13.9 / -17.1	14.6 to 17.9	16.3	17.9 / 14.6
HSC12KO	9 Oct. 1995	F	A	-15.5 to -14.0	-14.7	-14.0 / -15.3	15.5 to 17.2	16.4	17.1 / 15.6
HSC16KO	10 Oct. 1995	F	A	-14.6 to -13.6	-14.0		16.6 to 17.3	17.0	
HSC17KO	10 Oct. 1995	M	A	-15.7 to -13.9	-14.5	-14.0 / -15.6	16.1 to 18.9	18.0	18.9 / 16.1

The causes of these shifts are not currently known, but prey sampled outside Prince William Sound were more depleted in the heavy isotopes and we hypothesize that some seals may be foraging on isotopically depleted prey. Evidence of seals traveling outside the Sound was provided by satellite tag data (Frost and Lowry 1996). Prey data, e.g., herring and pollock, from T. Kline have shown very little isotopic fluctuation among locations within the Sound. However, Kline has found an isotopic gradient between *Neocalanus cristatus* from the northern Gulf of Alaska just south of Prince William Sound and *N. cristatus* within the Sound. A depletion of approximately 4‰ exists in $\delta^{13}C$ of the calanoid copepods outside the Sound, relative to those within (Kline 1997). Isotopic gradients have been identified by Schell et al. (in press) for zooplankton in the Bering Sea and Aleutian Islands, with on-shelf, productive waters being more enriched and deep, nutrient-poor waters being more depleted in $\delta^{13}C$ and $\delta^{15}N$ (Figures 2 and 3). Zooplankton samples collected from onshore to offshore transects throughout the Gulf of Alaska during 1996 revealed a similar isotopic gradient of enriched-to-depleted isotope values farther from shore (Figures 4 and 5).

The isotope fluctuations in the seal vibrissae were separated into maximum and minimum values based on differences greater than 1‰ in $\delta^{13}C$ and $\delta^{15}N$, respectively. Vibrissae, with fluctuations in $\delta^{13}C$ and $\delta^{15}N$ less than 1‰, had their ^{13}C and ^{15}N values averaged for the entire whisker. As depleted isotope values appear in sampled Gulf of Alaska prey, the enriched values along the vibrissae are expected to correspond to prey from Prince William Sound. Because harbor seals tend to have a strong site fidelity, it is expected that seals with constant isotope ratios forage near their haul-out sites in Prince William Sound (Pitcher and McAllister 1981).

Multiple tissues were collected from dead harbor seals to identify the isotope fractionation that occurs among different tissues during assimilation of food and tissue synthesis. Stable isotope values for muscle tend to most accurately reflect the stable isotope ratios for the whole animal (DeNiro and Epstein 1978). Tissue samples, which had to include muscle, were taken from fifty-three harbor seals killed by subsistence hunters in Ketchikan, Sitka and Prince William Sound. The $\delta^{13}C$ and $\delta^{15}N$ fractionation values were calculated as the difference in isotope ratios between each tissue and muscle from the same animal. Analysis of variance and Bonferroni post hoc tests were run for the entire data set to establish significant differences among tissues (SYSTAT 1997). The mean $\delta^{15}N$ of all seal tissues varied less than 1‰ in depletion or enrichment from muscle. The fractionation differences for harbor seal $\delta^{13}C$ range with increasing enrichment with blubber < brain < skin < collagen, kidney, liver, heart, blood < fur < vibrissae. The sample size for lung tissue was too small to test for significance. Tissues having the largest amount of lipid also had the greatest fractionation in $\delta^{13}C$ from muscle. This is to be expected because lipid synthesis discriminates against the incorporation of the heavier isotope, ^{13}C (DeNiro and Epstein 1977). These fractionation values were similar to those obtained in previous studies on gerbils (Tiezsen et al. 1983) and captive harp seals (Hobson et al. 1996). Least square means and standard errors were calculated and plotted for both $\delta^{13}C$ and $\delta^{15}N$ (Figures 6 and 7). Table 2 lists the fractionation values for eleven tissues collected from harbor seals.

Analysis of variance showed a significant shift in $\delta^{13}C$ from enriched to more depleted values for the combined collagen of all three pinniped species from 1950 through 1996 ($r^2 = 0.05$, $p = 0.034$) (Figure 12) (SYSTAT 1997). Harbor seals had a maximum $\delta^{13}C$ of -12.0‰ in 1970 and a minimum $\delta^{13}C$ of -15.5‰ in 1995. The $\delta^{13}C$ of northern fur seals ranged from a maximum value of -13.1‰ in 1976 to a minimum value of -16.7‰ in 1961. Steller sea lions had a maximum $\delta^{13}C$ of -12.5‰ in 1958 and a minimum $\delta^{13}C$ of -15.3‰ in 1989. The annual variance in the $\delta^{13}C$ of all three species ranged from less than 1‰ to as much as 5‰. Because of the large variance, each species was analyzed separately to test for significant changes. Only Steller sea lions showed a significant change in $\delta^{13}C$ ($r^2 = 0.39$, $p = 0.001$) (Figure 13). The sea lion $\delta^{13}C$ declined an average of 1.6‰ from 1950 to 1996 and the best fit of the data proved to be a line. Because of the lack of significant change in the harbor seal and northern fur seal $\delta^{13}C$ ($p = 0.265$, $p = 0.890$ respectively), the difference in the $\delta^{13}C$ for the combined pinniped data was driven solely by the significant decline in the $\delta^{13}C$ of the Steller sea lions (SPSS 1996).

A linear relationship between carbon isotope fractionation and diatom growth rates has been demonstrated by Laws et al. (1995). Bidigare et al. (1997) have shown that variations in carbon isotope fractionation occurred in marine systems due to fluctuations in algae growth rates. Schell (unpublished) used the laboratory and field results of Laws et al. and Bidigare et al. to explain the decline in the $\delta^{13}C$ in the baleen of bowhead whales. Schell used the isotope ratios in these whales, which feed primarily on zooplankton, as a proxy for primary production. Schell related the decline in the whale $\delta^{13}C$ since the 1960s to a reduction of more than 30% in the primary production in the Bering Sea since that time. A large amount of primary production is necessary to sustain top-trophic-level organisms like seals and sea lions. If primary production has decreased, then pinnipeds may be expending more energy in search of nutritionally rich prey. If those prey are not available in sufficient quantities, then the seals may be forced to feed on less optimal prey species. The underlying reasons behind the decline in the $\delta^{13}C$ are not yet known but are likely the result of changes in the physical environment.

Captive Animal Studies

Growth rate studies using Steller sea lions are being conducted for a related project and the data should prove useful in helping to interpret harbor seal growth rates. Regular oscillations in the stable isotopes of sea lion whiskers indicate the animals continue to grow whiskers for several years before the whisker is broken or lost. The growth rates of these annual oscillations have been compared with the limited growth information for sea lions in captivity. Six subadult Steller sea lions were being held in captivity at the Vancouver Aquarium in British Columbia, Canada. Vibrissae were clipped periodically during a three-year period and one animal had two successive whiskers cut, with an adequate overlap to estimate its rate of growth. The growth rate, averaged over fourteen months, was 0.14 mm/day. A second sea lion had a much shorter overlap of growth in two successive whiskers. The growth rate for the second animal, averaged over two winter months, was 0.17 mm/day. These data were contrasted with the average growth in the annual oscillations observed in Steller sea lion vibrissae from wild animals. Oscillation length varied from animal to animal and year to year. All the sea lions sampled in the Gulf of Alaska were adult females, while 72% of the sea lions from the Pribilof Islands in the Bering Sea were less than 5 years of age and almost exclusively male. Growth rates averaged over twelve months were 0.1-0.12 mm/day for all sea lions combined. Separation of growth rate by age has not been completed for the sea lions at this time. The range of growth from year to year averaged over twelve months was 0.05-0.18 mm/day. Growth rates for the captive sea lions were faster than those for wild animals. This was to be expected since these captive animals did not need to expend extra energy foraging for food and had not begun mating and gestating. We hope to continue sampling vibrissae from these captive sea lions once some of the animals have been moved to the Alaska SeaLife Center so that growth rate changes can be monitored seasonally as the animals' metabolic requirements change.

No conclusive growth rates have been determined for the captive harbor seals at Mystic MarineLife Aquarium in Connecticut. One dose of doubly-labeled glycine ($\delta^{13}C$ and $\delta^{15}N$) was administered to a captive harbor seal, "Norton," in January 1996 at Mystic MarineLife Aquarium. A second dose of doubly-labeled glycine was administered to "Norton" and an initial dose was administered to a second harbor seal, "Peter," in June 1996. A vibrissae was cut off "Norton" at the end of August and sent to us for stable isotope analysis. The rapid increase in ^{13}C and ^{15}N was incorporated into the whisker but only one peak was evident. We believe the peak is the result of the June injection of the labeled glycine and the rest of the whisker containing the January peak has broken off. That would mean the whisker grew 0.60 mm/day averaged from June through August (Figure 14). If this peak was the result of the January injection, then the June peak was in the portion of the vibrissae remaining in the cheek. In this instance, the growth rate would have been 0.37 mm/day from January through August. Both rates far exceed the growth rate for the recaptured adult male harbor seal in southeast Alaska whose growth rate during the winter, averaged over seven months, was only 0.07 mm/day (Figure 15). In 1997 a second harbor seal was recaptured and a whisker removed for isotope analysis two years after a whisker was initially sampled. Data from this whisker may provide further information on the difference in growth rates between captive and wild seals. "Norton's" growth also exceeded growth rates in the captive, subadult Steller sea lions, which ranged between 0.14 and 0.17 mm/day averaged over twelve months. Two additional harbor seals at Mystic MarineLife Aquarium have been added to the captive growth rate experiment. "Norton" and "Peter" were moved to facilities where it would have been difficult to continue the study (Table 3). In a complementary project, stable-isotope labeled amino acids have also been given to two subadult Steller sea lions at the Aquarium in order to estimate their vibrissae growth rates.

Table 3. Sequence of vibrissae growth rate experiment. "Norton" and "Peter" were given $\delta^{13}C$ and $\delta^{15}N$-labeled glycine while "Cecil" and "Snapper" were given only $\delta^{13}C$-labeled glycine.

	Norton	**Peter**	**Cecil**	**Snapper**
Delivery	Injection	Injection	Oral	Oral
Doses	2	2	1	1
Tissues	Blood, vibrissae	Blood, vibrissae	Blood	Blood
Delivery date	12 Jan 1996 4 June 1996	4 June 1996	12 May 1997	12 May 1997
Sample date	29 Aug 1996 5 Nov 1996	5 Nov 1996		

Metabolic processes regulate growth in animals and may differ between phocids and otariids. Physiological studies currently being done on these captive sea lions should soon provide researchers with metabolic data that can be correlated to growth rates. Metabolic studies on captive harbor seals showed the highest metabolic rates in April and August and the lowest rates in June and November. The highest rates corresponded to mating and pupping and the lowest rates corresponded to the cessation of these activities and to molting. A general decline in metabolic rates occurred with increasing seal age (Rosen and Renouf 1995). Seasonal variation in vibrissae growth rates is expected based on the aforementioned study, and would explain the variations in growth rates observed to date. Our captive seal study has been modified to try to elucidate seasonal changes in the vibrissae growth.

Interactions with Other Studies

Our main cooperative work has been and continues to be with K. Frost in conjunction with ADFG tagging and physiology studies on harbor seals. This work will be reported by that study component and is only briefly discussed here. Samples of seal blubber and potential prey items have been analyzed for fatty acid composition to estimate the sources of food being transferred up the food chain. The distinct changes in fatty acid composition across short geographic distances have been previously mentioned in the section regarding isotope ratio variations in the harbor seals. As a potentially excellent means of validating trophic insight from stable isotope ratios, subsets of the 1996 and 1997 seal vibrissae are being analyzed, added to existing databases, and contrasted with results from the fatty acid analyses.

The interaction with the modeling component of the SEA program has intensified. As the data have been acquired and compiled, we are able to test model assumptions and predictions by independent comparison using the isotopic model as a validation measure. Although similar carbon isotope labels in different members of the marine community may be indistinguishable, the trophic changes predicted will lead to testable shifts in the isotope ratios of nitrogen.

The wide selection of potential prey items in Prince William Sound that may be consumed by harbor seals has been collected over the past field seasons or was obtained from archived samples. These data are reported by T. Kline as part of the SEA program conducted by the Prince William Sound Science Center. Samples of harbor seal prey species (including forage fishes, salmon and herring) in the vicinity of major haul-outs and high population densities have been collected, analyzed and added to the database.

To date, the interaction with other studies on top consumers has been limited to the acquisition of vibrissae from sea otter carcasses and tissue from sea birds. Prey samples have been analyzed for the sea bird component of the ecosystem study. Currently available data are being synthesized by the principal investigators and will be reported by them.

CONCLUSIONS

The three aspects addressed by this program are progressing well and there are no perceived reasons for alteration of the scope of work at this time.

Analytical services for stable isotope ratio determinations: The mass spectrometry service has had full use in this project and in the SEA program and other oil-spill-related projects supporting sea otter and sea bird studies. At six months into the fiscal year, over 4000 samples have been run and new samples are being added as the spring field season gets underway. No serious machine problems have arisen during the past six months and all data have been made available to the PI and collaborators in a timely manner. A new mass spectrometry system has been added to the facility to provide greater sample capacity and increased sensitivity for small samples.

Harbor seal trophic energetics: All harbor seal tissues have been analyzed to determine the isotopic fractionation that occurs among differing tissues. These data will be of use to researchers who want to know the isotopic makeup of particular harbor seals but are limited by the available tissue. Some vibrissae remain to be analyzed and then completed data sets will be statistically analyzed. Certain prey items lacking from the Gulf of Alaska food web have been added to the database. Large fluctuations in harbor seal vibrissae have been contrasted with food webs in and outside Prince William Sound. These fluctuations seem to indicate the seals are relying upon more than one food web, whether they are pelagic vs. benthic or Prince William Sound vs. Gulf of Alaska. Comparisons of archived and modern seal tissues indicated no trophic shift occurred, but that a general decline in $\delta^{13}C$ took place between 1950 and 1996 in three species of pinnipeds in the Gulf of Alaska and the Bering Sea. The decline in $\delta^{13}C$ seems to lend supporting data to the hypothesis that primary production has declined in the North Pacific Ocean and may indicate a change in the carrying capacity of the ecosystem. Isotope data from subsets of the remaining 1996 and 1997 seals will be contrasted with the fatty acid composition information compiled by K. Frost of ADFG, to further detail food web structure and interannual variability within Prince William Sound.

Captive seal studies: Preliminary data from the captive harbor seals at Mystic MarineLife Aquarium indicate the stable-isotope-labeled glycine is an effective marker in the vibrissae for the growth rate studies. Some initial growth rate data have been calculated and contrasted with growth rates from a wild harbor seal, captive Steller sea lions and wild Steller sea lions. Growth rates in the captive harbor seal seem to surpass those of wild phocids and otariids and captive otariids. The growth rate experiment is ongoing and expected to be concluded in the next year. A dose of ^{13}C- and ^{15}N-labeled glycine was administered to one harbor seal at Mystic MarineLife Aquarium in January 1996 and to a second seal in June 1996. Two new harbor seals were added to the experiment in May 1997 and ^{15}N-labeled glycine was orally administered. A whisker from each seal is expected to be cut during the summer of 1998.

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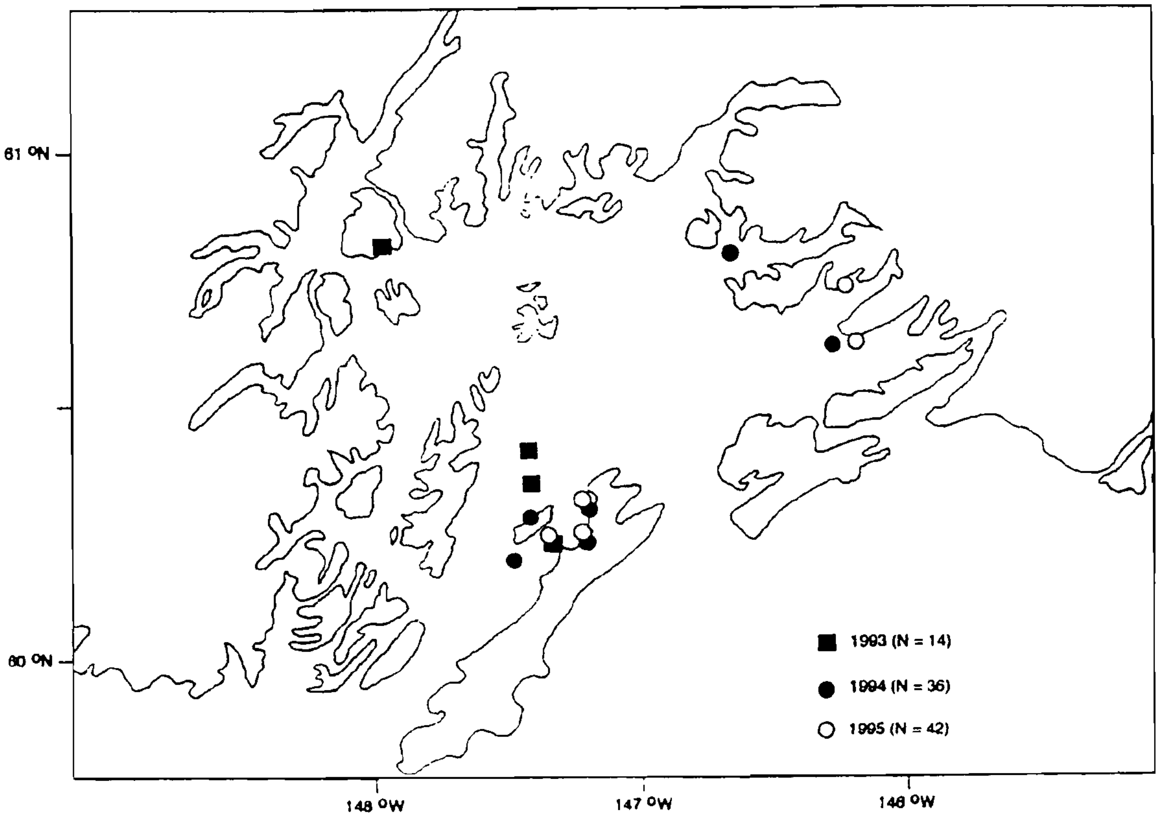

Figure 1. Sample locations for harbor seals in Prince William Sound, 1993-1995.

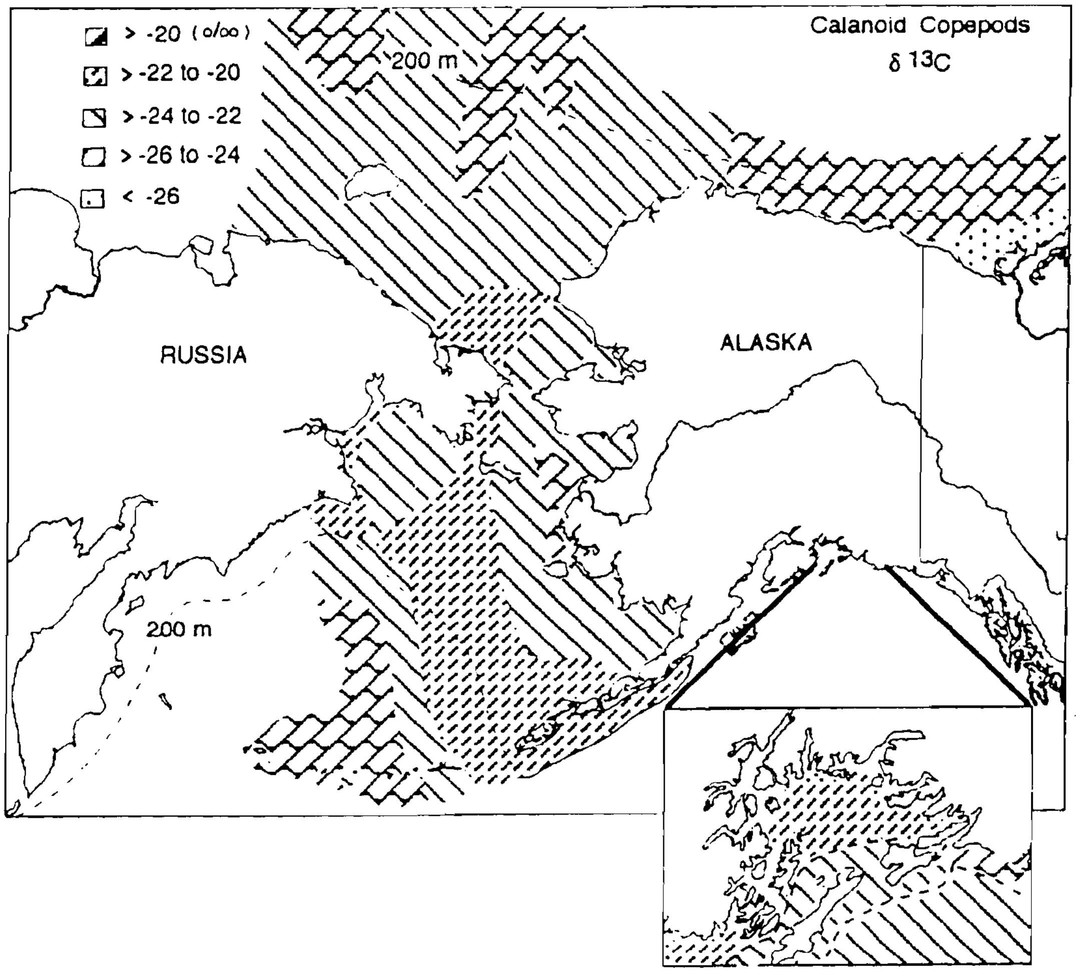

Figure 2. $\delta^{13}C$ isotope contours for calanoid copepods in the Bering, Chukchi and Beaufort seas.

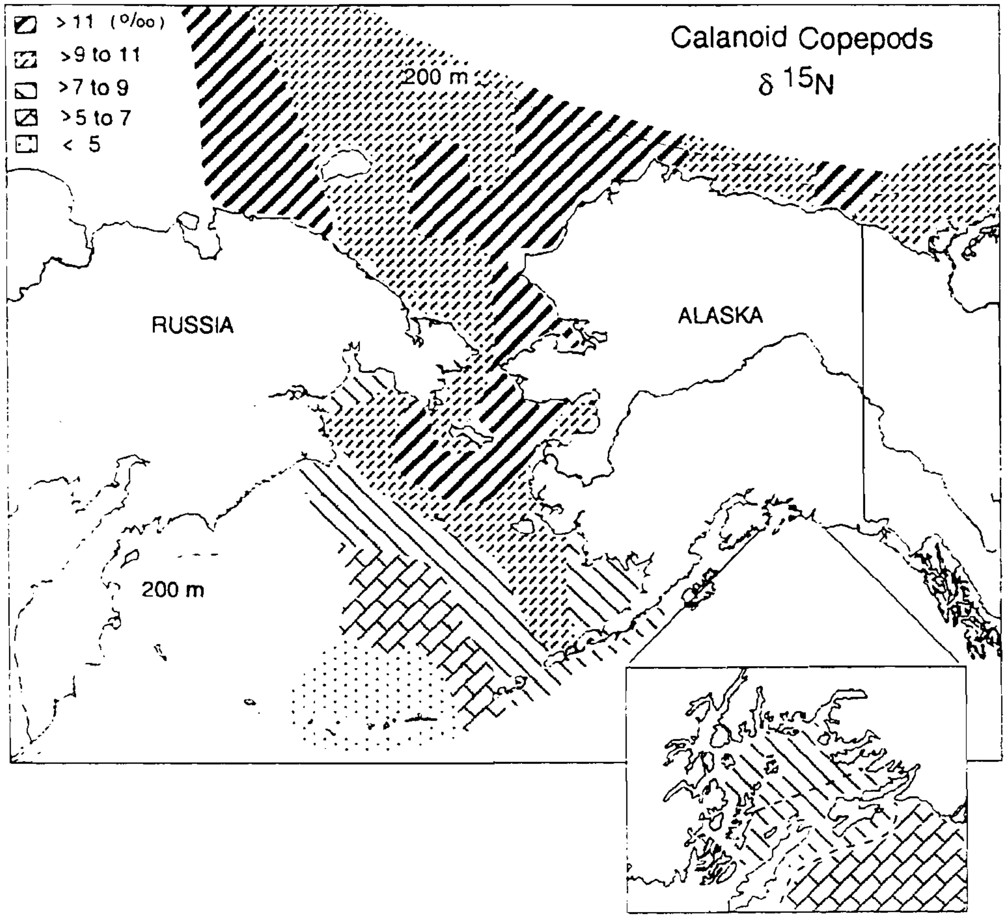

Figure 3. $\delta^{15}N$ isotope contours for calanoid copepods in the Bering, Chukchi and Beaufort seas.

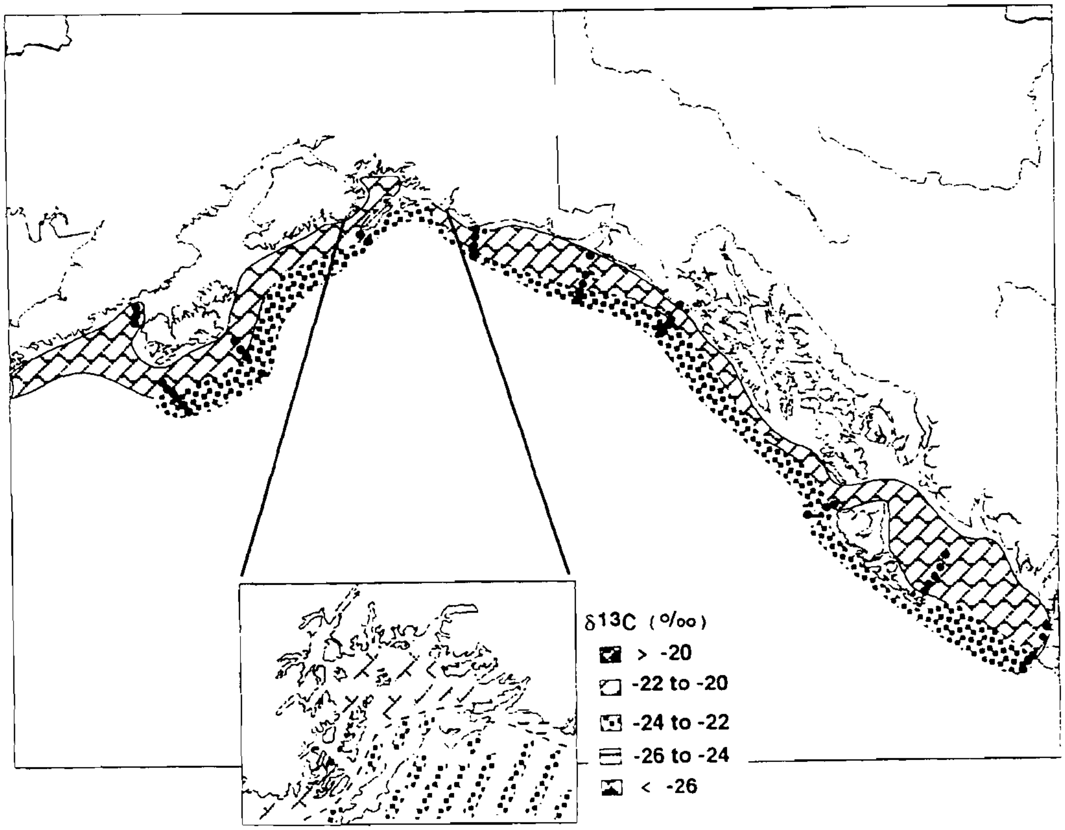

Figure 4. δ^{13}C isotope contours for calanoid copepods in the Gulf of Alaska and Prince William Sound.

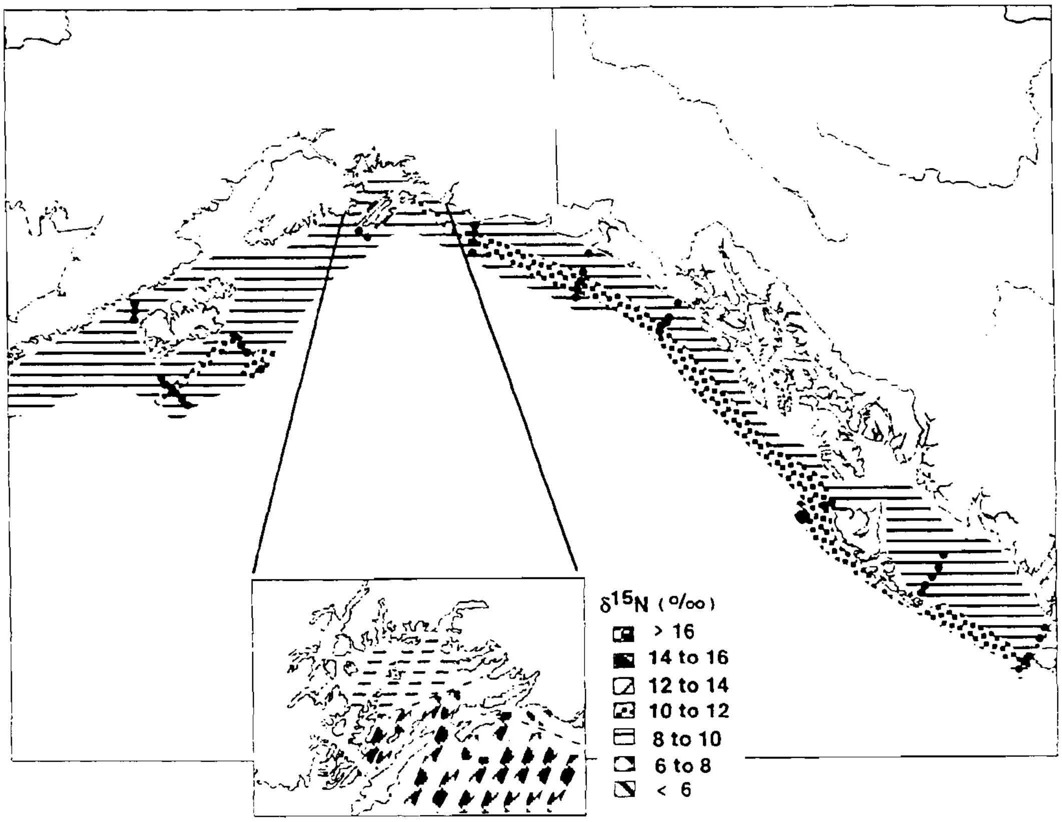

Figure 5. $\delta^{15}N$ isotope contours for calanoid copepods in the Gulf of Alaska and Prince William Sound.

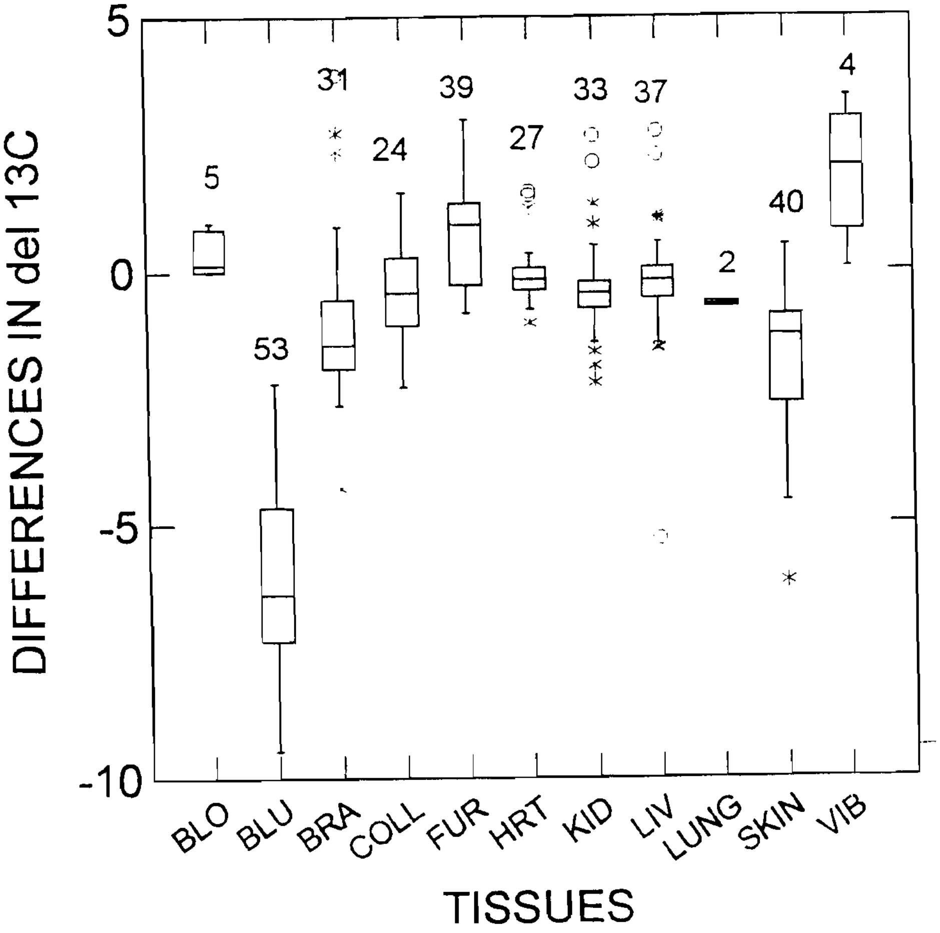

Figure 6. $\delta^{13}C$ fractionation of harbor seal tissues. blo = whole blood, blu = blubber, bra = brain, coll = collagen, hrt = heart, kid = kidney, liv = liver, vib = vibrissae. The sample size of each tissue is given above the box plot. * indicates values outside the first and third quartile of all values. o indicates values lower than 12.5% and greater than 87.5% of all values.

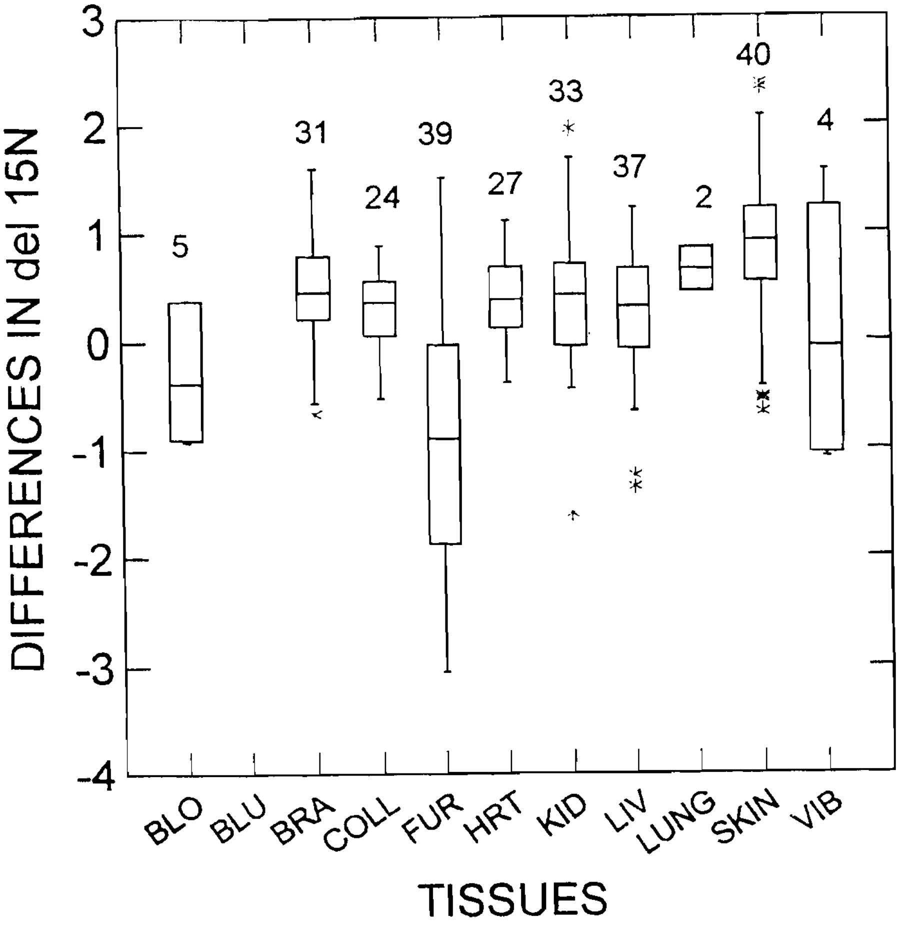

Figure 7. $\delta^{15}N$ fractionation of harbor seal tissues. blo = whole blood, blu = blubber, bra = brain, coll = collagen, hrt = heart, kid = kidney, liv = liver, vib = vibrissae. The sample size of each tissue is given above the box plot. * indicates values outside the first and third quartile of all values. o indicates values lower than 12.5% and greater than 87.5% of all values.

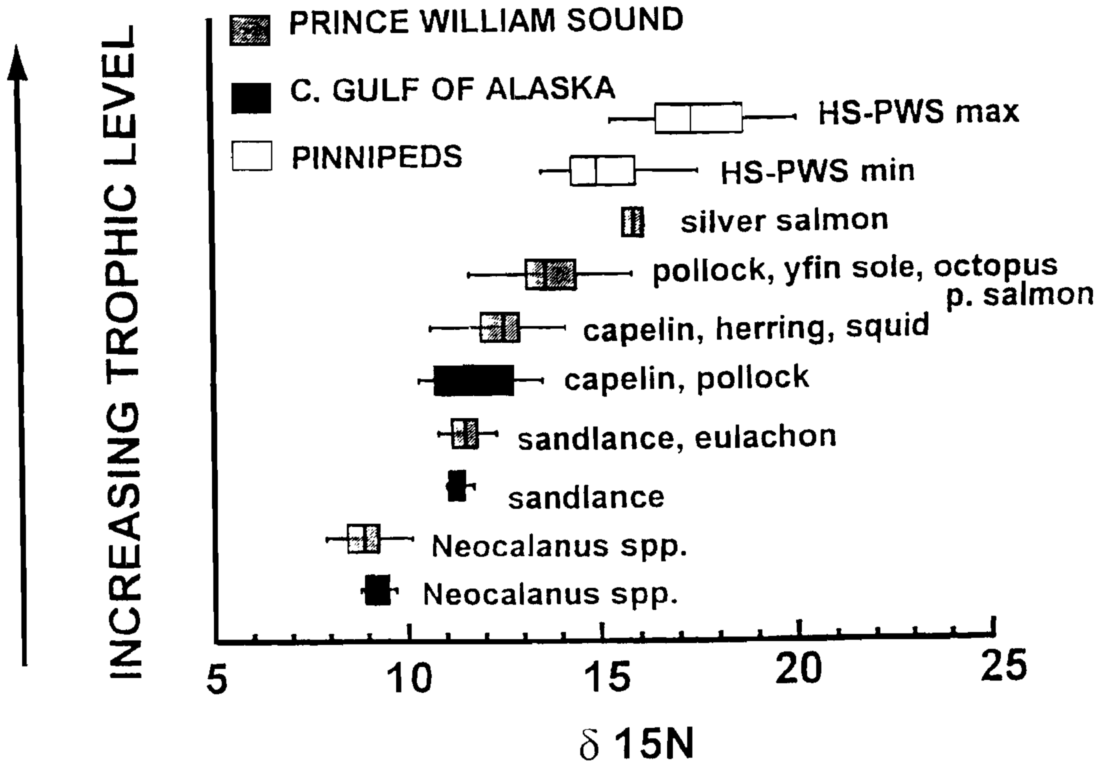

Figure 8. Maximum (max) and minimum (min) mean (± SE) $\delta^{15}N$ from Prince William Sound harbor seals (PWS HS) and mean (± SE) $\delta^{15}N$ from Prince William Sound and Gulf of Alaska fishes and invertebrates. Vibrissae values have been normalized to muscle. Sample sizes are ≥ 5.

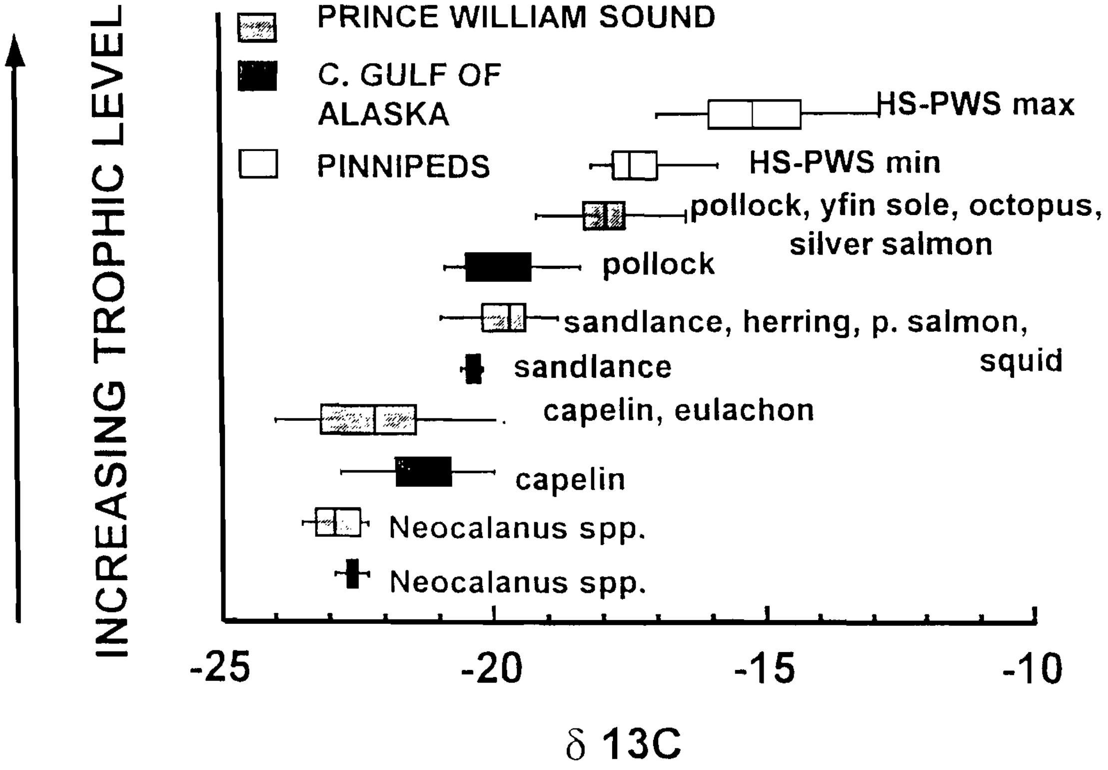

Figure 9. Maximum (max) and minimum (min) mean (± SE) $\delta^{13}C$ from Prince William Sound harbor seals (PWS HS) and mean (± SE) $\delta^{13}C$ from Prince William Sound and Gulf of Alaska fishes and invertebrates. Vibrissae values have been normalized to muscle. Sample sizes are ≥ 5.

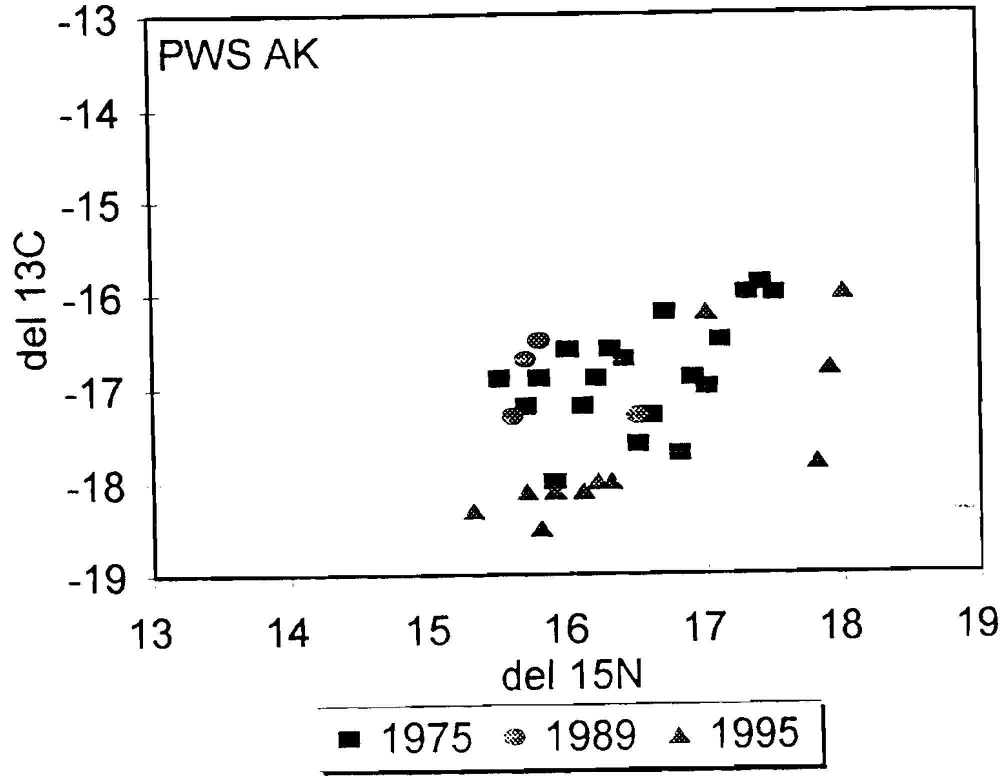

Figure 10. Stable carbon and nitrogen isotope ratios for Prince William Sound harbor seals. 1975 and 1989 values are from muscle and 1995 values are from vibrissae normalized to muscle.

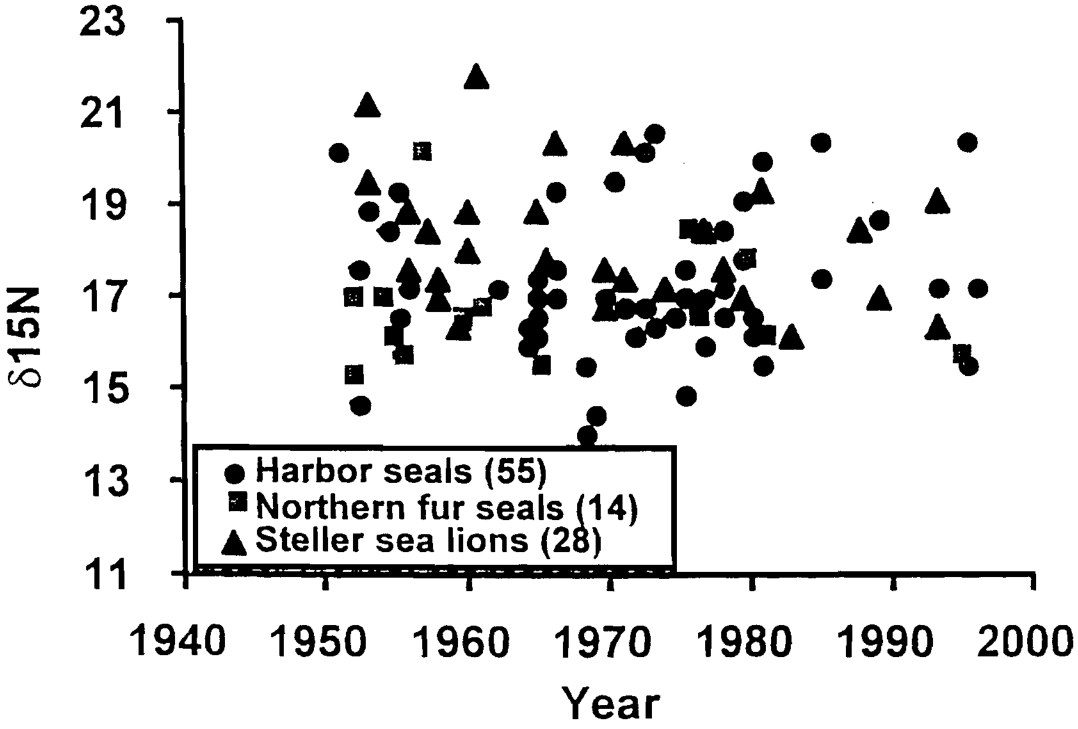

Figure 11. Bone collagen $\delta^{15}N$ values for harbor seals, Steller sea lions and northern fur seals from Prince William Sound, the Gulf of Alaska and the Bering Sea, 1950-1996.

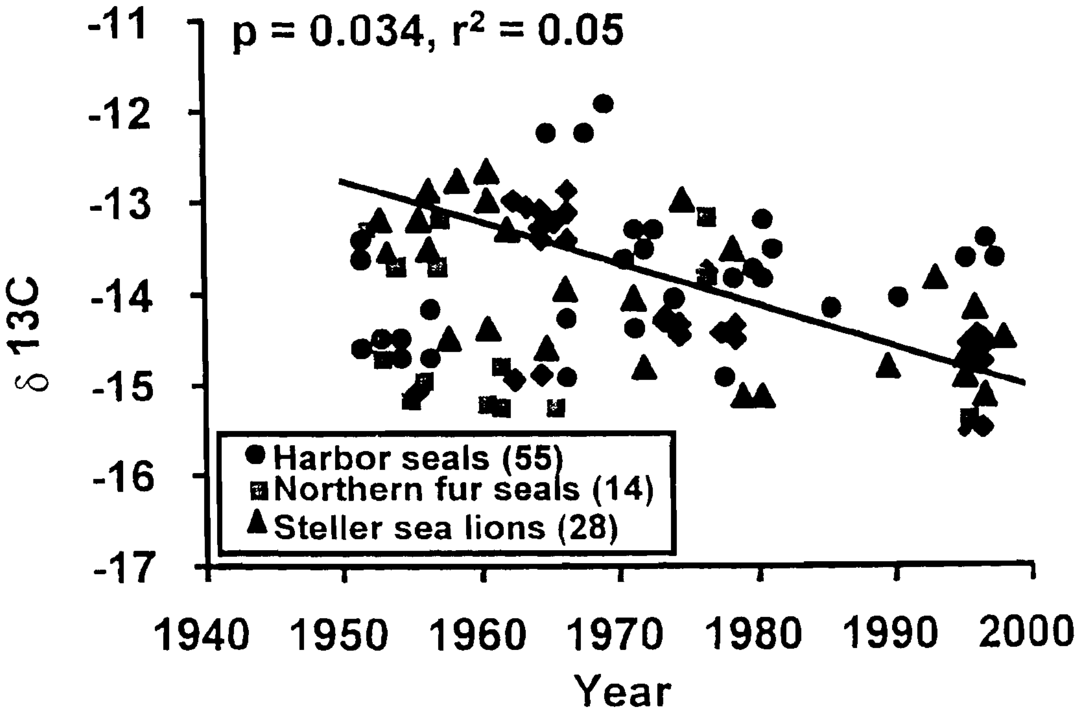

Figure 12. Bone collagen $\delta^{13}C$ values for harbor seals, Steller sea lions and northern fur seals from Prince William Sound, the Gulf of Alaska and the Bering Sea, 1950-1996.

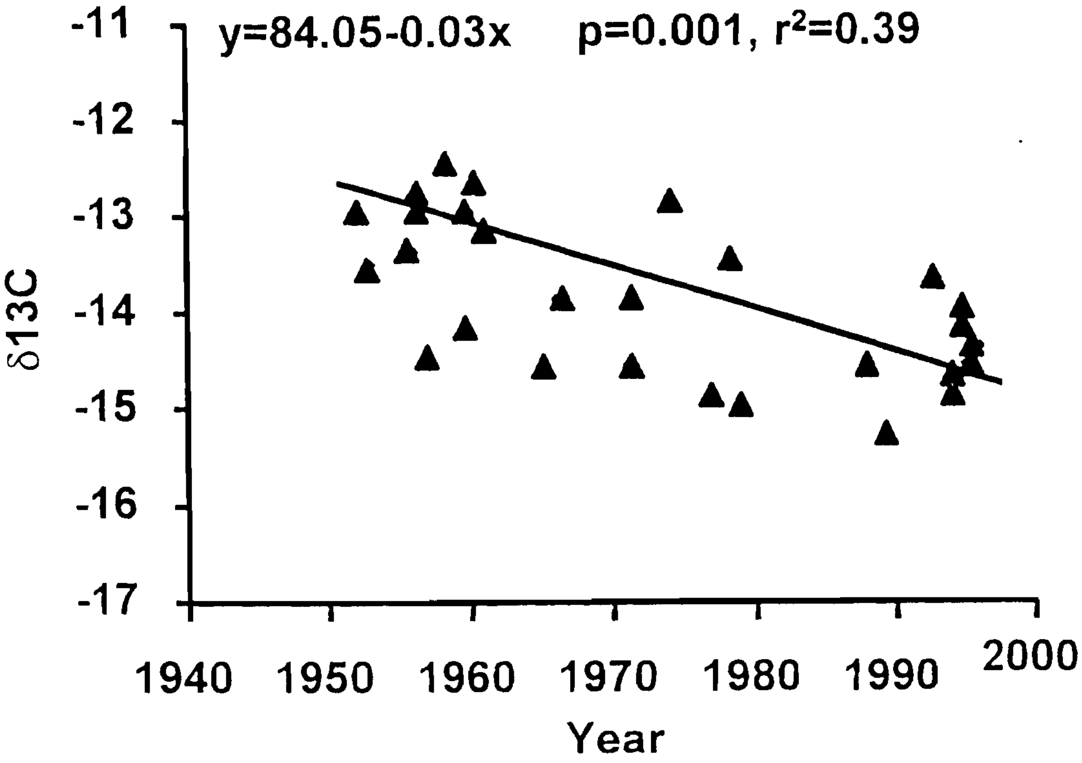

Figure 13. Bone collagen δ^{13}C values for Steller sea lions from the Gulf of Alaska and the Bering Sea, 1950-1996.

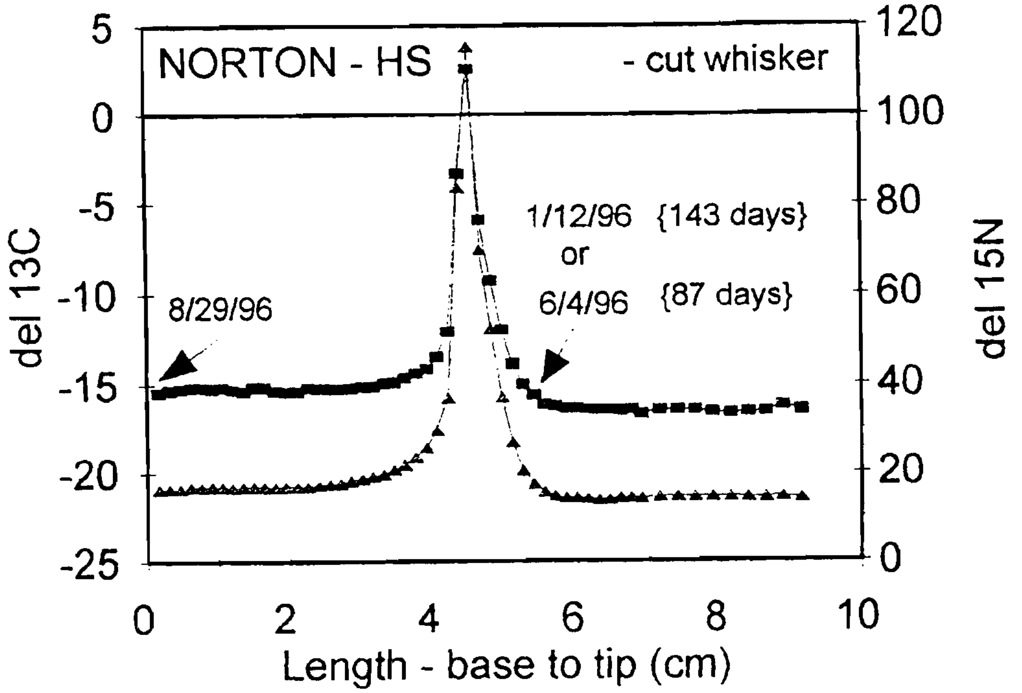

Figure 14. Vibrissae plot with doubly-labeled ($\delta^{13}C$ and $\delta^{15}N$) glycine peak for an adult harbor seal, "Norton", held in captivity at the Mystic Marinelife Aquarium, Connecticut.

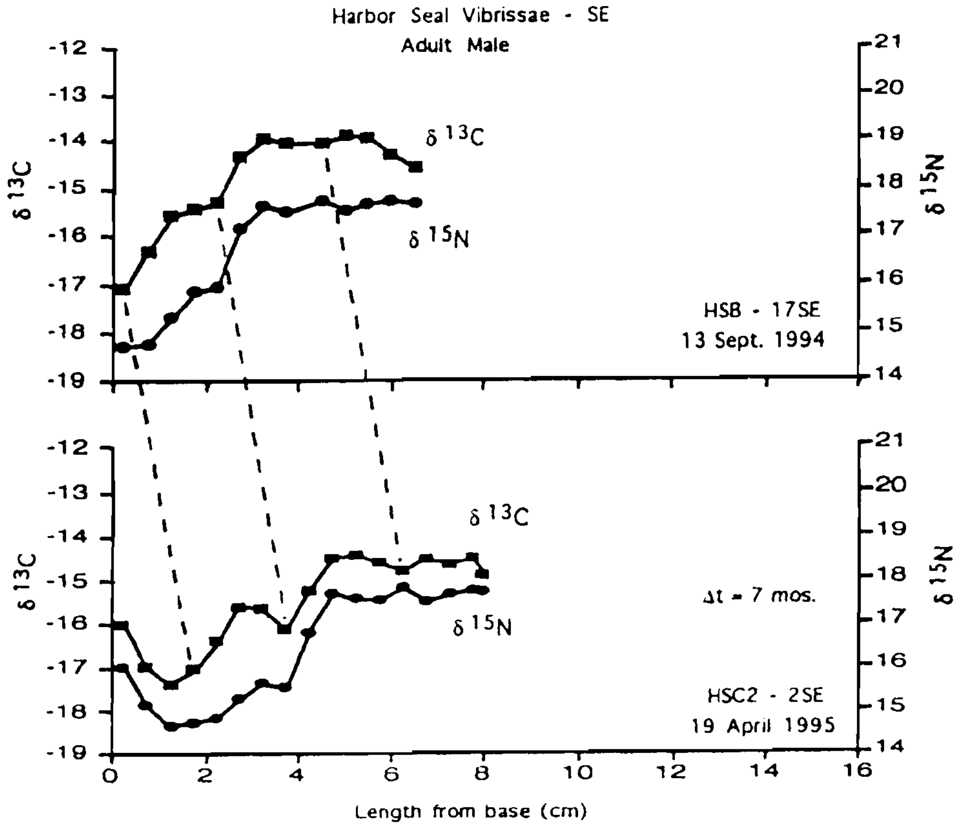

Figure 15. Vibrissae plots from a recaptured adult harbor seal in southeast Alaska. A vibrissae sampled in September 1994 (upper plot) is contrasted with a vibrissae taken from the same seal seven months later (lower plot).