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RETROSPECTIVE ISOTOPIC ANALYSES OF STELLER SEA LION TOOTH ANNULI AND SEA- BIRD FEATHERS: A CROSS-TAXA APPROACH TO INVESTIGATING REGIME AND DIETARY SHIFTS IN THE GULF OF ALASKA

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ABSTRACT

Stable isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) values of individual tooth annuli of female Steller sea lions ($n = 120$) collected from the 1960s through the 1980s were used for retrospective analyses of temporal changes in food webs in the Gulf of Alaska and North Pacific Ocean. We also examined isotopically contour feathers of tufted puffins ($n = 135$) and crested auklets ($n = 37$) through this period to test for broader isotopic patterns indicative of whole food web changes. Steller sea lions decreased slightly in $\delta^{13}\text{C}$ and increased in $\delta^{15}\text{N}$ values, suggesting an increasing trophic level and change in foraging location or oceanographic isotopic signature. Steller sea lion first and second tooth annuli were enriched in ^{15}N and depleted in ^{13}C compared with subsequent annuli, indicating the effects of maternal influence through weaning. The general pattern of increasing $\delta^{15}\text{N}$ values among Steller sea lions supports previous conclusions regarding a reduction or redistribution of forage fishes and an increase of demersal and semi-demersal species in the North Pacific ecosystem. There were no significant changes in $\delta^{15}\text{N}$ values for either bird species. However, $\delta^{13}\text{C}$ values in both bird species again suggested changes in foraging location or a shift in oceanographic currents.

Key words: *Aethia cristatella*, carbon-13, *Eumetopias jubatus*, feathers, *Fratercula cirrhata*, nitrogen-15, primary productivity, stable isotopes, teeth annuli.

The Gulf of Alaska and adjacent waters of the northeastern Pacific Ocean is part of a dynamic marine ecosystem that has experienced extreme fluctuation and depletion in several physical (e.g., inorganic nutrients, water temperature) and biological components commonly associated with a 1976 regime shift described by Ebbesmeyer *et al.* (1991). Changes in water temperatures along with compositional changes in key food web organisms (Anderson *et al.* 1997, Hollowed and Wooster 1995) might ultimately be linked to subsequent declines in predatory pinniped and bird populations (Loughlin and York 2000). One proposed mechanism for the declines in apex predator populations is the decrease or emigration of prey populations (Sinclair *et al.* 1994, Merrick *et al.* 1997, Hunt *et al.* 2002, Sinclair and Zeppelin 2002).

Stable-carbon and nitrogen isotope analyses provides a means of investigating diet of marine birds and mammals retrospectively since stable isotope ratios ($^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$) in consumer tissues reflect those values in their diet (DeNiro and Epstein 1978, 1981) and isotopic signatures can remain unchanged in various preserved tissues (van der Merwe 1982, Hobson and Montevecchi 1991, Schell 2000). Stable-nitrogen isotope ratios increase in consumer tissues on the order 3‰–5‰ with each trophic step (Michener and Schell 1994), and have thus proven to be a useful approach to delineating trophic position of consumers in marine food webs (Hobson and Welch 1992, Michener and Schell 1994). Stable-carbon isotope ratios are useful in providing information on the source of carbon to the diet (e.g., Hobson *et al.* 1995). For instance, benthic food webs are significantly enriched in ^{13}C compared to offshore or pelagic food webs (Hobson and Welch 1992, France 1995a, b). The combined use of both isotopes in marine food webs can thus provide useful information on relative trophic positions and location of feeding in marine consumers. In addition, different tissue types can represent different periods of dietary integration. We used this approach to investigate the association of food web changes and predator declines relative to the regime shift of 1976.

In this study, we base stable isotope analysis on the teeth of female Steller sea lions (*Eumetopias jubatus*) and feathers from tufted puffins (*Fratercula cirrhata*) and crested auklets (*Aethia cristatella*). These three species were chosen because they span three trophic levels in terms of size or type (vertebrate *vs.* invertebrate) of prey consumed, and each experienced variable population response following the 1976 regime shift. We reasoned that if fundamental isotopic changes occurred in the food web as a result of this regime shift, then such changes would be manifested across trophic levels. Such a cross-taxa approach was favored since the feeding behaviors of individual species can change in ways that might obscure overall food web isotopic changes. For example, if food webs became depleted in ^{15}N but the predator of interest shifted its trophic position upward, then overall we might not detect any isotopic change in the organism. Similarly, if ^{13}C became depleted in the food web but organisms shifted toward more inshore feeding, then again, this could go undetected isotopically. A dual-isotope, cross-taxa approach was adopted to maximize our detection of environmental changes following the regime shift. In addition, our choice of tissues for isotopic measurement allowed relatively fine-scale delineation of temporal isotopic or feeding patterns. For example, organic and

inorganic components of individual tooth annuli of marine mammals provide dietary integrations for that year in the animal's life (Hobson and Sease 1998). In the case of bird feathers, stable-isotope signatures represent diet of the bird over the period of feather growth (Hobson and Clark 1992, Mizutani *et al.* 1992).

METHODS

Tooth Sampling and Age Determinations

Upper canine teeth of 120 Steller sea lion females collected before and after the mid-1970s oceanographic regime shift were used in our analyses. Animals were collected between Cape Suckling (144°W) and the Shumagin Islands (~160°W) in the Gulf of Alaska. The year of birth was back-calculated for each animal based on collection year and age was determined by etching longitudinal thin sections of the canine teeth. Teeth from two to seven sea lions per birth year from 1965 to 1990 were selected for thin sectioning and dentine extraction.

To consistently produce thin sections for age determination and growth layer measurement, as well as retain a portion of each tooth for reliable dentine extraction, each tooth went through a series of procedures. Longitudinal thin sections were cut following Perrin and Myrick (1980). Non-decalcified sea lion teeth were mounted on wooden blocks and sectioned slightly to one side of the longitudinal midline using a rock saw. The larger portion, containing the longitudinal center of each tooth, was then polished, using a 400 grit disc polisher then mounted on a 2" × 3" glass slide with an optical grade epoxy. The tooth was then cut and polished again using a thin sectioning machine, resulting in a mounted thin section 120–140 microns thick. Sections were read under polarized light to allow clear reading of annual growth layer groups. Two readers conducted blind age estimates and determined a range in age of 2–17 yr for the animals sampled in this study.

Electronic images of each thin section were captured using a digital camera mounted on a microscope. Images were captured at 4× magnification with a polarizing filter to enhance growth-layer group definition. Cut surfaces were polished to remove saw marks and enhance growth-layer visibility. Working with a microscope, using electronic images as aides, growth layers were first marked and measured using *Optimas* (Version 6.51, Media Cybernetics) software. Growth-layer groups were marked in two places along the anterior and again along the posterior half of the tooth image. Lines were drawn perpendicularly across the growth layers at the enamel root junction, and again at the point where the first growth layer terminated in the root. This allowed for two measurements for the first growth layer and a maximum of four measurements of the second, third and fourth layers, depending on the definition of the layers and quality of the image. A total of 10 mg of dentine was then extracted from each of the first four growth-layer groups with a 1-mm engraving burr in a flexi-shaft Dremel tool.

Stable Isotope Analyses

Analyses of teeth followed methods described in Hobson and Sease (1998). The protein component of dentin was analyzed for stable-nitrogen isotope ratios by loading dentin samples into tin cups and combusting at approximately 1,800°C using continuous-flow isotope ratio mass spectrometry (CFIRMS) involving

a Europa 20:20 IRMS interfaced with a Robo Prep combustion system. Because we did not extract collagen *per se*, our $\delta^{15}\text{N}$ values were of whole protein composed primarily of collagen. The stable-carbon isotope ratios of the inorganic fraction were obtained by reacting powdered dentin samples with concentrated (100%) phosphoric acid in evacuated vacutainer tubes. The evolved CO_2 was sampled using either a breath sampler interfaced with a VG OPTIMA dual inlet or Europa 20:20 CFIRMS. Stable isotope ratios are expressed in delta (δ) notation relative to the Pee Dee Belemnite or AIR standards for carbon and nitrogen respectively (see Hobson and Sease 1998).

Feathers were cleaned of surface oils by soaking and rinsing with a 2:1 chloroform:methanol solution. They were then air dried under a fume hood to remove any solvent residue and 1 mg of feather vane was subsampled for isotopic analysis. These samples were loaded into tin cups and analyzed for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values using the Europa 20:20 isotope ratio mass spectrometer. Using replicate measurements on albumen (N,C) and calcium carbonate (C) standards, we estimated analytical error to be $\pm 0.3\text{‰}$ for nitrogen and $\pm 0.1\text{‰}$ for carbon for both sample types.

Statistical Analysis

To describe the temporal pattern in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and to detect changes in these values that could be concurrent with the 1976 regime shift, we fit models of stable-isotope values over time. The exact model depended on what data were available.

Stable isotope values in the teeth of each of the first four growth layer groups of female Steller sea lion were available for most years during 1960–1985. For these data, we fit orthogonal polynomials up to degree 5, and following the advice of Burnham and Anderson (1998), chose the model with the smallest value of the corrected Akaike Information Criteria (AICc). The maximum degree of 5 was somewhat arbitrary but was clearly sufficient to permit a wide range of scenarios and potential change-points. In addition, orthogonal polynomials have several advantages: among them are greater computing accuracy and reduced computing times. Since fitting of polynomial models can be affected by extreme values, we also fit the range of models after trimming 2.5% and 5% of the smallest and largest values. The polynomials allowed us to estimate the years when change points occurred (if any) by determining when the first derivative of the relationship $y = f(x)$ was equal to 0. In this manner, we were able to determine if there was a change in the stable isotope values around the time of the regime shift of 1976. We used the statistical package R (Ihaka and Gentleman 1996) for this purpose.

Stable isotope values of feathers of crested auklets were available for only a few years spread over time. This restricted our analysis to categorical models, allowing us to compare the levels of the mid-1970s and the mid-1980s. In addition, we were also able to examine whether there were sexual differences in stable isotope values. This analysis was done with a general linear model (GLM) using statistical package R (Ihaka and Gentleman 1996). The puffin data were available for a wide range of years, but the sample size was much smaller than the sea lion data set. In addition, these data were collected in different areas and both males and females were collected. We chose to model these data with categorical models, investigating differences in isotope values between pre- and post-1976, males and females, and area of collection (Gulf of Alaska *vs.* the Aleutians). Models were selected using the

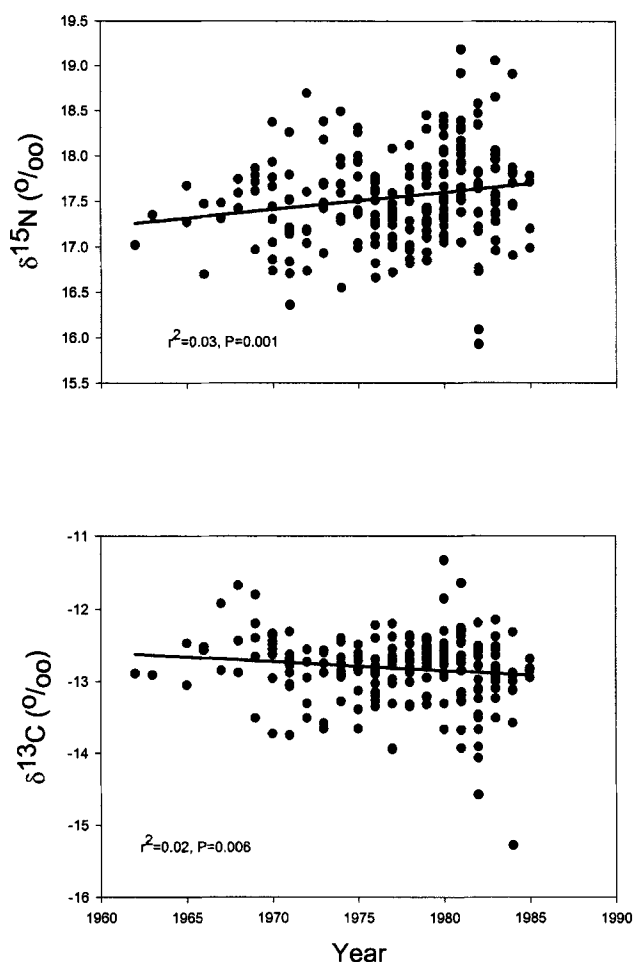


Figure 1. Relationship between tooth inorganic $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and year for Steller sea lions in the Gulf of Alaska for all growth-layer groups of all individuals combined (GLGs).

minimum AICc values among all models fit. Statistical differences were assessed using appropriate F -tests. If there were significant interactions ($P < 0.15$) present in the model, the parameters were estimated and separate tests done on each level of the interacting factor. For example, if there was a time period \times sex interaction, and we were interested in the effect of time-period, parameters were estimated separately for each sex and the time-period effect tested.

RESULTS

Steller Sea Lions

Overall, tooth annuli $\delta^{13}\text{C}$ values decreased slightly and $\delta^{15}\text{N}$ values increased significantly throughout our period of investigation (Fig. 1). However, because sea

Table 1. Effect of growth order on mean (\pm SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in tooth annuli for the pooled sample of Steller sea lions used in this study. Within columns, superscript letters indicate differences between annuli groups according to Tukey's HSD test.

Annulus age	<i>n</i>	$\delta^{13}\text{C}(\text{‰})$	$\delta^{15}\text{N}(\text{‰})$
0	113	-13.8 ± 0.7^a	18.7 ± 0.5^a
1	113	-13.1 ± 0.6^b	18.1 ± 0.7^b
2	113	-12.8 ± 0.5^c	17.6 ± 0.6^c
3	107	-12.8 ± 0.7^c	17.5 ± 0.7^c

lions receive nutrition through mother's milk prior to weaning, we investigated the effect of annulus year on stable isotope abundance. Overall, annulus order had a significant effect on both $\delta^{13}\text{C}$ ($F_{3,442} = 75.7$, $P < 0.0001$) and $\delta^{15}\text{N}$ ($F_{3,442} = 114.6$, $P < 0.0001$) values. Tukey's *post-hoc* tests on the first year, or growth-layer group one (GLG1), were more enriched in ^{15}N and depleted in ^{13}C than all other annuli. As Steller sea lions aged, $\delta^{15}\text{N}$ values decreased relative to GLG1 (Table 1), but increased overall when averaged as a function of time. Values of $\delta^{13}\text{C}$ increased within GLG 2, 3, and 4 compared to GLG1, but decreased as a function of time (Table 1; Fig. 2, 3).

We next modeled $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values within each growth-layer group as a function of time. For both isotopes, AICc values obtained for all order polynomials decreased with increasing trim level. Overall best-fit polynomials differed in order among growth-layer groups (Table 2). We investigated change points and overall patterns of relationships between stable isotope values with time as depicted by the best polynomial fit for each growth layer (Table 3). GLG1 showed increasing $\delta^{13}\text{C}$ values from 1960 to 1982 but $\delta^{15}\text{N}$ values showed a maximum in 1965–1966 and a minimum in 1976–1977. For GLG2, no change was observed through time for both isotopes; GLG3 showed no change in $\delta^{15}\text{N}$ values but an increasing trend in $\delta^{13}\text{C}$ values from 1960 to 1982; GLG4 showed increasing $\delta^{15}\text{N}$ values from 1960 to 1982 and two parsimonious models were possible for patterns in $\delta^{13}\text{C}$ values corresponding to no change and to an oscillating pattern with changes occurring in 1963, 1972, and 1978 (Table 3).

Crested Auklets

Crested auklet feather isotope values were quite variable (Table 4). We determined no significant effect of age, sex, or year group (1970s *vs.* 1980s) on $\delta^{15}\text{N}$ feather values (ANOVA, $P > 0.14$ in all cases; Fig. 4). However, we found significant year-group effects for $\delta^{13}\text{C}$ values, indicating 6.5% lower levels in the 1980s compared to the 1970s ($F_{1,33} = 13.57$, $P = 0.023$). There was a slight tendency for adults to be more enriched in both ^{13}C and ^{15}N compared to juveniles (Table 4).

Tufted Puffins

The results of our AIC approach to determining the most parsimonious model explaining isotopic changes in puffin feathers through time indicated that period (defined as before and after 1976) was the best fit for our $\delta^{13}\text{C}$ data and age the best fit for our $\delta^{15}\text{N}$ data (Table 5). We also examined these data using more conventional probability-based approaches.

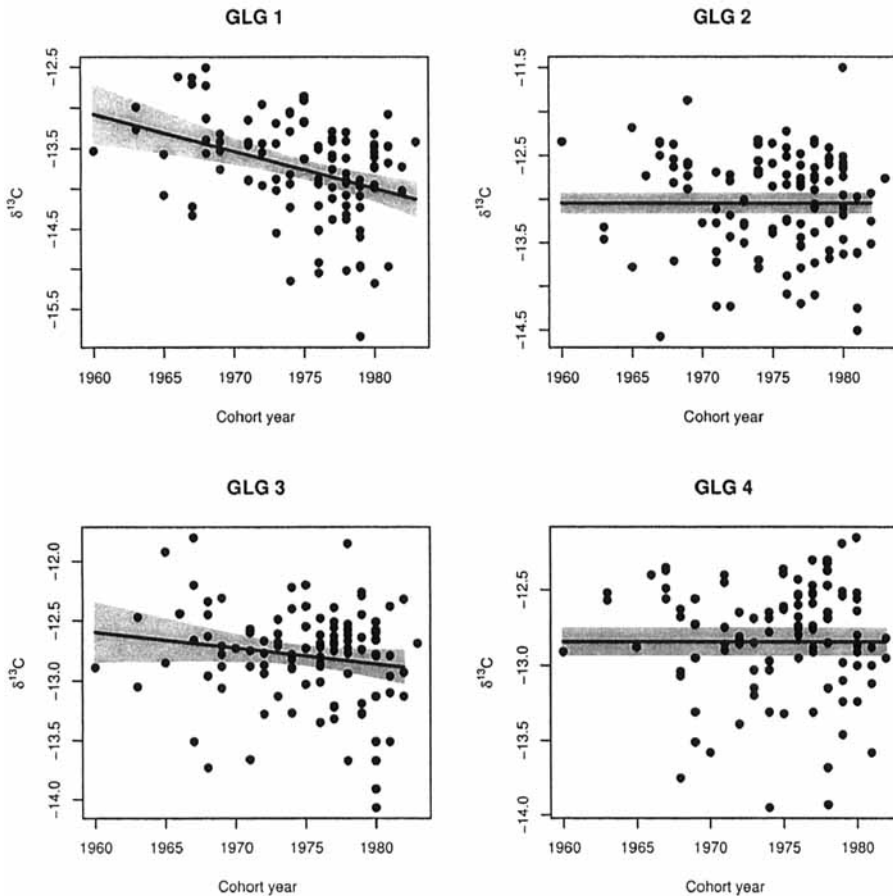


Figure 2. Relationship between tooth inorganic $\delta^{13}\text{C}$ values and year for Steller sea lions in the Gulf of Alaska according to tooth growth-layer group (GLG). The solid line is the best fitting polynomial of degree <5 chosen on the basis of the corrected Akaike Information Criteria. The shaded portion of the graph is the 95% prediction interval for the model.

Since our sample of puffins was comprised of birds from the western Aleutians and North Pacific as well as the Gulf of Alaska, we further analyzed these two groups separately (Table 4). For the Gulf of Alaska sample, there was no influence of year, age, or sex on $\delta^{15}\text{N}$ values ($F_{16,21} = 1.02$; $P = 0.48$). The overall $\delta^{15}\text{N}$ value was $15.4\text{‰} \pm 1.3\text{‰}$ (range 13.1‰ to 18.5‰ , $n = 42$) and no change occurred pre- and post-1976 (pre: $15.7 \pm 1.5\text{‰}$, $n = 4$; post: $15.5 \pm 1.3\text{‰}$, $n = 36$). For $\delta^{13}\text{C}$ values, we found a significant effect of age ($F_{2,21} = 4.61$, $P = 0.044$) and sex ($F_{1,21} = 3.69$, $P = 0.04$) but no influence of year ($F_{13,21} = 1.33$, $P < 0.279$). Although adult females ($r^2 = 0.16$, $P = 0.13$) and males ($r^2 = 0.01$, $P = 0.6$) showed no significant correlations of $\delta^{13}\text{C}$ values with year, the overall relationship for all age groups combined was significant ($r^2 = 0.17$, $P < 0.001$, Fig. 5). Adult females did not differ from adult males or juvenile females in $\delta^{13}\text{C}$ values but juvenile males and a single subadult female (-14.4‰) showed the most enriched $\delta^{13}\text{C}$ values.

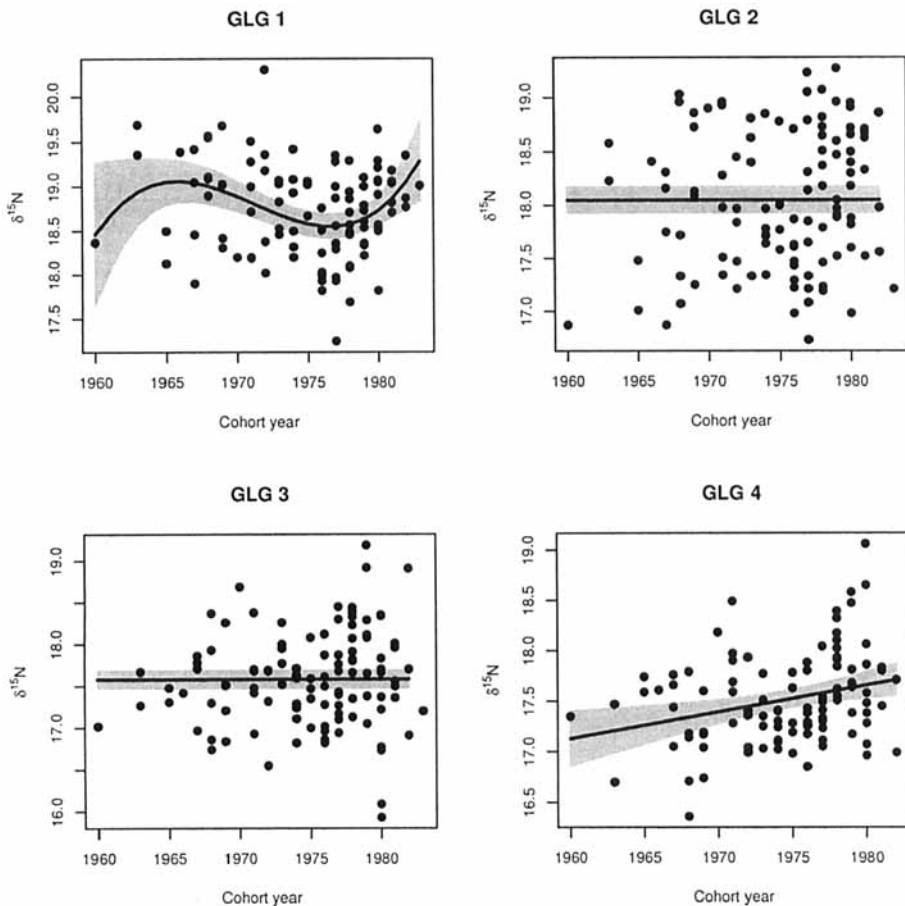


Figure 3. Relationship between tooth organic $\delta^{15}\text{N}$ values and year for Steller sea lions in the Gulf of Alaska according to tooth growth-layer group (GLG). The solid line is the best fitting polynomial of degree <5 chosen on the basis of the corrected Akaike Information Criteria. The shaded portion of the graph is the 95% prediction interval for the model (Chambers *et al.* 1983).

Pre-1976 birds ($-17.8 \pm 1.8\text{‰}$, $n = 4$) were more enriched in ^{13}C than post-1976 birds ($-20.2 \pm 1.8\text{‰}$, $n = 36$).

Patterns in the North Pacific and western Aleutians sample were similar to the Gulf of Alaska. However, we found no influence of age ($F_{2,48} = 1.9$, $P = 0.16$) or sex ($F_{1,48} = 0.14$, $P = 0.71$) on $\delta^{15}\text{N}$ values. Pre-1976, $\delta^{15}\text{N}$ values ($13.8 \pm 2.3\text{‰}$, 7.9‰ – 18.3‰ , $n = 43$) were not different to post-1976 values ($12.6 \pm 2.1\text{‰}$, range 8.8 – 16.7‰ , $n = 47$) and no overall correlation between $\delta^{15}\text{N}$ values and year was found (Fig. 6). $\delta^{13}\text{C}$ values were correlated with year (Fig. 6; $r^2 = 0.25$, $P < 0.001$), declining over time. Similarly, the ANOVA model showed a significant effect of age ($F_{2,48} = 3.15$, $P = 0.05$) and year ($F_{35,48} = 7.87$, $P < 0.001$), but no effect of sex on $\delta^{13}\text{C}$ values ($F_{1,48} = 0.36$, $P = 0.55$). Adult females were similar in $\delta^{13}\text{C}$ values to adult males and subadult females but tended to be more enriched in ^{13}C compared to juvenile and subadult males (Table 4).

Table 2. Sea lion polynomial modeling results. For each growth layer, corrected values of AICc for polynomials of stable isotope values modeled as polynomials up to degree 5 (degree 0 is the constant model). Trim = 0, all data used, Trim = 5%, 2.5% of highest and lowest values removed, Trim = 10%, 5% of highest and lowest values removed. Lowest AICc values for each isotope are bolded.

Polynomial degree	AICc $\delta^{15}\text{N}$ (‰)			AICc $\delta^{13}\text{C}$ (‰)		
	(trim = 0)	(trim = 0.05%)	(trim = 0.10%)	(trim = 0)	(trim = 5%)	(trim = 10%)
GLG1						
0	171.976	138.278	113.585	232.462	169.893	134.997
1	171.962	140.147	115.620	225.109	162.558	129.721
2	171.969	140.378	115.713	227.001	164.610	131.836
3	164.718	133.992	109.612	227.179	163.680	132.665
4	166.549	136.063	111.745	228.890	164.000	131.199
5	168.655	137.822	113.882	230.305	166.245	133.086
GLG2						
0	218.218	190.817	171.112	196.320	157.275	129.616
1	218.455	192.781	173.035	197.446	158.856	130.345
2	220.529	194.086	173.244	199.513	160.561	132.289
3	221.188	196.049	175.399	201.310	162.672	134.452
4	221.519	197.562	176.681	203.333	164.797	136.671
5	221.251	189.022	168.242	204.778	165.687	135.970
GLG3						
0	189.162	139.963	114.352	144.103	82.269	48.433
1	189.787	140.769	114.345	143.414	83.392	50.464
2	191.708	142.082	116.312	144.844	85.434	52.388
3	193.851	144.245	118.391	146.928	87.596	54.551
4	194.982	144.450	117.216	148.882	89.528	56.554
5	197.009	145.291	116.527	147.718	89.731	58.559
GLG4						
0	132.034	87.003	54.983	141.235	68.044	45.210
1	125.593	87.435	54.533	141.723	69.951	46.063
2	126.787	88.794	56.391	143.777	72.023	48.093
3	128.907	90.964	58.561	143.678	71.676	48.679
4	128.910	89.459	56.000	138.116	68.780	44.399
5	126.307	89.387	55.946	139.447	68.945	44.721

DISCUSSION

The objective of our research was to use stable isotope signatures in teeth annuli and feathers to establish a temporal isotopic record of central and high trophic-level consumers in the North Pacific through the regime shift of 1976. Changes in stable isotope values of such consumers can reflect real dietary changes as well as changes in foraging location, or changes in the stable isotope composition of primary producers.

Our study has provided evidence for an overall decline in average $\delta^{13}\text{C}$ values for two species of marine birds and Steller sea lions, in the Gulf of Alaska and adjacent waters of the eastern North Pacific and Aleutians during the late 1960s through the late 1980s. Results of $\delta^{13}\text{C}$ analysis suggests that either the signature of the marine

Table 3. Summary of model results for isotopic changes in all Steller sea lion tooth annuli growth layers for both isotopes. The polynomial degree corresponds to the best fit AIC criteria. Change points are based on the requirement that the first derivative of the temporal response of isotope values equals zero.

GLG	Isotope	Polynomial degree	Estimated change point(s)	Description
1	^{13}C	1		Increasing 1960–1982
	^{15}N	3	1966, 1977	Maximum in 1965–1966; minimum in 1976–1977
2	^{13}C	0		No change
	^{15}N	0		No change
3	^{13}C	1		Increasing 1960–1982
	^{15}N	0		No change
4	^{13}C	0		No change
	^{13}C	4	1963, 1972, 1978	Oscillating; minimum for animals born in 1972, relative maximum for 1963 and 1978 cohorts
	^{15}N	1		Increasing 1960–1982

food web in this region declined causing a consequent broad isotopic change across trophic levels, or that all three species underwent a simultaneous shift to more pelagic prey due either to a change in foraging distribution or a shift in oceanic currents or conditions as discussed above. The latter explanation is plausible since pelagic food webs tend to be more negative in carbon isotope signature compared with inshore or benthic food webs (Hobson *et al.* 1994, France 1995a,b). The slight (on the order of 0.5‰) declines in Steller sea lion $\delta^{13}\text{C}$ values with age are also plausibly explained by known patterns of increased pelagic foraging with age (Merrick *et al.* 1997).

If the patterns in $\delta^{13}\text{C}$ values represent an overall change in the marine food web, one possible mechanism is a decline in cellular growth rate of phytoplankton at the base of the food web (Laws *et al.* 1995, Bidigare *et al.* 1997). Such a decline can result from decreased availability of carbon dioxide, nutrients, and light for photosynthesis. Food web carbon isotopic signatures can change due to a variety of processes including water temperature and availability of inorganic nutrients (Michener and Schell 1994) that may mediate phytoplankton growth rates (Schell 2000). Recently, Cullen *et al.* (2001) have hypothesized that changes in atmospheric CO_2 sources to marine waters, namely the Seuss effect, may be responsible for long-term declines in marine food web $\delta^{13}\text{C}$ signatures (but see Hirons *et al.* 2001, Schell 2001). Other possible linkages between declining $\delta^{13}\text{C}$ values in the Gulf of Alaska and oceanic processes include a long-term decrease in the mixed-layer depth in the North Pacific Ocean (Freeland *et al.* 1997, Wu *et al.* 1999). This, in turn, may have resulted in a corresponding decrease in nitrate supply to the euphotic zone thereby altering growth rates of primary productivity and yielding a subsequent decrease in food web $\delta^{13}\text{C}$ values. Increased stabilization of the surface layer may have also caused synergistic coupling of lowered productivity and increased Seuss effect on stable isotope ratios of dissolved inorganic carbon (DIC) and particulate organic carbon (POC) (Schell 2001). Changes in stratification arising from changing runoff patterns and impacts on the Alaska Coastal Current in which apex predators such as sea lions feed, are other possible mechanisms influencing food web isotopic

Table 4. Isotopic differences among seabirds sampled in the Gulf of Alaska and North Pacific (including Aleutians). Values are means \pm SD.

Sample	<i>n</i>	$\delta^{13}\text{C}(\text{‰})$	$\delta^{15}\text{N}(\text{‰})$
Crested Auklet:			
Adult male	13	-18.9 ± 1.7	14.5 ± 2.3
Adult female	9	-18.7 ± 1.8	13.5 ± 2.3
Juvenile male	9	-20.2 ± 1.2	12.6 ± 2.0
Juvenile female	6	-19.5 ± 1.2	12.6 ± 1.9
Tufted Puffin			
Gulf of Alaska			
Adult male	15	-18.6 ± 0.6	15.5 ± 1.4
Adult female	15	-18.5 ± 1.1	15.4 ± 1.4
Juvenile male	3	-16.0 ± 1.9	16.0 ± 1.4
Juvenile female	3	-17.2 ± 0.9	15.5 ± 1.1
North Pacific			
Adult male	32	-18.7 ± 0.8	13.4 ± 2.5
Adult female	21	-18.4 ± 0.7	13.4 ± 2.5
Juvenile male	3	-19.8 ± 0.6	12.1 ± 1.9
Subadult male	17	-19.7 ± 1.2	13.2 ± 1.8
Subadult female	14	-19.0 ± 1.7	12.5 ± 2.3

signatures. For birds, we found about a 1.5‰–2‰ decline in $\delta^{13}\text{C}$ values over a twenty-year period. Schell (2000) has recently correlated long-term changes in $\delta^{13}\text{C}$ values in the baleen of bowhead whales with declines in productivity in the Bering Sea and estimates a 40% reduction in productivity in that system. Our seabird data at first may suggest a similar decline in the Gulf of Alaska and Aleutians although closer examination of the tufted puffin data suggests that the observed isotopic decline is, in part, due to differences between the sexes and among age classes.

Hirons *et al.* (2001) examined isotopic changes in bone collagen of Steller sea lions and two other pinnipeds in the Gulf of Alaska and Bering Sea for the period 1951 through 1996 and determined an average decline in $\delta^{13}\text{C}$ values of 2‰. However, their combined sample of animals from both the Bering and Gulf of Alaska precludes analysis of effects in either system separately. Secondly, age and sex data were not available for several of their animals. Finally, the use of collagen, while representing dietary averages over the lifetime of the animal in older individuals, is biased toward earlier periods of growth in younger individuals (*i.e.*, when most of the initial collagen is formed). Until these effects are considered in detail, it will be difficult to compare our results with theirs. Where possible, we recommend the use of individual tooth annuli *vs.* bone collagen for these sorts of retrospective investigations.

Recently, Cullen *et al.* (2001) challenged Schell's hypothesis of isotopic evidence for a productivity change in the Bering Sea food web and argued that the Suess effect of input from anthropogenically derived ^{13}C -depleted CO_2 into surface waters may be a more parsimonious explanation for long-term ^{13}C depletion in that marine system. Although this viewpoint was countered by Schell (2001), both groups agreed that further studies in other ocean systems might well result in a better delineation of local *vs.* more global effects. While our results for the Gulf of Alaska region similarly suggest long-term ^{13}C depletion in the marine food web,

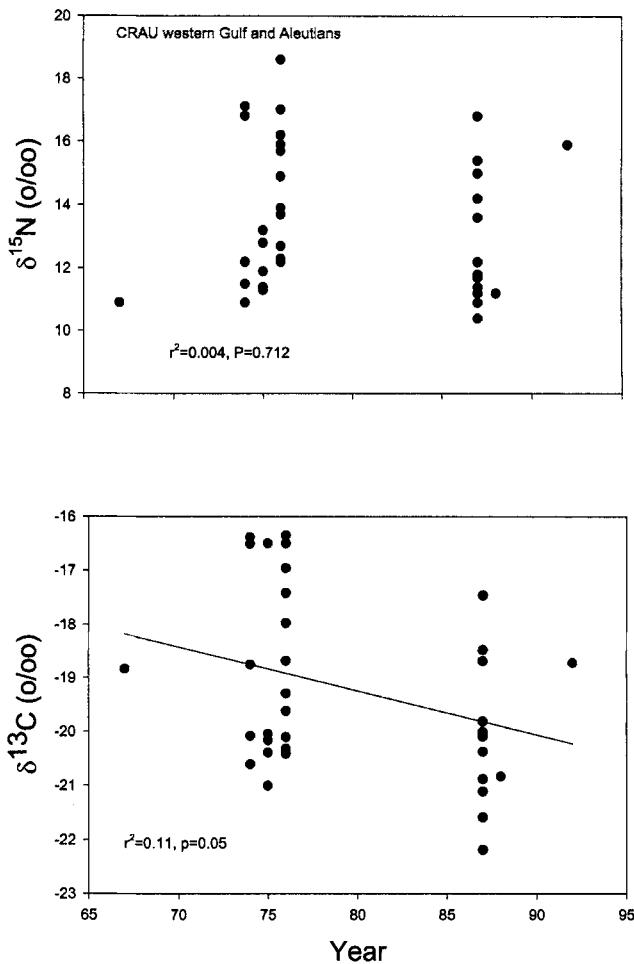


Figure 4. Relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ feather values and year for crested auklets in the western Aleutians.

we agree that the potential for changes in spatial use of marine environments by volant predators (*i.e.*, their differential exploitation of inshore *vs.* offshore resources, and at different life stages) underlines the need for either a multispecies approach or the choice of sessile benthic clams as proxy measures of environmental isotopic change (Hirons *et al.* 2001, Schell 2001).

In general, stable nitrogen isotope analysis of animal tissues provides an indication of trophic level. The isotopic enrichment factor between consumer tissues and their prey depends on tissue type (Hobson and Clark 1992). For marine birds, the best estimate of this trophic enrichment in $\delta^{15}\text{N}$ values is 4.4‰ (Mizutani *et al.* 1992). This suggests that, during body feather molt, tufted puffins in the Gulf of Alaska fed on prey with an average $\delta^{15}\text{N}$ value of 11.0‰ and those in the North Pacific and western Aleutians on prey averaging 8.2‰–9.4‰. Similarly, the mean prey $\delta^{15}\text{N}$ value estimated for crested auklets during molt ranged from 8.2‰ for juveniles to

Table 5. Results of AICc criteria tests of models explaining isotopic variation in puffin feathers. Age (adult vs. non-adult); sex (M, F); period (before 1976, after 1976). Lowest AICc values bolded.

Model parameter	AICc $\delta^{13}\text{C}$ (‰)	AICc $\delta^{15}\text{N}$ (‰)
Null	138.187	154.727
Age	137.791	153.374
Sex	140.149	156.476
Period	134.777	154.416
Full	142.938	158.200
Age*sex	141.694	155.947
Age + sex	139.726	154.140
Age + period	136.449	154.766
Age*period	137.153	156.092
Sex + period	136.771	155.917
Sex*period	138.541	157.537

10.1‰ for adult males. Although our knowledge of $\delta^{15}\text{N}$ values for various prey types in this area is incomplete, data suggest that tufted puffins fed on a mixture of fish and invertebrates (Hobson *et al.* 1994, 1997). Crested auklets, as expected, had feather $\delta^{15}\text{N}$ values consistent with a diet of primarily invertebrate prey. Our data provide insight to feeding ecology of these species during the post-breeding period which is generally poorly understood in seabirds (Hobson *et al.* 1994). Within species, dietary differences between sexes and age groups are also not well understood for most temperate or high-latitude seabirds.

We found no evidence for changes in $\delta^{15}\text{N}$ values in crested auklets or tufted puffins over the same period. However, changes in $\delta^{15}\text{N}$ values for Steller sea lions were significant and variable with age and time contributing to isotopic evidence for a regime shift occurring in the Gulf of Alaska since 1976. The first (GLG1) and fourth (GLG4) tooth annulus of Steller sea lions most strongly evidenced these patterns around two or more change points including the mid 1970s. Here, $\delta^{15}\text{N}$ values tended to increase after decreasing up to 1976, supporting diet studies indicating that Steller sea lions, like other apex predators in the North Pacific and Bering Sea, saw a reduction in availability of forage fish and increased consumption of large semi-demersal fish such as walleye pollock (Hunt *et al.* 2002, Sinclair 1988, Sinclair *et al.* 1994, Merrick *et al.* 1997, Sinclair and Zeppelin 2002; Table 2). Further, our determination that the first two annuli of Steller sea lion teeth, corresponding to the first two years of growth, were enriched in both ^{13}C and ^{15}N compared with subsequent annuli across all years, is consistent with previous findings (Hobson *et al.* 1997). These years correspond to periods when maternal influence on trophic level occurs through weaning (*contra* Jenkins *et al.* 2001). Thus, it is possible that the foraging ecology of females may have changed during the mid 1970s prior to or during the weaning period, or that the foraging ecology of neonates changed. However, we stress that critical information is lacking in terms of our understanding of processes that may have contributed to the temporal patterns in isotopic signatures we measured. That the isotopic patterns were not consistent across all growth-layer groups points to an interaction between year and the ecophysiology of the individuals examined. That we do not necessarily see similar isotopic effects to those in GLG1 in other years is complicated by several

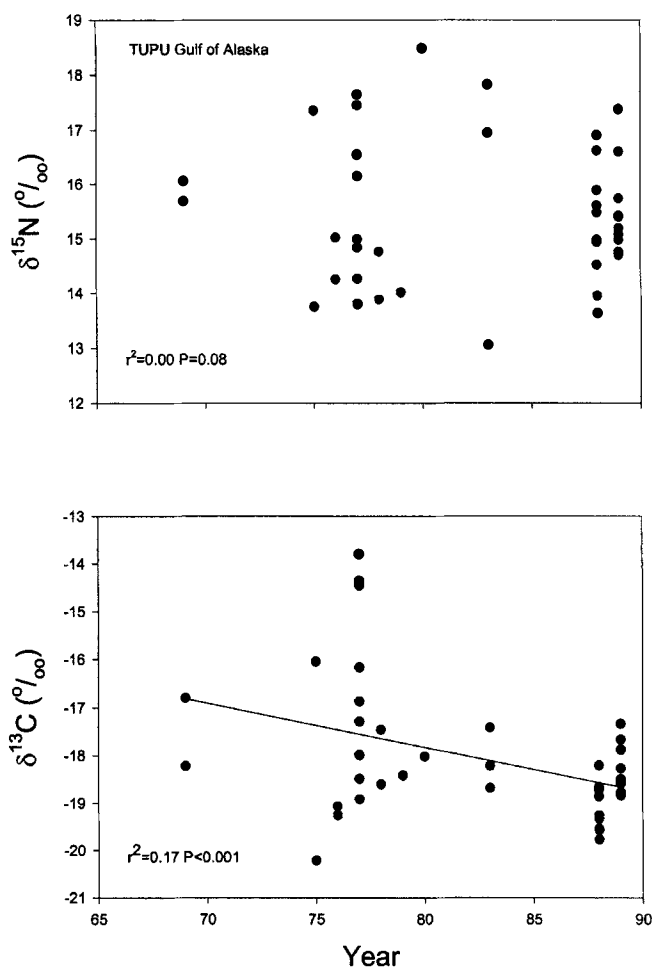


Figure 5. Relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ feather values and year for tufted puffins in the Gulf of Alaska.

factors. Not all older animals in our data set (*i.e.*, corresponding to GLG layers of 4 and higher) necessarily reproduced successfully in later years. In addition, nutritional metabolic and isotopic pathways to young *via* suckling do not necessarily correspond to identical patterns in adult females. Thus, nutrient transfer to young can involve dietary metabolic pathways that differ from metabolic pathways to the nursing mothers (see Hobson and Stirling 1997 for a discussion on metabolic routing).

Patterns of isotopic fractionation between diet and tooth dentine have not been studied extensively, but Schoeninger and DeNiro (1984) suggested an enrichment of +3‰ in $\delta^{15}\text{N}$ values for bone and tooth collagen. Applying this value to our data suggests that Steller sea lions consumed prey with a mean $\delta^{15}\text{N}$ value of 14.6‰. This corresponds to several possible diets of fish in various combinations but is also consistent with a diet of adult walleye pollock. Stable nitrogen isotope ratios of red

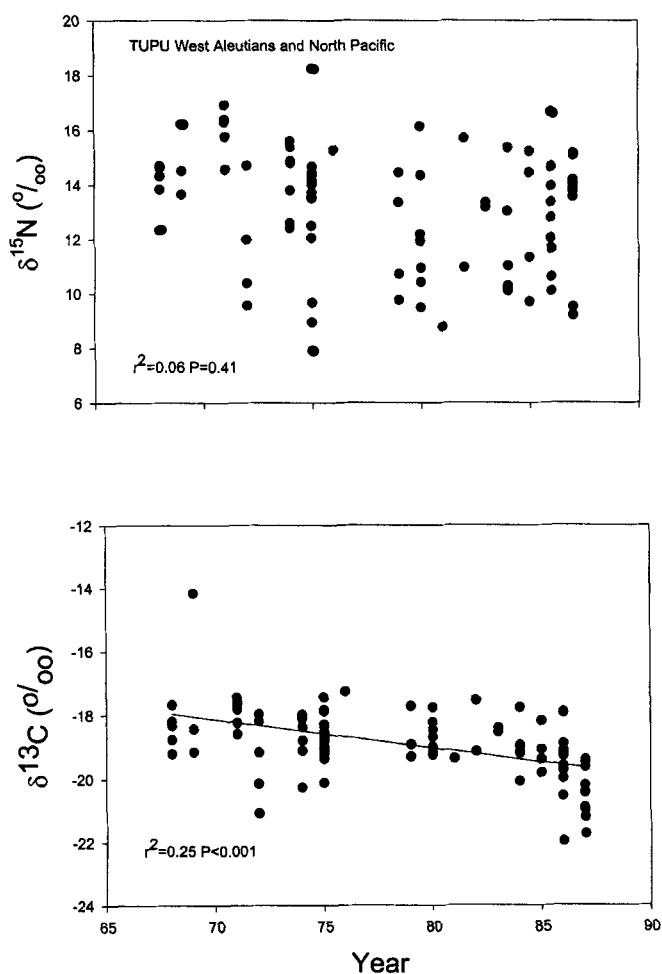


Figure 6. Relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ feather values and year for tufted puffins in the North Pacific and western Aleutians.

blood cells, plasma, and serum collected from Steller sea lions in the 1990's (Kurl and Sinclair 2003) closely corresponds to diet studies conducted in the same area over the same time period (Sinclair and Zeppelin 2002). Steller sea lions currently consume a diet rich in walleye pollock (*Theragra chalcogramma*) and other large demersal and semi-demersal fishes such as Pacific cod (*Gadus macrocephalus*) and arrowtooth flounder (*Atheresthes stomias*) in the Gulf of Alaska and northern North Pacific. The slight increase in $\delta^{15}\text{N}$ values throughout the study period in the analyses presented here is also consistent with diet studies in Steller sea lions indicating greater incorporation of walleye pollock over capelin and herring since the regime shift of 1976 (Sinclair and Zeppelin 2002).

Although our study has not provided unequivocal support for a uniform food web response to the Gulf of Alaska regime shift of 1976, our approach does reveal the advantages to a cross-taxa isotope study that also combines dietary integrations

for specific years *vs.* the lifetime of the individual. In addition to providing support for an overall decline in productivity in the Gulf, we now identify the possibility that food web changes may have resulted in changes in sea lion maternal nutrient transfer through weaning. Since offspring survival beyond weaning represents a critical demographic phase in this population, we suggest that more research be conducted to investigate this possibility (also see Merrick *et al.* 1997).

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