Centennial Decline in the Trophic Level of an Endangered Seabird after Fisheries Decline

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Abstract: *Coastal marine ecosystems worldwide have undergone such profound transformations from overfishing that trophic interactions observed today might be artifacts of these changes. We determined whether the trophic level of an endangered seabird, the Marbled Murrelet (*Brachyramphus marmoratus*), has declined over the past 100 years after the collapse of Pacific sardine (*Sardinops sadax*) fisheries in the late 1940s and the recent declines of similar fisheries in central California. We compared stable-isotope signatures of* $\delta^{15}N$ *and* $\delta^{13}C$ *in feathers of museum specimens collected before fisheries decline with values in murrelet feathers collected recently. Values of* $\delta^{15}N$ *in prebreeding diets declined significantly, 1.4‰ or 38% of a trophic level, over the past century during cool ocean conditions and by 0.5‰ during warm conditions, whereas postbreeding values of* $\delta^{15}N$ *were nearly constant. The* $\delta^{13}C$ *values in prebreeding diets declined by 0.8‰, suggesting an increased importance of krill in modern compared with historic prebreeding diets, but postbreeding diets did not change. Stable-isotope mixing models indicated that the proportion of energetically superior, high-trophic-level prey declined strongly whereas energetically poor, low-trophic-level and midtrophic-level prey increased in the prebreeding diet in cool years when murrelet reproduction was likely to be high. Decreased prey resources have caused murrelets to fish further down on the food web, appear partly responsible for poor murrelet reproduction, and may have contributed to its listing under the U.S. Endangered Species Act.*

Key Words: endangered species, Marbled Murrelet, marine food web, seabird diet, stable isotopes

Declinación Centenaria en el Nivel Trófico de una Especie de Ave Marina en Peligro después del Colapso de las Pesquerías

Resumen: *A nivel mundial, los ecosistemas marinos costeros han sido sometidos a transformaciones tan profundas por la sobreexplotación pesquera que las interacciones tróficas que se observan actualmente pueden ser artefactos de esos cambios. Determinamos si el nivel trófico de una especie de ave marina en peligro,* Brachyramphus marmoratus*, ha declinado durante los últimos 100 años después del colapso de las pesquerías de sardina del Pacífico (*Sardinops sadax*) en la década de 1940 y las declinaciones recientes de pesquerías similares en California central. Comparamos las firmas de isótopos estables de* $\delta^{15}N$ *y* $\delta^{13}C$ *en plumas de especimenes de museo recolectados antes del colapso de las pesquerías con las de plumas recolectadas recientemente. Los valores de* $\delta^{15}N$ *en dietas de individuos pre-reproductivos declinaron significativamente, 1.4‰ o 38% de un nivel trófico, a lo largo del siglo pasado durante períodos con condiciones frías en los océanos y 0.5‰ durante condiciones más cálidas, mientras que los valores post reproductivos de* $\delta^{15}N$ *fueron casi constantes. Los valores de* $\delta^{13}C$ *en dietas pre-reproductivas declinaron 0.8‰, lo que sugiere una mayor importancia del kril en las dietas pre-reproductivas modernas en comparación con las históricas, pero que las dietas post reproductivas no han cambiado. Los modelos de combinación de isótopos estables indicaron la que la proporción de presas de nivel trófico alto y energéticamente superiores declinó fuertemente mientras que las presas de nivel trófico bajo y medio y energéticamente inferiores incrementaron en la dieta pre-reproductiva en los años fríos cuando*

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era probable que la reproducción de B. marmoratus *fuera alta. La disminución de las presas ha causado que* B. marmoratus *pesque más abajo en la red alimenticia, y parece ser la responsable de la baja reproducción de* B. marmoratus*, y puede haber contribuido a su inclusión en el Acta de Especies en Peligro de E.U.A.*

Palabras Clave: *Brachyramphus marmoratus*, dieta de ave marina, especie en peligro, isótopos estables, red alimenticia marina

Introduction

Coastal marine ecosystems worldwide have undergone dramatic changes because of overfishing, pollution, habitat destruction, exotic species introductions, and climate warming (Pauly et al. 1998*b*; Myers & Worm 2003; Ward & Myers 2005). Of these impacts, perhaps the most pervasive is overharvesting of species at higher trophic levels, the effects of which cascade to lower trophic levels by changing community structure, species dominance, and ecosystem characteristics. "Fishing down the food web" directly reduces the average trophic level of marine organisms by selectively harvesting fishes that are larger and on a higher trophic level, reduces catch biomass and mean organism size, and periodically requires harvesters to shift to new, often lower-trophic-level fishery resources (Pauly et al. 1998*a*, 1998*b*; Myers & Worm 2003). Changes relatively high in a marine trophic web could cascade primarily down but perhaps also up the web, as a suite of predator-prey relationships shifts to accommodate the new structure (Pauly & Watson 2003). The impacts of overfishing, however, can sometimes be difficult to distinguish from natural variability in fish stocks in part because of long-term variation in ocean climate, such as ocean warming or regime shifts of the Pacific Decadal Oscillation (PDO) (Mantua et al. 1997; Francis et al. 1998), that affects community composition (Finney et al. 2002).

Trophic interactions observed in marine food webs today might be artifacts of these recent, large structural changes to marine communities. Two cases of long-term diet shifts in marine predators have been attributed to legacy effects of whaling. Diet shifts have been detected in a top marine predator, the killer whale (*Orcinus orca*), when its preferred whale prey was overharvested recently, causing large declines in populations of replacement prey (Springer et al. 2003; Williams et al. 2004). A trophic-level decline in Northern Fulmars (*Fulmarus glaciali*) was attributed to a decrease in the availability of whale offal during the past century (Thompson et al. 1995). Haddock (*Melanogrammus aeglefinus*) diets declined by two-thirds of a trophic level between 1929 and 1987 in response to large-scale changes in the food web of the Georges Bank in the North Atlantic associated with fishing pressure and long-term climatic variation (Wainright et al. 1993). However, Stellers sea lions (*Eumetopias jubatus*), northern fur seals (*Callorhinus ursinus*), and harbor seals (*Phoca vitulina*) in the Gulf of Alaska and Bering Sea have shown either no change or a slight increase in trophic level over the past 50 years (Hirons et al. 2001; Hobson et al. 2004).

Little is known about the impacts of structural changes to marine communities at midtrophic levels or whether the omnivorous diet of most midtrophic species such as seabirds may buffer them against diet change, trophic cascades, and population declines (Bascompte et al. 2005). Seabirds act as environmental samplers that track and consume the most abundant or energetically valuable prey items because they vary seasonally and annually (Ainley et al. 1995, 1996*a*, 1996*b*; Litzow et al. 2002).

We investigated whether the trophic level of an endangered marine seabird, the Marbled Murrelet (Alcidae: *Brachyramphus marmoratus*), has changed over the past 100 years after the collapse of the sardine fishery in central California, immortalized by the characters of *Cannery Row* in Steinbeck (1945), and recent harvesting of similar fisheries eaten by seabirds. Seabird (family Alcidae) prey in the California Current system (CCS) cluster into three distinct groups (Fig. 1), as classified by *k*-means cluster analysis of $\delta^{15}N$ and $\delta^{13}C$ (B.H.B. and S.R.B., unpublished data), that differ from adjacent groups by about one-half a trophic level and are affected differentially by harvesting and climatic variability. High-trophic-level prey commonly taken by both seabirds and fisheries include Pacific sardines (*Sardinops sadax*), the northern anchovy (*Engraulis mordax*), and market squid (*Loligo opalescens*) (Leet et al. 2001; Love et al. 2002; Starr et al. 2002). Ocean cooling and overharvest appear to have caused the collapse of the sardine industry in central California that occurred in the late 1940s, when yields at canneries declined tenfold from a mean of 372,000 t/year from 1935 to 1945 to 32,000 t/year from 1945 to 1955, and sardine populations have yet to recover to precollapse levels (Leet et al. 2001; Lluch-Belda et al. 2001; Chavez et al. 2003*a*). Other fishing impacts on high-trophic-level prey in this region include a nearly eightfold increase in market squid landings over the past 20 years and an anchovy stock that has declined by 75% since 1974 (Leet et al. 2001; Ish et al. 2004).

Prey items at a midtrophic level (Fig. 1) include juvenile rockfishes (*Sebastes* spp.), sandlance (*Ammodytes hexapterus*), and mysid shrimp (*Mysis* spp.). Some midtrophic-level prey are not taken by fisheries (e.g., mysids), whereas others have been heavily exploited only recently (e.g., rockfishes), leading, in conjunction with

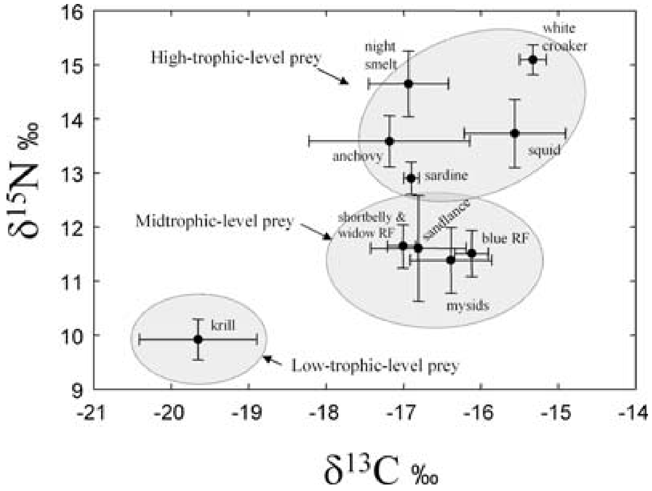

Figure 1. Dominant prey of seabirds in central California (RF, rockfish). Prey fall into three distinct groups labeled high-, mid-, and low-trophic-level prey based on k-means *clustering (Systat 2004) of $\delta^{15}N$ and $\delta^{13}C$ composition ($\chi^2_{20} = 146.25$, $p < 0.001$). Groups differ from adjacent groups by about one-half a trophic level. Classification success was 90% for low-trophic-level items, 60–100% for midtrophic-level items, and 74–100% for high-trophic-level items. Murrelet-sized prey items were collected in the Monterey Bay Region from 1997–2002. Error bars represent ±1 SE.*

ocean warming, to massive population declines and recent fisheries closures (Leet et al. 2001; Miller & Sydeman 2004).

Unlike high- and midtrophic-level seabird prey, low-trophic-level prey (i.e., euphausids or krill) have never been exploited heavily in California, but climatic variability greatly affects their population dynamics and in turn the dynamics of higher-level prey (Ainley et al. 1995; Abraham & Sydeman 2004; Ish et al. 2004). A 90% decline in CCS zooplankton occurred over the past 50 years because of ocean warming and a deepening thermocline (Roemmich & McGowan 1995). Mesozooplankton (e.g., amphipods) and macrozooplankton (e.g., krill) abundance increases dramatically in the CCS during cool PDOs or La Niña years, resulting in a burst of prey fish availability near the onset of seabird nesting and high seabird fecundity (Francis et al. 1998; Sydeman et al. 2001). Conversely, during warm periods fewer zooplankton and prey fishes are available and seabird fecundity is low (Ainley 1990; Ainley et al. 1995). Thus fishing pressure generally exerts a top-down effect on seabird prey, whereas ocean climate exerts a bottom-up effect (Micheli et al. 2001; Ware & Thomson 2005).

We tested whether the trophic level of Marbled Murrelets has declined over the last 100 years by comparing diets of 136 murrelets collected along the central California coast before intensive fishery exploitation and declines (historic era: 1895–1911) to 201 murrelets studied recently in the same region (modern era: 1998–2002). Marbled Murrelets are seabirds that typically forage <5 km from shore and nest in cryptic, inaccessible sites high in old-growth trees of great commercial value in coastal forests (Ralph et al. 1995). They are endangered in the United States and Canada and are thought to have declined primarily as a result of deforestation, nest predation, and oil spills.

Food may be an important factor limiting murrelet reproduction in central California (Peery et al. 2004). Murrelets appear to be primarily piscivores during the breeding season and to increase consumption of invertebrates during the winter (Hobson et al. 1994; Gaston & Jones 1998). Evidence from a few stomachs collected in central California from 1910–1911 indicates murrelets ate primarily sardines (Carter & Erickson 1992; Burkett 1995). Yet, modern stable isotope studies found murrelet diets before breeding were composed of a high proportion of mid- and low-trophic-level prey such as young-of-year rockfish, sandlance, mysids, and krill (*Thysanoessa spinifera),* which occur over the continental shelf within foraging range of murrelets in the CCS, while fall post-breeding diets were at a higher trophic level (B.H.B. and S.R.B., unpublished data). Approximately 80 krill or 3.5 rockfish are required to equal the energy (kilojoules) of one Pacific sardine of the size (30–60 mm) eaten by a small seabird, and 45 average-sized krill or 2 young-of-year rockfish are equal to the kilojoules in an average-sized northern anchovy (B.H.B. and S.R.B., unpublished data), so murrelets should select low- and midtrophic level prey if their availability and ease of capture outweigh the costs of finding larger, energetically superior prey. Perhaps murrelets might not have consumed as much krill and midtrophic-level prey before the reduction in availability of high-trophic-level prey due to overharvesting and natural ecosystem variability such as PDO cycles (Chavez et al. 2003*a*).

We determined whether historic trophic levels were similar to modern patterns explained by interactions between ocean conditions and prey availability with stable-isotope ratios, which are derived from food ingested during molt, preserved in feathers, and track seasonal and annual variation in diet (Hobson & Welch 1992; Hobson et al. 1994; Thompson & Furness 1995). Comparing the stable isotope signatures from the same tissues collected at different time intervals provides an assessment of temporal changes in diet (Dalerum & Angerbjorn 2005). In marine ecosystems stable-isotope ratios of nitrogen ($^{15}N/^{14}N$ expressed as $\delta^{15}N$) and carbon ($^{13}C/^{12}C$ expressed as $\delta^{13}C$) in predators predictably reflect those of their prey (Hobson 1993; Michener & Schell 1994; Forero et al. 2004). In marine birds $\delta^{15}N$ enriches by about 3.1‰ with each step in trophic level (Hobson et al. 1994; Kelly 2000), and $\delta^{13}C$ distinguishes krill from other items in this food web (Fig. 1). Examined together, these two isotopes can distinguish the major features of the diet and trophic level of Marbled Murrelets in the CCS (Fig. 1). We hypothesized that if cyclic oceanic change affects historic murrelets in the same manner as modern birds, seasonal shifts in trophic level should be similar in both historic and modern eras, with prebreeding diets at a similar or lower trophic level than postbreeding diets (B.H.B. and S.R.B., unpublished data). Alternatively, if seasonal changes in modern diets occur because of reduced abundance of energetically superior high- and some midtrophic-level prey, historic prebreeding diets should include a greater proportion of high- and midtrophic-level fishes and be at a higher trophic level than current diets.

Methods

Feather Collection and Isotope Analysis

We collected whole breast feathers and the tip of a fifth secondary feather from adult Marbled Murrelets caught in Año Nuevo Bay (37.1°N, 122.3°W), about 30 km north of Monterey Bay in central California (U.S.A.), from 1998 to 2002 and from adult murrelet specimens in the American Museum of Natural History, University of California Berkeley Museum of Vertebrate Zoology, and the California Academy of Sciences that were collected in the same region from 1895 to 1911. Murrelets molt their breast feathers to achieve both basic (winter) and alternate (breeding) plumage, and wing feathers (primaries and secondaries) are replaced only during the prebasic molt (Carter & Stein 1995). Brown-tipped breast feathers represent the prebreeding diet (March–April), and all secondary and all-white breast feathers represent the postbreeding diet (August–September).

We cleaned feathers with a methanol:chloroform:water solution, rinsed the solution with distilled water, and air dried the feathers (Wunder et al. 2005). Approximately 1.2 mg of dried feather (Thompson & Furness 1995) were loaded into tin capsules and analyzed for δ^{15}N and δ^{13}C with a Europa 20/20 continuous-flow isotope-ratio mass spectrometer (Europa Scientific, Vandalia, Ohio). Peach leaves and bovine liver from the National Institute of Standards and Technology (Boulder, Colorado) were used as standards for C and N, respectively (Jardine & Cunjak 2005). Analytical precision (SD) of analyses was always $<\pm 0.25$‰ for δ^{15}N and ± 0.10‰ for δ^{13}C. We analyzed standards between every eight feather samples and used a least-squares linear model to correct minor drift during the analysis (Jardine & Cunjak 2005). Isotopic ratios are expressed in the δ notation (parts per thousand—‰) relative to atmospheric N (for δ^{15}N) or Pee Dee Belemnite (for δ^{13}C).

Data Analysis

We used the PDO as a proxy for CCS sea surface temperature. In central California, January–April oceanographic variables such as upwelling and sea surface temperature are correlated with food-web development, diets during nesting, and reproductive success of seabirds (Ainley et al. 1995; Chavez et al. 2003*a*; Abraham & Sydeman 2004), including murrelets (B.H.B. and S.R.B., unpublished data). We used the mean of the monthly PDO values from January through April to characterize temperature for each year (Mantua et al. 1997; Mantua 2001) rather than as an indication of a long-term warm or cool regime. Although the Northern Oscillation Index or local sea surface temperatures may be a better proxy for local oceanographic conditions in a given year, these indices do not extend prior to 1948 and 1925, respectively, and monthly PDO from January through April is moderately correlated with Northern Oscillation Index ($r = -0.525, p < 0.001$). Thus PDO is the best alternative available to characterize general oceanographic conditions for each year. Values of PDO before 1900 are unknown, so we used tree-ring reconstructions of PDO for 1895 and 1896 (D'Arrigo et al. 2001). Negative PDO years were classified as cool years and positive values as warm years. Years grouped as follows: historic cool (1907, 1910, 1911), historic warm (1895, 1896, 1909), modern cool (1997, 1999, 2000, 2002), and modern warm (1998, 2001). Historic era years were 1895–1911 and modern era years were 1997–2002.

Although some commercial fishing began in 1903 in the study area, all the historic isotope data we used for diet reconstruction precede the earnest beginnings of the sardine fishery in 1919 (Williams 2003). Sardine harvest was not monitored before 1911, when the last historic specimen in our study was collected, and canneries did not concentrate in Monterey until after 1915 (Williams 2003). Annual sardine harvests in central California (San Francisco, Monterey Bay, and floating processing plants) between 1915 and 1920 (mean = 27,958 tons) were <8% of levels recorded during the period of intense exploitation from 1930 to 1945 (mean = 372,000 t). Greater harvests were due both to an increase in the number of fishing boats and more efficient fishing technology (Chavez et al. 2003*b*; Williams 2003). Therefore the trophic level and diets of murrelets before 1911 should be minimally affected by fishing.

Multivariate general linear models were used to test for era (pre- or post-1911), season (pre- or postbreeding), and annual temperature state (warm or cool) effects on δ^{15}N and δ^{13}C. We used three-way multivariate analysis of variance (MANOVA) models to analyze both isotopes simultaneously to test for overall significance and then used separate three-way analysis of variance (ANOVA) tests for each element. The latter tests, which yielded results identical to MANOVA, are presented because they are more easily interpreted. For ANOVA, we assumed all effects were fixed. By classifying temperature as a categorical variable, all levels of the factor were represented in the analysis, so it is a fixed effect (Littell et al. 1996). Temperature could arguably be classified as a random effect if it was treated as a continuous variable, although the 12 years over which feathers were collected may not represent a random sample of ocean temperature. Nevertheless, we used SAS to explore models with temperature coded as a continuous variable and treated as a random effect (Littell et al. 1996). All analyses yielded virtually identical inferences about the significance and relative importance of each effect for both isotopes, so we present only results from fixed-effects models. We used Bonferroni multiple-comparisons tests for post hoc tests of differences among means.

An IsoError dual-isotope, three-source mixing model (Phillips 2001; Phillips et al. 2005) was used to calculate the proportion of high-, mid-, and low-trophic-level prey in murrelet diets for each of the eight possible combinations of season, era, and ocean temperature. We did not use concentration-dependent models because all prey items and bird feathers had similar C:N ratios. We used a diet-feather fractionation value of 3.7‰ for δ^{15}N and 1.0‰ for δ^{13}C. This was based on the diet-feather fractionation in closely related Common Murres (Alcidae: *Uria aalge*) (Becker 2001) and is similar to values published for δ^{15}N (3.0–5.3‰) and δ^{13}C (0.4–3.8‰) for other fish-eating seabirds (Mizutani et al. 1992; Thompson & Furness 1995; Kelly 2000; Vanderklift & Ponsard 2003). We used these values in the mixing model, along with the isotopic means for each combination of season, era, and ocean temperature, to estimate the proportion of prey items from each trophic-level grouping that murrelets ingested. Varying the fractionation estimate does not change the relative differences in murrelet diets among seasons, temperatures, and eras, although it would alter the proportional estimates for each dietary source. The percent change in trophic level of Marbled Murrelets over time between a purely high and a purely low trophic-level diet was calculated by dividing the difference in δ^{15}N between eras by the 3.7‰ diet-feather fractionation.

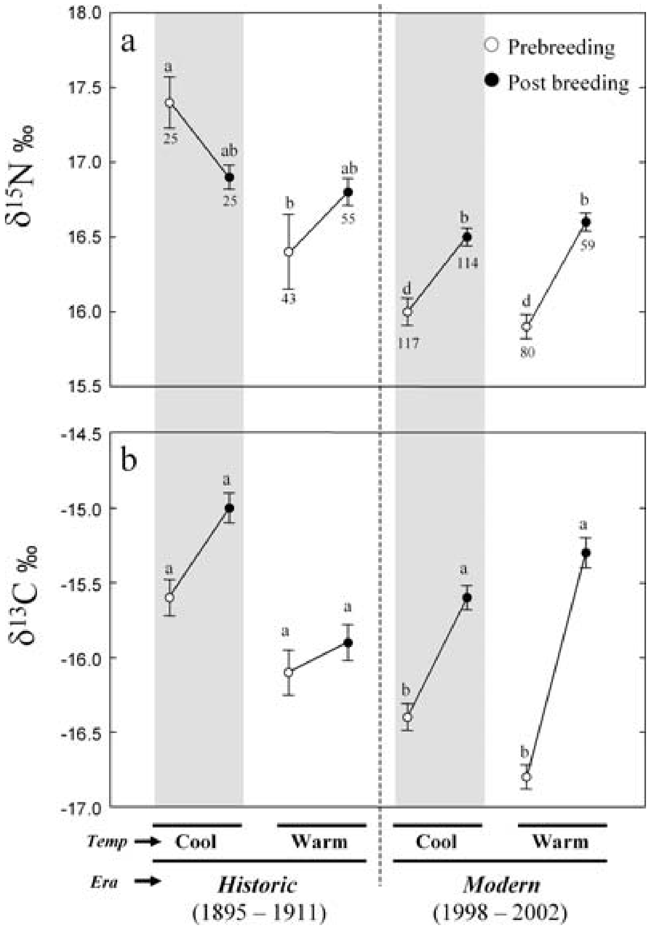

Figure 2. Levels of (a) δ^{15}N and (b) δ^{13}C in the diets of historic and modern Marbled Murrelets. Diet shown for prebreeding (open circle) and postbreeding (filled circle) seasons grouped by cool and warm water years (based on annual mean monthly Pacific Decadal Oscillation values from January through April). Means with different letters within panels differ significantly (Bonferroni adjusted pairwise comparisons, $p <$ 0.05). Numbers below points represent sample size, and error bars are ±1 SE.

Results

Diets of modern murrelets declined significantly in both δ^{15}N and δ^{13}C compared with diets of historic murrelets (Fig. 2; three-way MANOVA for all main effects and interactions, $p \leq 0.001$). Three-way ANOVAs for single isotopes showed significant differences among all three independent variables and most interactions for both isotopes (Table 1).

The δ^{15}N values in prebreeding diets declined significantly over the past century by 1.4‰ (38% of a trophic level) during cool ocean conditions and by 0.5‰ (14% of a trophic level) during warm conditions. In comparison, postbreeding δ^{15}N was nearly constant across eras (Fig. 2a). The effect of era on δ^{15}N in murrelet diets was far greater than effects of ocean temperature and season (as indicated by its large mean-squared error term in Table 1); adjusted least-squared mean δ^{15}N declined by 0.6‰ from the historic to modern era. The significant interaction between era and season was due to murrelets feeding at a higher trophic level before breeding in the era before extensive fish harvest. Post hoc comparisons confirmed that δ^{15}N in all historic prebreeding diets differed significantly from modern prebreeding diets, and indicated that modern prebreeding diets contained significantly less δ^{15}N than modern postbreeding diets (Fig. 2a).

The δ^{13}C values in prebreeding diets also declined greatly (0.8‰) between eras (Fig. 2b, Table 1), suggesting that the decline in δ^{15}N could have been due to an increased importance of krill in modern compared with

Table 1. Testing effects (analysis of variance) of era (historic vs. modern), season (pre- or postbreeding), and temperature (warm or cool) on $\delta^{15}N$ and $\delta^{13}C$ ratios in Marbled Murrelet feathers collected from birds in central California.*

Isotope	*Source*	*df*	*MS*	F	p <
$\delta^{15}N$	era (historic or modern)	1	39.45	55.36	0.001
	temperature (warm or cool year)	1	5.69	7.98	0.005
	season (pre or post breeding)	1	6.49	9.11	0.003
	era * temperature	1	6.42	9.00	0.003
	era * season	1	10.25	14.38	0.001
	season * temperature	1	5.83	8.18	0.004
	era * season * temperature	1	4.27	5.99	0.015
	error	510	0.71		
$\delta^{13}C$	era (historic or modern)	1	15.01	20.34	0.001
	temperature (warm or cool year)	1	11.14	15.09	0.001
	season (pre or postbreeding)	1	58.49	79.24	0.001
	era * temperature	1	10.79	14.58	0.001
	era * season	1	15.41	20.88	0.001
	season * temperature	1	0.53	0.72	0.397
	era * season * temperature	1	8.43	11.42	0.001
	error	510	0.74		

*$\delta^{15}N$: $r^2 = 0.19$; $\delta^{13}C$: $r^2 = 0.29$

historic prebreeding diets. Compared with prebreeding diets, postbreeding $\delta^{13}C$ values changed very little between eras (0.005‰). The $\delta^{13}C$ values were affected most strongly by season (as indicated by the largest mean squared error term in Table 1) and secondarily affected by era and temperature. Most important, the magnitude of this seasonal difference in $\delta^{13}C$ values increased in modern compared with historic diets (Fig. 2b), which accounts for the strong era * season interaction (Table 1). Post hoc comparisons indicated that $\delta^{13}C$ in historic diets differed significantly from modern prebreeding, but not from postbreeding, diets (Fig. 2a). Overall, murrelet diets were 0.4‰ greater in $\delta^{13}C$ in the historic than the modern era.

Results from linear, three-source, dual-isotope mixing models show that the proportion of high-trophic-level prey in murrelet diets declined strongly from the historic to the modern era and that the proportion of low-trophic-level prey generally increased (Fig. 3). Compared with historic diets, typical modern prebreeding diets during cool conditions were composed of 42% less high-trophic-level prey, a 26% increase in krill, and a 16% increase in midtrophic-level prey (Table 2). Similarly, during warm years, modern prebreeding diets showed a 23% increase in krill intake compared with historic diets, a 17% decline in consumption of midtrophic-level prey, and a 6% decline in high-trophic-level prey. Declines in trophic level from historic to modern era in prebreeding diets exceeded 1

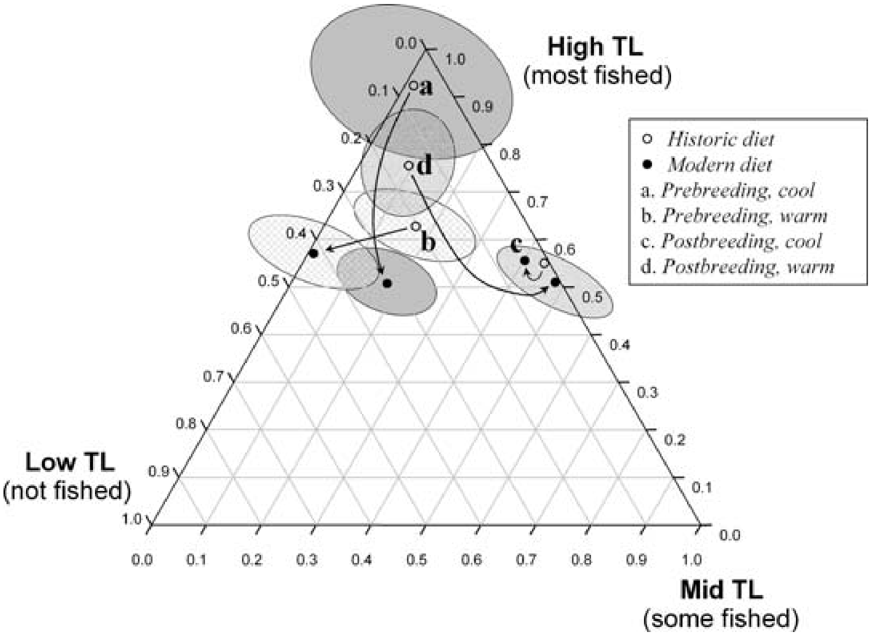

Figure 3. Historic shifts in proportion of high-, mid-, and low-trophic-level (TL) prey in Marbled Murrelet diets. Shifts from the historic to modern era were calculated from dual-isotope mixing models incorporating $\delta^{13}C$ and $\delta^{15}N$ for (A) cool prebreeding conditions, (B) warm prebreeding conditions, (C) cool postbreeding conditions, and (D) warm postbreeding conditions. Ellipses represent approximate standard errors and sample sizes as in Fig. 2. To simplify the illustration an ellipse for cool postbreeding conditions is not shown because diet changed little (Table 2).

Table 2. Proportional change among high-, mid- and low-trophic-level (TL) prey in dietary intake of Marbled Murrelets between historic (1895–1911) and modern (1998–2002) eras predicted from linear three-source, dual-isotope mixing models.

		Proportional change in prey		
Season	*Temperature*	*high TL*	*mid TL*	*low TL*
Prebreeding	cool	−0.42*	0.16	0.26*
	warm	−0.06	−0.17	0.23*
Postbreeding	cool	−0.05	−0.10	0.15
	warm	−0.22*	0.41*	−0.18*

**Proportional change* > *1 SE.*

SE under both cool and warm conditions. Postbreeding diets showed little change in composition between eras during cool years, but during warm years modern diets had sizable declines in the proportion of low (−18%) and high (−22%) trophic-level prey that was offset by a 41% increase in midtrophic-level prey.

Discussion

Our results indicate that large changes in the trophic level and diet of an endangered seabird have occurred over the past century in the Monterey Bay ecosystem (Figs. 2 & 3). The prebreeding diet of Marbled Murrelets declined by nearly one-half of a trophic level over this period, a −1.4‰ and −0.8‰ decline in δ^{15}N and δ^{13}C, respectively. Both era (pre- vs. postfishery decline) and ocean temperate were significantly related to the changes in Marbled Murrelet diets over the past century, but era had a much greater impact and accounted for more of the variation in trophic level (Table 1). Historically, murrelets ate primarily high-trophic-level prey in cool years when energetically superior fishes were likely to have been more abundant (Figs. 2 & 3). Now breeding murrelets appear to eat fewer of these fishes and more smaller, less energetically valuable, midtrophic-level fishes and krill during cool ocean conditions when their reproductive success is greatest (B.H.B. and S.R.B., unpublished data). Postbreeding diets exhibited less change in trophic level, perhaps because krill and year-of-young rockfishes are less available in late summer and early fall (Smith & Adams 1988) and thus may be less important prey items at this time regardless of fishing pressure or oceanographic conditions. Alternatively, murrelets may have altered their postbreeding diet items in a manner that still maintained the same mean δ^{15}N and δ^{13}C.

The magnitude of decline in trophic level observed for murrelets was similar to or exceeded measures of long-term change in trophic level in other marine vertebrates based on shifts in isotopic signatures. Northern Fulmars declined by −1.16‰ in δ^{15}N and by −0.95‰ in δ^{13}C between 1940 and 1993 in the North Atlantic. Although these changes were attributed to a reduction in the availability of whaling offal (Thompson et al. 1995), overfishing could also be a cause. A two-thirds decline in trophic level (−2.45‰ δ^{15}N) in haddock was associated with fishing pressure and climatic variation (Wainright et al. 1993). No change in δ^{15}N of Tufted Puffins (*Fratercula cirrhata*) or Crested Auklets (*Aethia cristatella*) occurred in the Gulf of Alaska as a result of PDO regime shifts, but δ^{13}C declined, suggesting a change in foraging location (Hobson et al. 2004). This analysis, however, was over a 20-year period (1970s and 1980s), so it could test only for relatively short-term change. Values of δ^{13}C declined over the latter half of the century in high-latitude Pacific marine pinnipeds by nearly 2‰ (Hirons et al. 2001; Hobson et al. 2004) and in whales by 2.7‰ (Schell 2000), but evidence for a change in trophic level was equivocal. The δ^{15}N in North Pacific pinnipeds and whales was relatively stable or slightly increasing (Schell 2000; Hirons et al. 2001; Hobson et al. 2004), but δ^{15}N declined by 1.3‰ in whales of the Bering and Chukchi seas (Schell 2001).

In these studies, differences in δ^{13}C (but not δ^{15}N) over time may have been due to recent changes of δ^{13}C in ocean waters (Cullen et al. 2001). Values of δ^{13}C have declined by an average 0.16‰ per decade in ocean waters because of anthropogenic CO_2 inputs from burning of fossil fuels; this is known as the "Suess effect" (Kroopnick 1985; Gruber et al. 1999; Quay et al. 2003). For whales and pinnipeds, however, the magnitude of isotopic change exceeds baseline shifts because of the Suess effect (Hirons et al. 2001; Schell 2001).

There is no evidence that changes in isotopic signatures of murrelet feathers reported here were due to long-term changes in baseline δ^{15}N and δ^{13}C in the CCS. Monterey Bay zooplankton δ^{15}N values have not shown isotopic changes over the past 50 years, spanning both warm and cold PDO cycles (Rau et al. 2003). Likewise, δ^{13}C values of the same zooplankton showed no long-term trend (G. Rau et al., unpublished data), but accuracy of these measurements may have been affected by the preservative used in sample storage (Rau et al. 2003). Although some long-term decline in δ^{13}C in murrelet diets could be due to the Suess effect, it seems an unlikely cause of the long-term changes in isotopic signatures observed in murrelets because it cannot explain why murrelet prebreeding δ^{13}C and δ^{15}N declined over time but postbreeding values remained constant (Fig. 2).

Our samples represent snapshots of murrelet trophic levels before and during pervasive changes to the prey base in the CCS. The process of murrelet trophic level decline may have begun with collapse of the sardine fishery in the 1940s (Leet et al. 2001; Lluch-Belda et al. 2001) and then continued with increased fishing pressure on squid, anchovy, and juvenile rockfish that has occurred since the 1980s (Leet et al. 2001; Ish et al. 2004). Stomach contents from a few individuals captured in Monterey Bay from 1910–1911 and in the 1970s suggest that murrelets switched their diet from sardines to less energetically valuable anchovies following the collapse of the sardine fishery (Carter & Erickson 1992; Burkett 1995). Increased fishery pressure on squid and rockfishes since the 1980s has further reduced desirable high- and some midtrophic-level prey for murrelets during the prebreeding season.

Marbled Murrelets in the Monterey Bay ecosystem now fish farther down the food web and, just as humans have periodically done (Pauly et al. 1998*a*, 1998*b*), have shifted to lower-trophic-level food items (i.e., krill, sandlance, and rockfishes) in response to the reduction of high-trophic-level prey during the past century after fisheries declined in the region (Figs. 2 & 3). Although some impacts of commercial fishing, positive and negative, on seabird demography are well documented (Tasker et al. 2000; Furness 2003; Votier et al. 2004), much less is known of the long-term impacts of fishing on seabird trophic level. Warming sea surface temperatures were related to a change in the diet of Northern Gannets (*Sula bassana*) over a recent 30-year period from mostly migratory to cold-water prey fishes (Montevecchi & Myers 1997), although the effect on trophic level was not measured. Changes in trophic level recorded for murrelets in central California have occurred at the limit of this species' range and at the margin of an oceanic biogeographic region (Point Conception), where birds might be more susceptible to changes in prey fluctuations (Barrett & Krasnov 1996).

The decline in murrelet trophic level was most pronounced in the prebreeding diet, which may be related to the crucial role prebreeding diets play in alcid life history. Like most species in the Alcidae (Gaston & Jones 1998), murrelets lay a single egg weighing about 25% of their prebreeding body mass, which suggests that egg production is energetically costly and breeding may be easily disrupted by lack of adequate prey. A large proportion (50–90%) of murrelets forgo breeding annually in central California and may do so because they cannot find sufficient food resources (Peery et al. 2004). Prior to fisheries declines and deforestation in central California, productivity of murrelets (estimated by the ratio of juveniles to adults in museum collections) was similar to values predicted by comparative life-history analysis from 29 other avian species but was eight times greater than productivity estimates for murrelets obtained from 1995 to 2003 (Peery et al. 2006; M. Z. Peery & S.R.B., unpublished data). The increased proportion of low- and midtrophic level organisms currently in the diet of murrelets suggests that fisheries declines may have fundamentally altered seabird prey availability and the trophodynamics of these marine predators and could have contributed to their listing as an endangered species in conjunction with cutting of coastal old-growth forests.

Finally, our results suggest that long-term diet shifts need not be restricted to top carnivores but may also change trophic relationships of omnivores like seabirds in the middle of food webs (Springer et al. 2003; Williams et al. 2004; Bascompte et al. 2005). The prey items we studied are critical components for the transfer of energy from phytoplankton to marine predators such as seabirds and marine mammals in the CCS (Ainley 1990). Seabird reproductive success in this region is highly correlated with the availability of prey species such as krill, juvenile rockfish, mysids, sardines, anchovies, and squid (Ainley et al. 1995; Sydeman et al. 2001; Miller & Sydeman 2004). Long-term changes in the abundance and availability of high- and midtrophic-level prey may have also affected diets of other seabird species and their population dynamics over the past century. Although high-trophic-level seabird prey in the Humboldt Current and California Current have always fluctuated with climate changes (Ainley et al. 1995; Sydeman et al. 2001; Chavez et al. 2003*a*), large-scale seabird population crashes have primarily occurred after the onset of industrial fishing (Duffy 1983), perhaps because fishing pressure may have reduced the mean prey population size and co-opted the superabundance of food that helped seabirds adjust to changing climates (Furness & Monaghan 1987). Placement of marine protected areas in locations that improve the recruitment and survival of seabird prey or that contain bathymetric habitats that aggregate seabird prey and attract seabirds (Becker & Beissinger 2003; Yen et al. 2004) could be important for restoring marine food webs and conserving seabirds.

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