Exxon Valdez Oil Spill
Restoration Project Annual Report

Isotope Ratio Studies of Marine Mammals in Prince William Sound

Restoration Project 96170
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: 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, a stable isotope study of harbor seals and potential prey species was begun in Prince William Sound (Restoration Project 95320I). T. Kline, then of the University of Alaska Fairbanks, was a co-investigator but upon taking a position with the Prince William Sound Science Center, the project was split into two parts. T. Kline collected data on lower trophic levels while this project is focused on harbor seals and prey species as needed. In FY96, this project (96170) was separated completely, with responsibility 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 consists 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 of 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 the sound and the adjacent Gulf of Alaska. 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 Gulf of Alaska) 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 observed in the western Gulf of Alaska 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: Data consists 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. The data are in spreadsheets and tabular format in Corel QuattroPro and Microsoft Excel and will be included in refereed publications and a graduate dissertation. The project PI will maintain these data files and can be contacted at the following: Dr. Donald M. Schell, P.O. Box 757220, Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, Alaska 99775-7220; email: ffdms1@aurora.alaska.edu, 907/474-7978 (phone), 907/474-5863 (fax).

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TABLE OF CONTENTS

LIST OF TABLES

Tables — Page

LIST OF FIGURES

Figure — Page

EXECUTIVE SUMMARY

This report describes the preliminary results of the study on the food webs supporting harbor seals in Prince William Sound. The integrating methodology for this task is the use of natural stable isotope abundances as tracers of carbon and nitrogen transfers through the food webs. 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, while harvested or dead animals had all vibrissae removed for analysis. To date, approximately 100 seals have been sampled and most of these have been analyzed. The data from these vibrissae reveal a temporal record allowing comparisons of interannual changes in feeding. When possible, samples from different organ tissues, e.g. muscle and blubber, were also taken. A variety of tissues from a single animal were analyzed to determine isotopic fractionation among the tissues. This has 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 and a whisker was clipped on 29 August 1996 for analysis. The added label was visible but surprisingly, the January marker had already grown to the tip of the vibrissae and was lost. In contrast, one 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 1.5 cm in seven months time. The marked contrast between these two results implies that whisker growth rates in harbor seals are highly seasonal and 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.

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. Our findings, although preliminary at this point, include several interesting findings. 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 have large changes 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 K. Frost in a collaborating study and have been found to be very different among regions, supporting 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. Samples collected in recent years have similar $\delta^{15}N$ values as archived specimens but show depleted $\delta^{13}C$ values, indicative of prey derived either from offshore areas or resulting from a general decrease in primary productivity in Prince William Sound.

A conceptual model of harbor seal feeding has been constructed based on the known isotope ratios in lower trophic levels and fishes (primarily capelin, herring and pollock). 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. Sampling of these potential prey species will be a major focus in 1997.

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 the studies by the 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. 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 between trophic levels (phytoplankton to zooplankton to fishes to top consumers). 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. 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 ä with an accompanying loss of the lighter isotope through excretion. 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 calibrate responses to changing isotopic composition in diet and 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 in cooperation with the marine mammal component and is described in the report accompanying this section.

3. As the major isotope ratio analysis facility, we have provided analytical services for carbon and nitrogen isotope ratios to other PI's involved with spill-related studies and assisted with the interpretation of the acquired data. This task has required approximately 1020% 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 will be collected from native hunters. These samples will be 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 and aid 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 being fed known diets, establish the relationships between whisker growth rate and temporal changes and the fractionation factors between the $\delta^{13}C$ and $\delta^{15}N$ values of diet and consumer.

7. Compare the isotope-ratio derived food web models to predictions by the ÒLake-RiverÓ 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, claws, etc.) (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 have been provided by ADFG personnel and combined with other lower trophic level organisms to assist in assigning trophic status. National Marine Fisheries Service personnel provided forage species from inshore and offshore waters in southeast Alaska. Isotopic values for these species are 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. These prey are being used as indicators of regional isotopic differences. These regions are used to help locate areas of foraging by seals traveling outside Prince William Sound. A National Marine Fisheries Service triennial survey of the entire Gulf of Alaska took place during the summer of 1996 and provided prey for areas where data was lacking.

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 are being used to determine the range of the isotopic gradient between the sound and locations in the Gulf of Alaska. These regional isotopic difference will be exhibited in higher order consumers due to trophic transfers in food webs. Data collected by Schell (1996) and Kline (1997) have shown these regional differences exist throughout the Bering Sea and between Prince William Sound and one area of the Gulf of Alaska.

A few grams of muscle tissue were extracted from several samples of each 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 muscle 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. Multiple tissue types were collected from each animal to identify the isotope fractionation that occurs among differing tissues. Stable isotope values for muscle tissue were assumed representative of the values for a whole animal. During the past three 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 taken for analysis.

Vibrissae and tissues from ninety-eight harbor seals have been or continue to be 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 other segment 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 Alaska Department of Fish and Game 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. The University of Alaska Museum provided bone tissue from harbor seals from various regions of the Gulf of Alaska and Bering Sea from 1950 to 1996. Bone collagen was extracted using the methods of Matheus (1995) and Stafford et al. (1988). The stable isotope ratios of these tissues were used to compare and contrast to the stable isotope ratios of present samples. By obtaining seal tissues from multiple regions prior to the population decline (pre-1970), any significant changes in these ratios may be an indication of changes in ecosystem productivity over 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 were subsequently led into the mass spectrometer by capillary 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.

A second type of growth rate experiment was conducted simultaneously at the Vancouver Aquarium in British Columbia, Canada on subadult Steller sea lions. Vibrissae have been cut from the muzzle of each of the six animals periodically during the past three years. The vibrissae were analyzed for their stable isotopes and all the whiskers from an animal are plotted together. Overlap in growth from one vibrissae to the next is measured from a 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, tissue samples have been collected and analyzed from over 100 harbor seals. Additionally, vibrissae samples have been collected from over 140 harbor seals, sixty percent of those vibrissae have been analyzed. Analyzed vibrissae from harbor seals are listed in Table 1 with the range and mean stable isotope ratios. These illustrate 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 ADF&G seal surveys in Prince William Sound and body tissues were collected by native subsistence hunters in cooperation with ADF&G.

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

Table 1. Harbor seal vibrissae from Prince William Sound. Age designation refers to adult (A), subadult (SA) and pup (P) seals. Samples for which data are not reported are currently being analyzed.

Harbor Seal	Sample Date	Sex	Age	Range $\delta^{13}C$	$x\delta^{13}C$	Range $\delta^{15}N$	$x\delta^{15}N$	
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	15.3 to 19.0	17.7
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	15.8 to 17.9	16.7	
HSA5PWS	7 May 1993	F	SA	-16.0 to -15.4	-15.8	15.8 to 18.8	17.1	
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	13.4 to 18.0	16.0	
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	13.3 to 16.2	15.0	
HSB7PWS	28 April 1994	F	A	-17.8 to -12.5	-15.2	13.7 to 17.4	15.6	
HSB8PWS	28 April 1994	M	SA	-17.7 to -15.5	-16.3	13.7 to 16.9	15.6	
HSB9PWS	28 April 1994	M	SA	-18.1 to -16.4	-17.1	13.6 to 16.8	15.4	
HSB10PWS	28 April 1994	M	A	-17.7 to -14.5	-15.8	15.2 to 17.8	16.2	
HSB11PWS	18 Sept. 1994	F	A	-17.9 to -16.3	-17.1	14.7 to 17.1	15.4	
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	14.8 to 16.1	15.4	
HSB15PWS	18 Sept. 1994	F	SA	-17.0 to -13.2	-15.2	15.8 to 18.9	17.7	
HSB16PWS	18 Sept. 1994	F	SA	no vibrissae				
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	15.6 to 17.1	16.4	
HSB22PWS	18 Sept. 1994	M	SA	-18.2 to -13.5	-15.1	15.4 to 19.2	17.5	
HSB23PWS	18 Sept. 1994	M	A	-17.9 to -16.2	-17.6	14.0 to 15.4	14.4	
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	16.6 to 17.9	17.1	
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	14.9 to 17.5	16.4	
HSB28PWS	22 Sept. 1994	M	A	-17.5 to -15.6	-16.4	14.6 to 16.4	15.7	
HSB29PWS	22 Sept. 1994	M	P	-16.7 to -15.2	-15.9	17.5 to 19.2	18.4	
HSB30PWS	22 Sept. 1994	F	A	-17.8 to -15.2	-16.9	14.5 to 16.8	15.2	
HSB31PWS	22 Sept. 1994	F	SA	-17.7 to -16.1	-16.8	14.6 to 16.7	15.7	
HSB32PWS	22 Sept. 1994	F	A	-17.8 to -13.8	-16.1	14.3 to 17.1	15.5	
HSB33PWS	22 Sept. 1994	F	SA	-17.8 to -14.3	-16.4	14.7 to 16.6	15.9	

Table 1. (Continued)

HSB34PWS	22 Sept. 1994	M	A	-17.2 to -14.4	-15.3	14.7 to 17.2	16.0
HSB35PWS	22 Sept. 1994	F	A	-18.1 to -15.6	-16.8	15.0 to 17.4	15.9
HSB36PWS	22 Sept. 1994	M	A	-17.9 to -16.8	-17.6	14.5 to 16.2	15.1
TATHS1PWS	27 Sept. 1994	F	SA	-18.1 t -16.7	-17.5	14.4 to 17.8	15.8
TATHS2PWS	29 Sept. 1994	F	SA	no vibrissae			
TATHS3PWS	29 Sept. 1994	F	A	-17.5 to -15.5	-17.0	14.3 to 17.1	14.9
TATHS4PWS	30 Sept. 1994	M	A	-16.4 to -16.1	-15.6	16.1 to 18.7	17.3
TATHS5PWS	30 Sept. 1994	M	A	-17.9 to -15.7	-16.4	14.4 to 16.1	15.6
TATHS6PWS	1 Oct. 1994	F	P	-17.8 to -16.1	-16.5	16.0 to 18.3	16.8
TATHS7PWS	1 Oct. 1994	M	P	-17.8 to -14.9	-15.7	14.3 to 19.8	17.5
HSC1PWS	9 May 1995	M	SA	-17.3 to -15.5	-16.1	15.3 to 17.6	16.3
HSC2PWS	9 May 1995	M	SA	-17.5 to -13.4	-14.9	14.6 to 20.0	17.9
HSC3PWS	9 May 1995	M	SA	-16.3 to -15.0	-15.4	16.4 to 19.5	18.4
HSC4PWS	9 May 1995	M	SA	-17.5 to -16.1	-16.6	14.1 to 17.2	15.8
HSC5PWS	9 May 1995	M	SA	-17.5 to -15.6	-16.2	14.6 to 16.9	15.8
HSC6PWS	11 May 1995	F	SA	-17.2 to -15.4	-16.2	15.3 to 16.8	16.1
HSC7PWS	11 May 1995	M	SA	-17.6 to -15.1	-16.2	14.2 to 16.9	15.7
HSC8PWS	11 May 1995	F	A	-17.8 to -14.3	-16.4	14.1 to 16.8	15.3
HSC9PWS	11 May 1995	F	SA	-18.0 to -15.1	-15.9	16.5 to 18.8	17.8
HSC10PWS	11 May 1995	M	SA	-17.2 to -12.8	-14.1	16.0 to 18.9	17.9
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	11 May 1995	F	SA				
HSC14PWS	11 May 1995	M	A				
HSC15PWS	12 May 1995	M	A				
HSC16PWS	12 May 1995	M	A				
HSC17PWS	12 May 1995	F	SA				
HSC18PWS	12 May 1995	M	SA				
HSC19PWS	12 May 1995	F	SA				
HSC20PWS	14 May 1995	F	A				
HSC21PWS	14 May 1995	F	SA				
HSC22PWS	14 May 1995	M	SA				
HSC23PWS	25 Sept. 1995	F	SA				
HSC24PWS	25 Sept. 1995	F	P				
HSC25PWS	26 Sept. 1995	F	SA				
HSC26PWS	26 Sept. 1995	F	A				
HSC27PWS	26 Sept. 1995	F	A				
HSC28PWS	26 Sept. 1995	M	SA				
HSC29PWS	26 Sept. 1995	M	SA				
HSC30PWS	26 Sept. 1995	F	A				
HSC31PWS	26 Sept. 1995	M	A				
HSC32PWS	26 Sept. 1995	M	A				
HSC33PWS	26 Sept. 1995	F	SA				
HSC34PWS	26 Sept. 1995	F	SA				
HSC35PWS	26 Sept. 1995	F	P				
HSC36PWS	26 Sept. 1995	F	SA				
HSC37PWS	27 Sept. 1995	M	A				
HSC38PWS	27 Sept. 1995	F	A				
HSC39PWS	27 Sept. 1995	F	SA				
HSC40PWS	27 Sept. 1995	M	A				
HSC41PWS	28 Sept. 1995	M	SA				
HSC42PWS	28 Sept. 1995	M	SA				

Alaska and Prince William Sound were significantly different by region $F_{4,98} = 6595.92$, p = <0.001. Harbor seals in southeast Alaska and Kodiak were significantly different by region $F_{4,62} = 5648.64$, p = <0.001. Harbor seals in Prince William Sound and Kodiak were significantly different by region, $F_{4,92} = 12555.49$, p = <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 $\delta^{15}N = 17.29 \pm 0.17‰$. 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 nearshore. More nutrients may be transported by the Alaska Coastal Current as it travels westward along the Gulf coast of Alaska and 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 (Laws et al. 1995).

Seals from eleven sites have been 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 are significantly different by area $F_{16,1896} = 19.11$, p = <0.001; sex $F_{2,955} = 11.05$, p = <0.001 and age $F_{4,1908} = 45,953$, p = <0.001. The two areas in northeastern PWS are significantly different from each other $F_{2,86} = 11.79$, p = <0.001. There is a significant difference in age $F_{4,170} = 9.43$, p = <0.001 but not between sexes (Systat for Windows 1992). Further analyses are being conducted individually for each of the eleven sampling areas. The stable isotope differences observed in seals from different locations appear to agree with some of the location differences defined by the fatty-acid analysis (Iverson et al. 1997). These differences may result from juveniles of a species being eaten in one region of the sound while adults of the same species are eaten in another region.

Stable isotope ratios within harbor seal vibrissae do not appear to oscillate with any regular periodicity, although some seals do have large changes between enriched and depleted values. Harbor seals sampled 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 primary 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 simultaneously 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. Six of the twelve whiskers 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.

The causes of these shifts are not currently known but we hypothesize that prey outside Prince William Sound are more depleted in the heavy isotopes and that some seals may be foraging on ^{13}C-depleted prey. Evidence for travel outside the sound is 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. Approximately a 4‰ depletion exists in $\delta^{13}C$ of the calanoid copepod outside the sound relative to those within the sound (Kline 1997). Isotopic gradients have been identified by Schell (1996) for zooplankton in the Bering Sea and Aleutian Islands with onshelf waters being more enriched and deep water regions being more depleted in $\delta^{13}C$ and $\delta^{15}N$. Prey samples collected within and south of Prince William Sound during the 1996 National Marine Fisheries Service Gulf of Alaska survey are expected to reveal if an isotopic gradient is evident in higher trophic organisms and if they are isotopically congruous as food sources for harbor seals within the sound.

Currently, the maximum and minimum isotope values, observed in seal whiskers having isotope fluctuations greater than 1‰, are being separated into two groups. Each group of isotope values will be included in a Prince William Sound food web and a northern Gulf of Alaska food web once prey analyses are complete. Because depleted isotope values are expected in the Gulf of Alaska prey, the enriched values along the vibrissae are expected to correspond to prey from Prince William Sound. Vibrissae, with fluctuations in $\delta^{13}C$ and $\delta^{15}N$ less than 1‰, will have their ^{13}C and ^{15}N values averaged for the entire whisker. These values will be added to both food webs, but 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.

Harbor seal tissues were collected with the assistance of ADF&G personnel and native subsistence hunters. Multiple tissues were collected from each animal 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 sixty 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 of each tissue to muscle from the same animal. An Analysis of Variance and Bonferroni post hoc tests were run for the entire data set to establish significant differences among tissues. Least square means and standard errors were calculated and plotted (Figures 2 and 3). Table 2 lists the fractionation values for eleven tissues collected from harbor seals.

Archived Seal Samples

Stable isotope values of archived muscle tissue from PWS harbor seals, 1975 and 1989, were compared with vibrissae values from animals sampled from the same region in 1995 (Figure 4). Vibrissae isotope values were adjusted for keratin enrichment relative to muscle, using the values in Table 2. The $\delta^{15}N$ values all remained in one trophic level, as defined by a change of 3‰, and there were no significant differences among the three years. A one-way ANOVA and Bonferroni post hoc test detected a significant difference in $\delta^{13}C$ between 1975 and 1995 ($F_{2,31} = 4.76$, $p = 0.016$).

Table 2. $\delta^{13}C$ and $\delta^{15}N$ fractionation of harbor seal tissues from muscle using least squares means.

Tissue	**N**	**$\delta^{13}C$** Mean, ‰	**SE** ‰	**$\delta^{15}N$** Mean, ‰	**SE** ‰
blood, whole	5	0.40	0.22	-0.29	0.29
blubber	53	-5.99	0.26	--	--
brain	31	-1.04	0.30	0.52	0.10
collagen	24	-0.39	0.20	0.31	0.07
fur	39	0.69	0.16	-1.0	0.18
heart	27	-0.06	0.12	0.40	0.08
kidney	33	-0.38	0.17	0.38	0.11
liver	37	-0.24	0.21	0.25	0.10
lung	2	-0.68	0.06	0.65	0.20
skin	40	-1.83	0.24	0.86	0.12
vibrissae	4	1.90	0.72	0.10	0.67

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 back to 1950. A total of twelve harbor seals (Ketchikan - 5, Cordova -3, Kodiak - 2, Pribilof Islands - 2), nine Steller sea lions (Cook Inlet - 3, Kodiak - 1, Alaska Peninsula - 2, Pribilof Islands - 3) and ten northern fur seals (Cook Inlet -2, Alaska Peninsula - 3, Pribilof Islands - 5) had collagen extracted from bone samples free of humus and tissues. Data from the bone collagen was combined with data from muscle tissue collected in the 1970s and 1980s and vibrissae collected in the 1990s. All tissues were normalized to muscle using the data shown in Table 2 to compensate for internal fractionation between tissue types. The $\delta^{15}N$ values remained within one trophic level and indicate that no trophic shift occurred during the forty-seven years samples were available (Figure 5). This does not mean that prey variability did not occur but that the predominant prey in the diets of these phocids and otariids were consistently from the same trophic level. A rapid depletion did take place in the $\delta^{13}C$ of all three species between the years of 1950-1971 and 1975-1996 (Figure 6). The timing of this shift corresponds with the time of other observed changes in the physical and biological environment from the North Pacific Ocean (Ebbesmeyer et al. 1991, Trenberth and Hurrell 1994). This data, in combination with that of Laws et al. (1995) and Schell (unpublished) may be an indicator that the carrying capacity of the North Pacific Ocean has declined since the 1970s. The reasons for this change in the $\delta^{13}C$ are not yet known but likely result from changes in the physical environment.

Isotope Ratios in Prey Species

The Prince William Sound prey plot (Figure 7) was created using $\delta^{13}C$ and $\delta^{15}N$ values for nine potential prey species for harbor seals. *Neocalanus* spp. was included in the food web as a first order consumer within the sound. For the sake of clarity, only a random sampling of harbor seals were added to the plot. Based on the natural history of harbor seals, including information from stomach content analyses, pollock, herring, squid, octopus, salmon and capelin were evident most often in seal stomachs from Prince William Sound (Pitcher 1980). The pleuronectid, yellowfin sole, has been observed being taken by seals in an area west of Montague Island. A few samples were collected and added to the plot as well as some available samples of the high-lipid eulachon. This plot is not meant to represent the absolute prey variety in the diet but more as likely sources of prey for seals foraging within the sound.

Based on a trophic level enrichment of 3‰ for $\delta^{15}N$ and 1‰ for $\delta^{13}C$, the majority of seals plotted ($\delta^{13}C$ = ~-18‰ and $\delta^{15}N$ = ~16‰) are likely feeding on a mix of adult herring, squid and juvenile pollock in Prince William Sound. The more enriched seals represented in the plot may be feeding on adult pollock, octopus and yellowfin sole. More samples of squid, octopus and sole have recently been acquired. Once they have been analyzed, their isotope values will be added to this food web. Some harbor seal isotope ratios are more enriched in ^{13}C than prey represented here. The source of these enriched values may be from the consumption of benthic organisms for which samples are not available at this time. Benthic environments tend to have more enriched values due to recycling of nutrients and the presence of a bacterial food web (Coffin et al. 1994). The addition of benthic organisms will be added to the modeled food web as they become available. Analyses of potential prey collected outside Prince William Sound are nearing completion. During the National Marine Fisheries Service 1996 Gulf of Alaska survey, pollock, capelin and sandlance were collected from Gulf of Alaska water outside Prince William Sound at depths between 50 and 140 m. We have speculated that the isotopic shifts seen in some harbor seal vibrissae may result from the seals foraging in isotopically-depleted waters outside the sound. The stable isotope ratios for these Gulf of Alaska species will be compared with the values for the same species found in various locations within Prince William Sound to see if an isotopic gradient exist between the inshore and offshore waters. The large, depleted values observed in the seal vibrissae will be added to the Gulf of Alaska food web to determine if offshore foraging can explain the depletion.

Similar to work done by Schell et al. (1989, 1993, 1996) in the Bering Sea, areas of the Gulf of Alaska are being refined into smaller, isotopic regions to better define feeding areas for traveling phocids or prey transport into Prince William Sound (Figures 8 and 9). Benthic and pelagic organisms from Chatham Straits in southeast Alaska (Figure 10), collected with the assistance of National Marine Fisheries Service - Auke Bay, provide information on prey species "upstream" of Prince William Sound. Certain species may travel the Alaska Coastal Current and act as a food source for Prince William Sound seals. Additional samples of lower trophic level organisms, primarily from outside the sound, will be collected and analyzed during the coming year to be utilized in defining isotopic regions. Stable isotope values for Prince William Sound prey species were provided and also reported by Dr. Tom Kline as part of the SEA program conducted by the Prince William Sound Science Center.

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 lions whiskers indicate the animals continue to grow their 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 are being held in captivity at the Vancouver Aquarium in British Columbia, Canada. Vibrissae have been clipped periodically during the past three years and one animal had two successive whiskers cut which had an adequate overlap of growth to estimate the growth rate of the whiskers. The growth rate, averaged over fourteen months, was 0.14 mm/day (Figure 11). 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. This data was 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 sea lions from the Pribilof Islands in the Bering Sea were a mix of subadults and adults and almost exclusively male. Age confirmation using teeth has not yet arrived so the proportion of ages for the Bering Sea animals cannot be given at this time. Growth rates averaged over twelve months were 0.11 - 0.12 mm/day for all sea lions combined. The range of growth from year to year averaged over twelve months was 0.05 - 0.18 mm/day. Growth rates of captive sea lions were faster than for wild animals. This was to be expected since these captive animals do not need to expend extra energy foraging for food or have not begun mating and gestating. We hope to continue sampling vibrissae from these captive sea lions in order to determine if growth rates change seasonally with changing metabolic requirements.

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 is 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 12). This rate far exceeds 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 13). "Norton's" growth also exceeded growth rates in the captive, subadult Steller sea lions which ranged between 0.14 to 0.17 mm/day averaged over twelve months.

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 which 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, pupping and molting and the lowest rates corresponded to the cessation of these activities. A general decline in metabolic rates occurred with increasing seal age (Rosen and Renouf 1995). Seasonal variation in vibrissae growth rates are 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.

Isotope Ratios in Potential Prey

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 by us and are currently being analyzed.

Interactions with Other Studies

Our main cooperative work has been and continues to be with K. Frost of the ADF&G in conjunction with their 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 has 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, 1996 and 1997 seal samples will be analyzed and contrasted with the results from the fatty acid analyses.

The interaction with the modeling component of the SEA program has intensified. As the data are acquired and compiled, we will be 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.

To date, the interaction with other studies on top consumers has been limited to the acquisition of vibrissae from sea otter carcasses and sea bird tissue. 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.

Captive seal studies: Preliminary data from the captive harbor seal 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. Another dose of ^{15}N-labeled glycine in scheduled to be administered in April 1997. A whisker from each seal is expected to be cut during the summer of 1997.

Analytical services for stable isotope ratio determinations: The mass spectrometry service has had full usage by this project, 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 a new backlog is building 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. The funding by the National Science Foundation of a new mass spectrometry system will insure more sample capacity and increased sensitivity for small samples. This instrument has been ordered and is due for installation in summer 1997.

Harbor seal trophic energetics: All harbor seal tissues have been analyzed to date while some vibrissae remain to be analyzed. Data sets are being statistically analyzed and the time series data sets are being compiled and prepared for analyses. Harbor seal tissues have been analyzed to identify the isotopic fractionation that occurs among differing tissues. These data will be of use to researchers wanting to know the isotopic makeup of particular harbor seals but are limited by the available tissue. Prey items lacking from food webs will be added during the upcoming sampling season. Large fluctuations in harbor seal vibrissae are being 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. A comprehensive analysis of the prey data is expected this year. Comparisons of archived and modern seal tissues indicate a rapid depletion in $\delta^{13}C$ took place between the years of 1950-1971 and 1975-1996. The timing of this shift corresponds with other observed changes in the physical and biological environment from the North Pacific Ocean. The reasons for this change are not yet known but the data may indicate a change in the carrying capacity of the ecosystem. Isotope data from the remaining 1995 and 1996 seals will be contrasted with the fatty acid composition information compiled by K. Frost with ADF&G to further detail food web structure within Prince William Sound.

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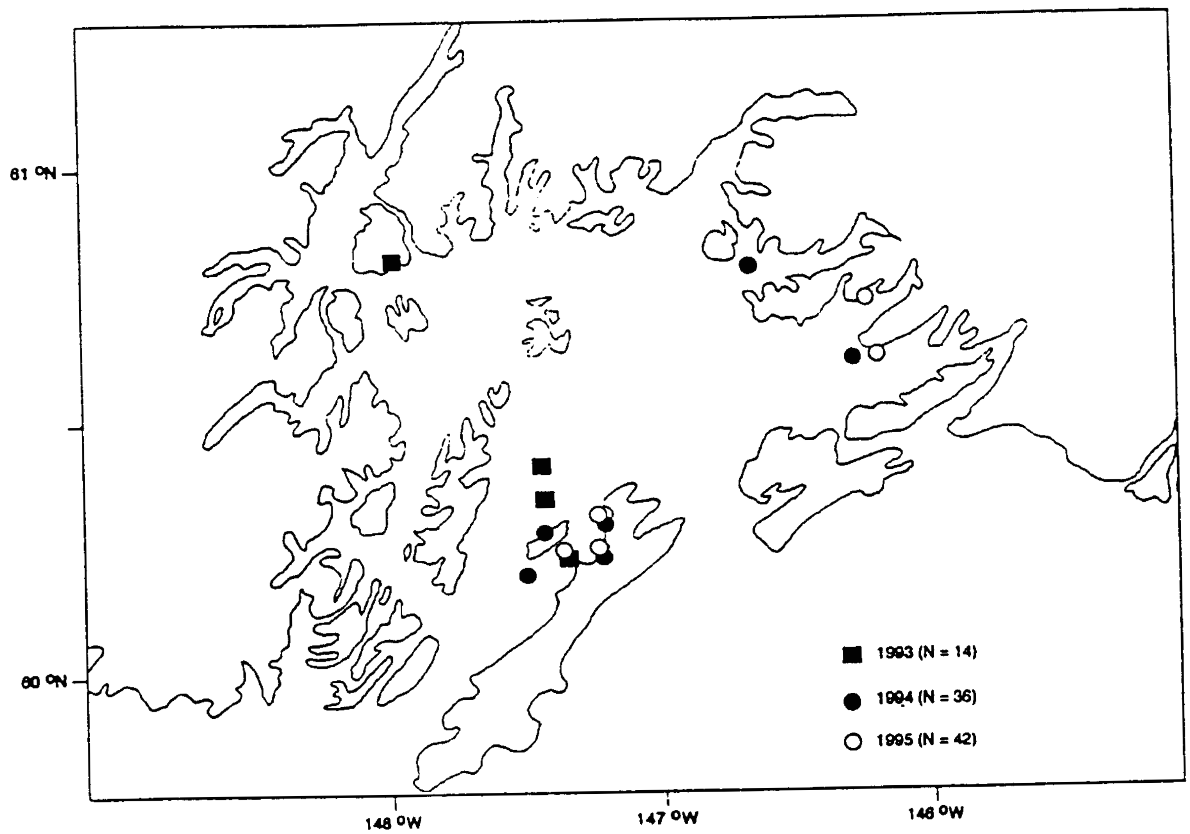

Figure 1. Sample locations for harbor seals in Prince William Sound, 1993-1995.

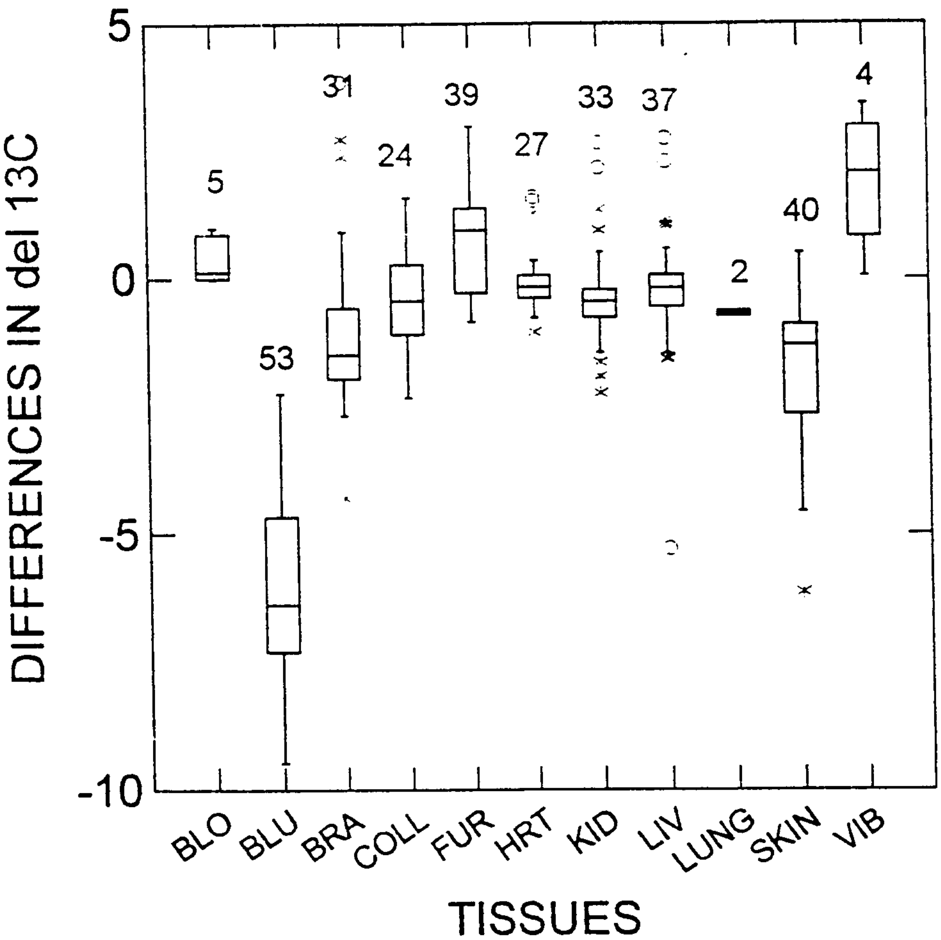

Figure 2. $\delta^{13}C$ fractionation of harbor seal tissues. blo = whole blood, blu = blubber, bra = brain, coll = collagen. hrt = heart. kid = kidney, liv = liver, vib = vibrissae. The sample size of each tissue is given above the box plot. * indicates values outside the first and third quartile of all values. o indicates values lower than 12.5% and greater than 87.5% of all values.

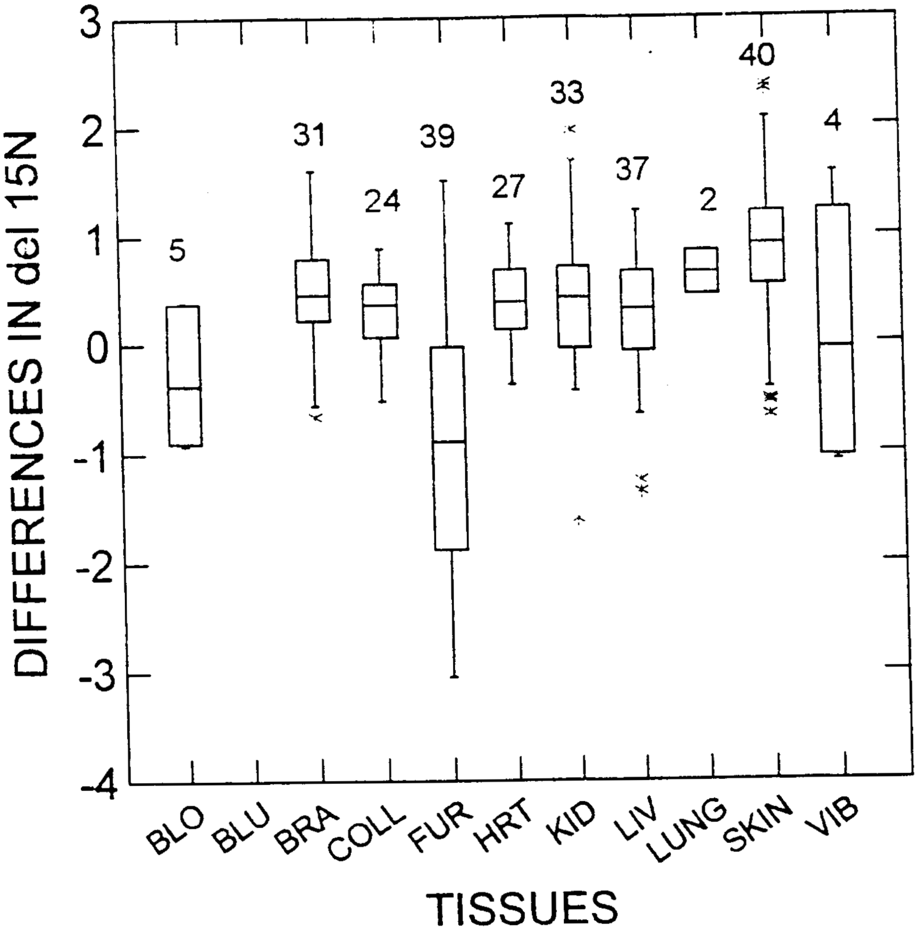

Figure 3. $\delta^{15}N$ fractionation of harbor seal tissues. blo = whole blood, blu = blubber, bra = brain, coll = collagen, hrt = heart, kid = kidney, liv = liver, vib = vibrissae. The sample size of each tissue is given above the box plot. * indicates values outside the first and third quartile of all values. o indicates values lower than 12.5% and greater than 87.5% of all values.

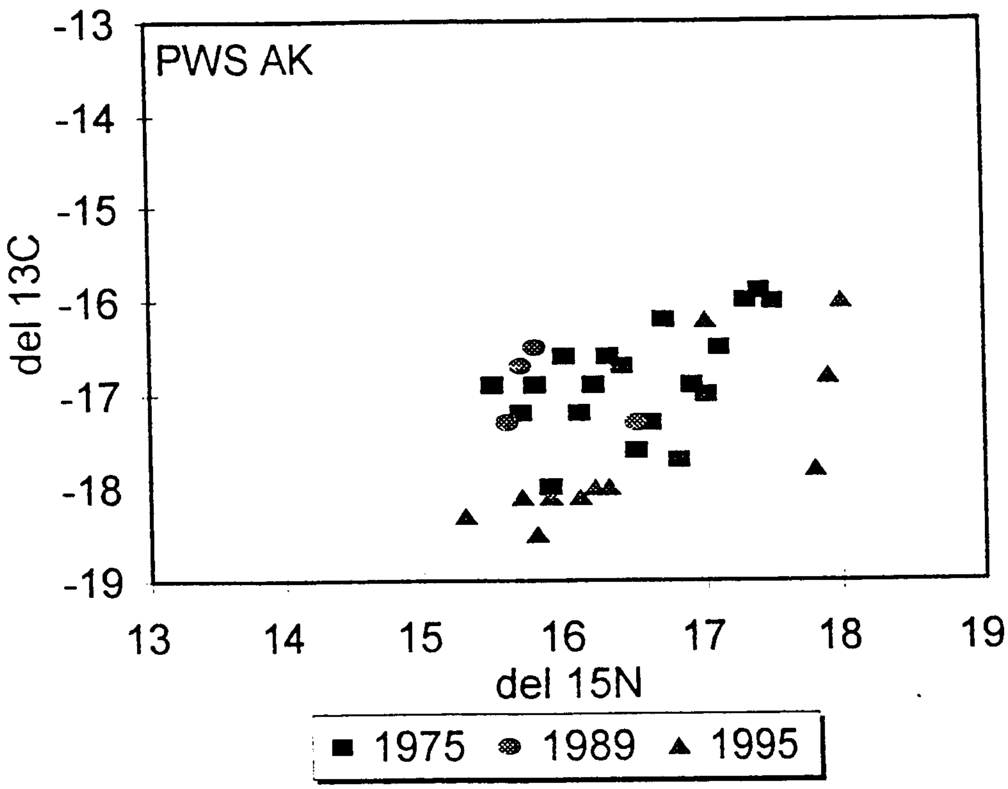

Figure 4. Stable isotope values for Prince William Sound harbor seals. 1975 and 1989 values are muscle. 1995 values are vibrissae normalized to muscle.

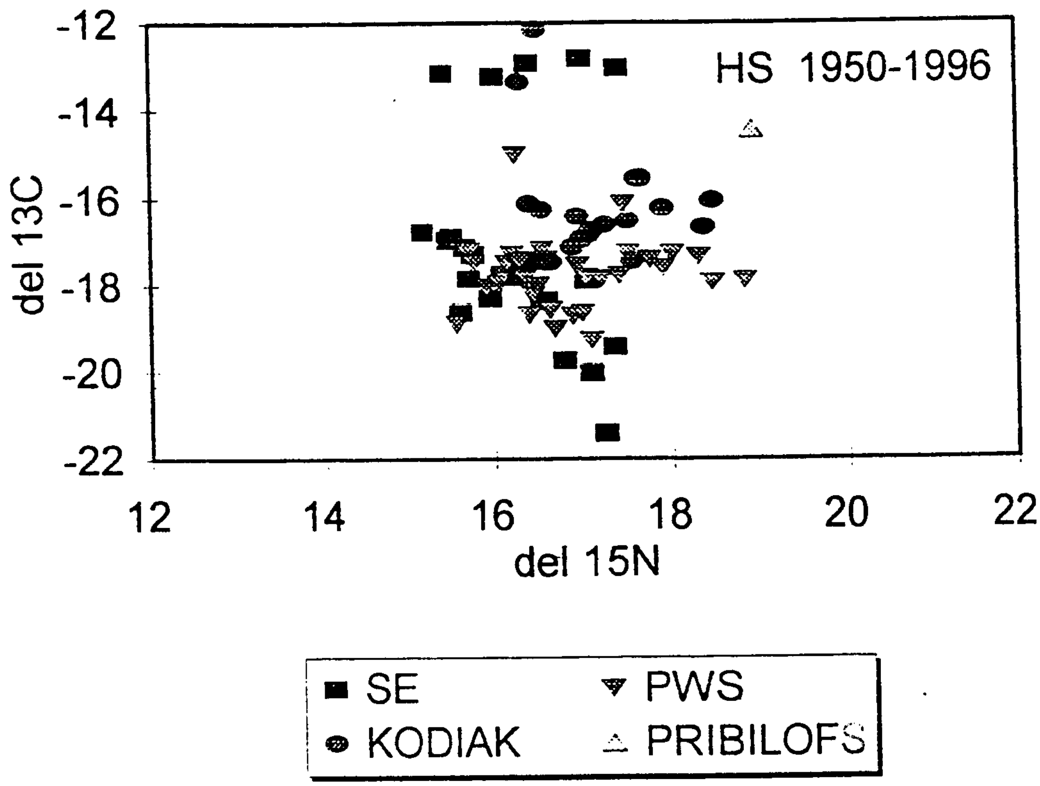

Figure 5. Stable isotope values for harbor seals, 1950-1996. Tissues consist of bone collagen, muscle and vibrissae. Collagen and vibrissae have been normalized to muscle.

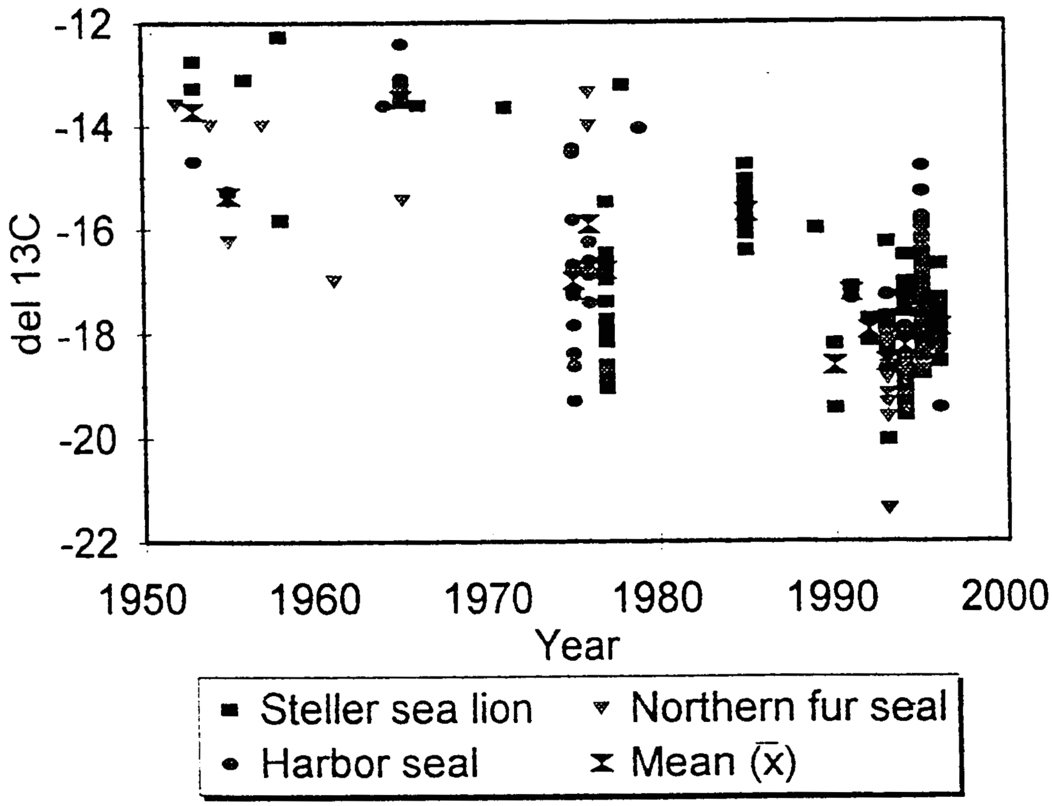

Figure 6. Harbor seal, Steller sea lion and northern fur seal $\delta^{13}C$ values for the Gulf of Alaska and the southeastern Bering Sea, 1950-1996. . Tissues consist of bone collagen, muscle and vibrissae. Collagen and vibrissae have been normalized to muscle.

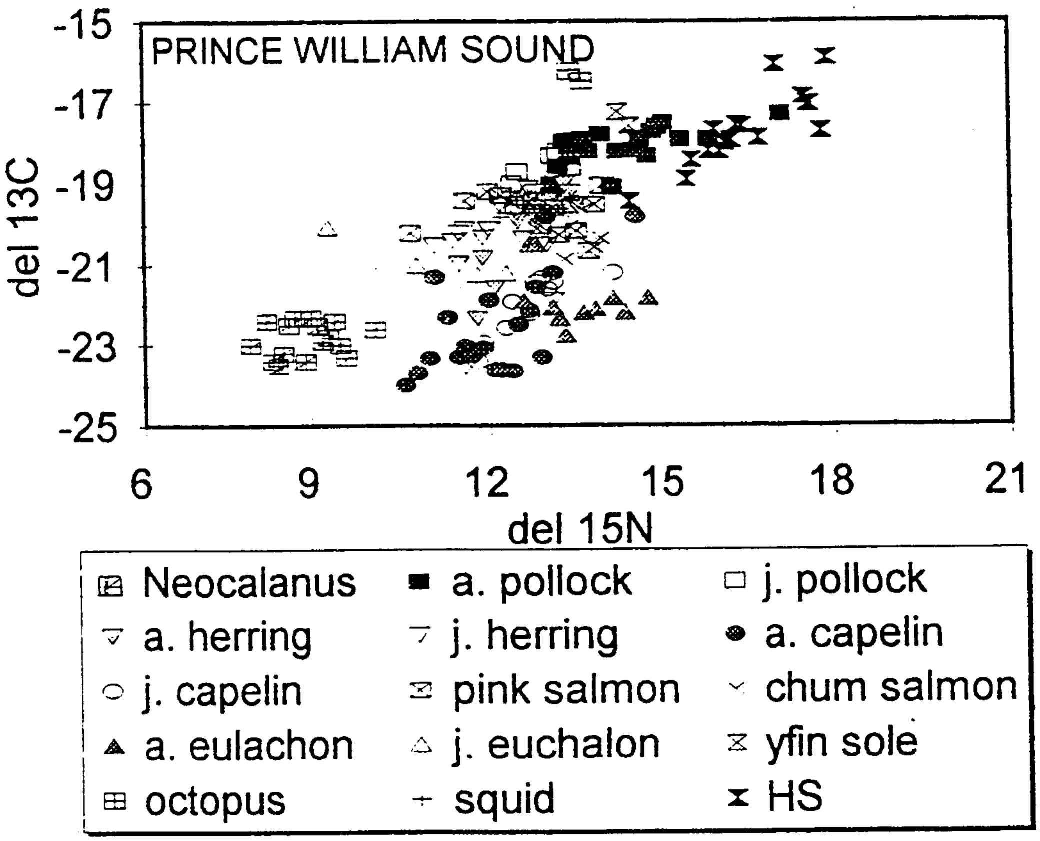

Figure 7. Prince William Sound food web using carbon and nitrogen stable isotope ratios.

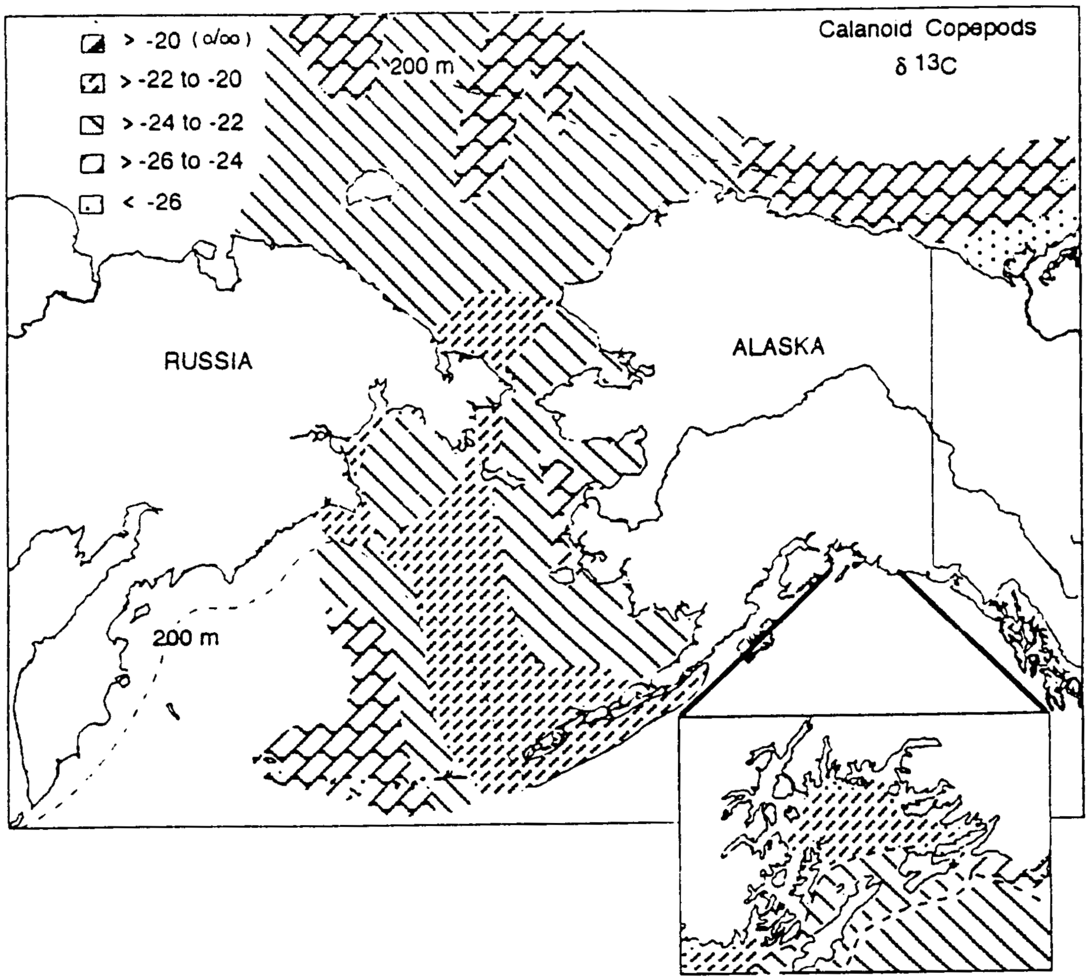

Figure 8. $\delta^{13}C$ isotope contours for calanoid copepods in the Bering and Chukchi seas. The Prince William Sound insert shows estimated contours based on analyzed lower trophic level organisms.

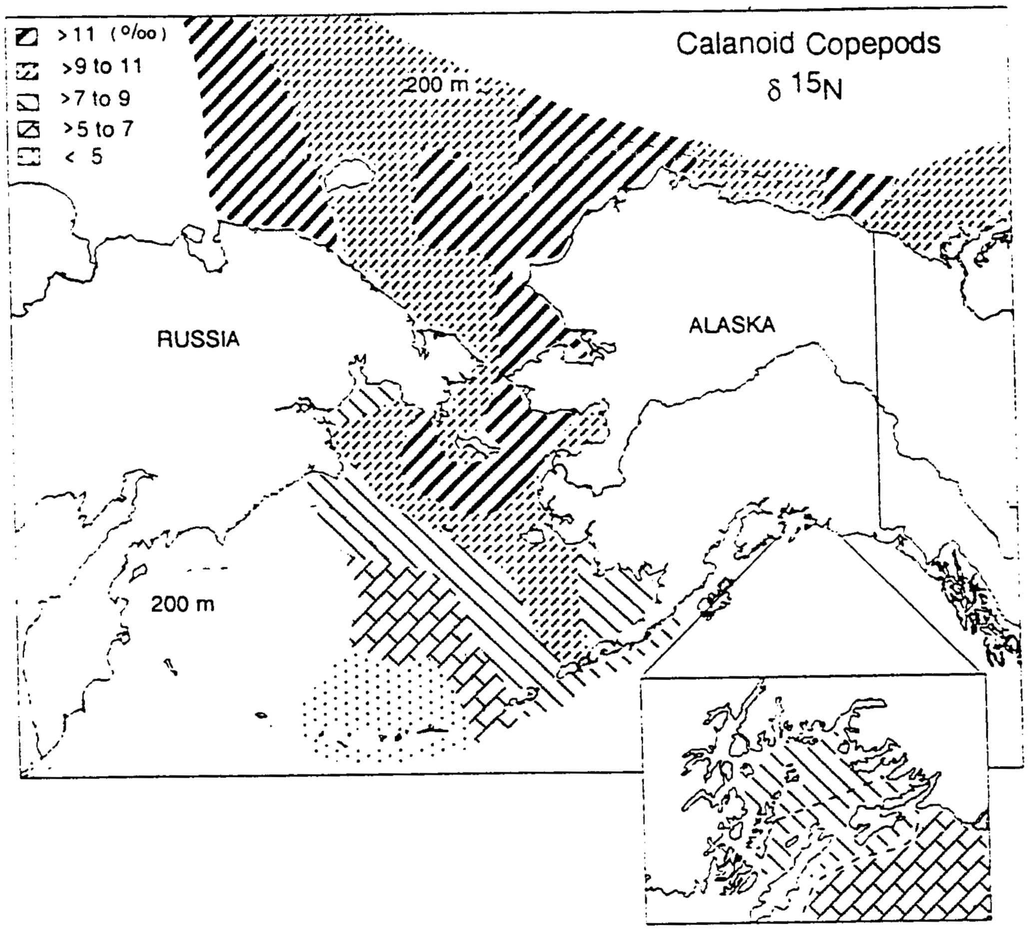

Figure 9. $\delta^{15}N$ isotope contours for calanoid copepods in the Bering and Chukchi seas. The Prince William Sound insert shows estimated contours based on analyzed lower trophic level organisms.

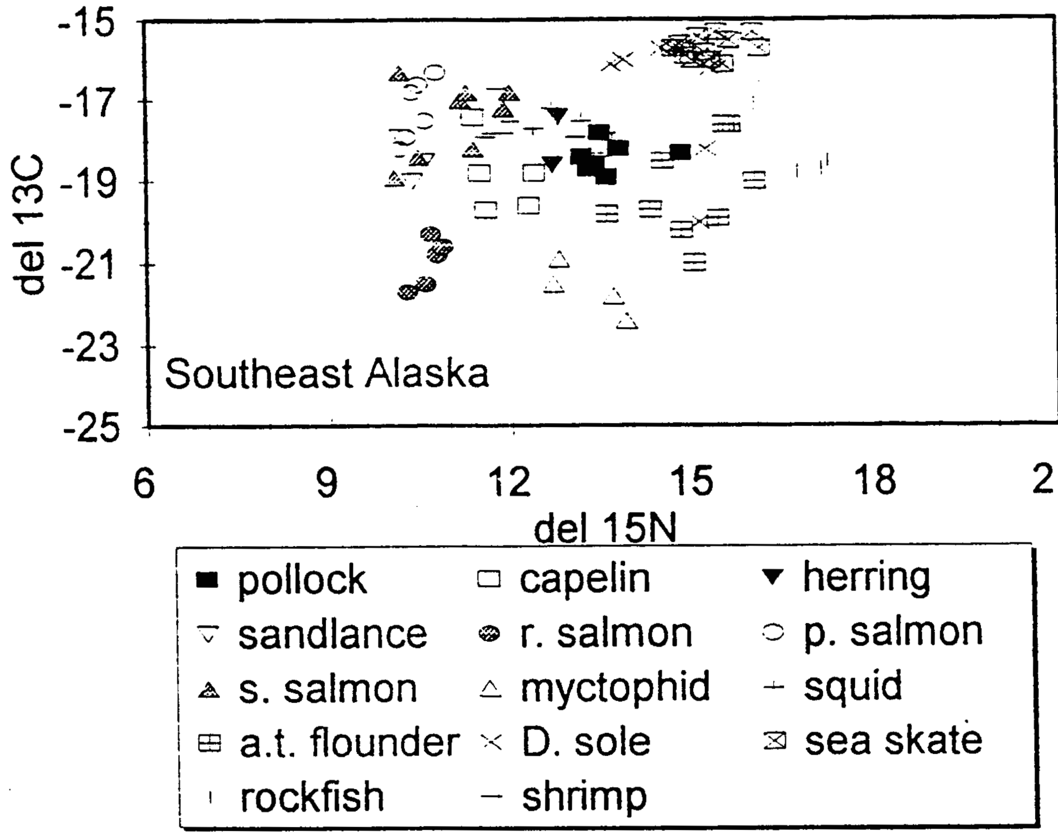

Figure 10. Chatham Straits, Southeast Alaska food web using carbon and nitrogen stable isotope ratios.

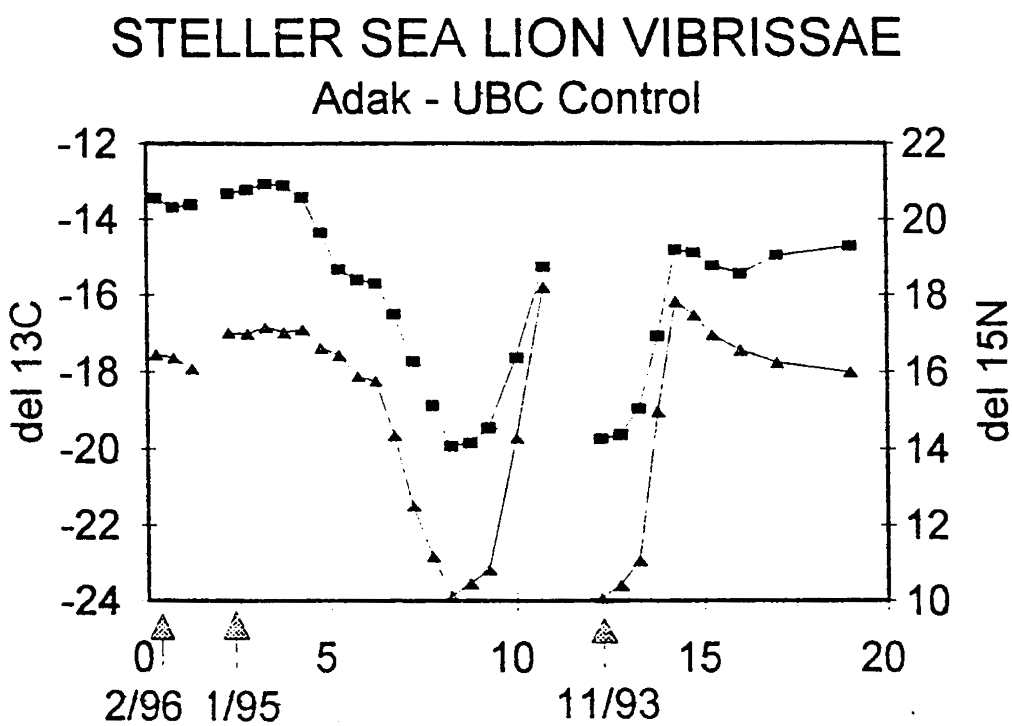

Figure 11. Vibrissae segments used to estimate growth rate of a subadult Steller sea lion held in captivity at the Vancouver Aquarium, British Columbia.

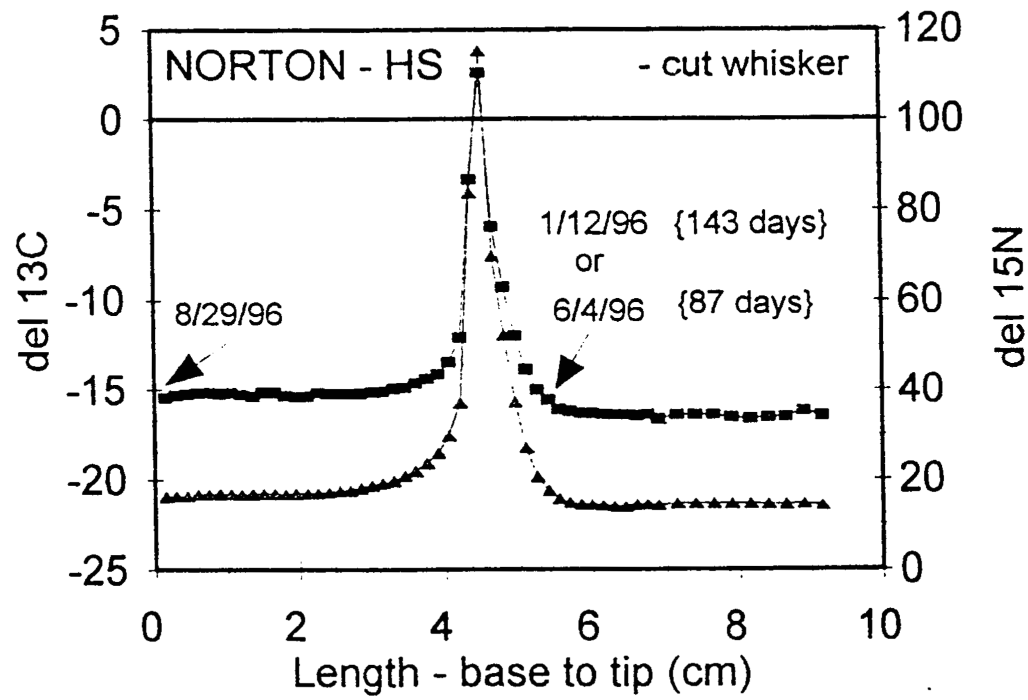

Figure 12. Vibrissae plot with doubly-labeled ($\delta^{13}C$ and $\delta^{15}N$) glycine peak of an adult harbor seal held in captivity at the Mystic Aquarium. Connecticut.

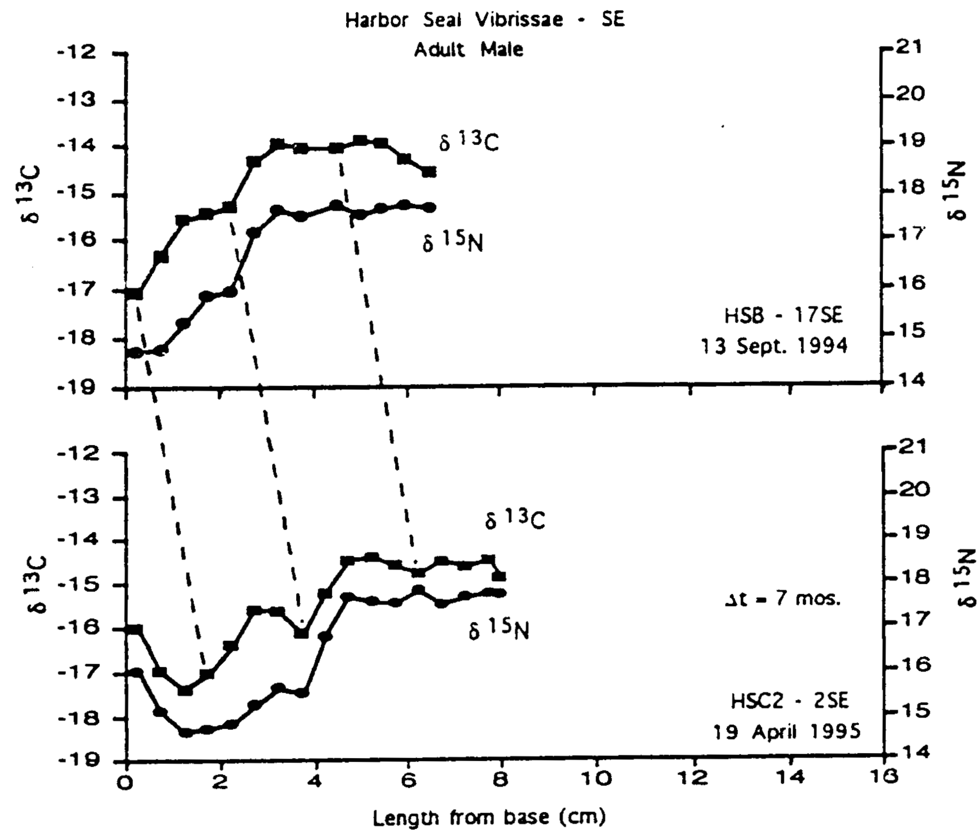

Figure 13. Vibrissae plots from a recaptured adult harbor seal in Southeast Alaska. Vibrissae sampled in September 1994 (upper plot) is contrasted with a vibrissae taken seven months later (lower plot).