Ocean climate and prey availability affect the trophic level and reproductive success of the marbled murrelet, an endangered seabird

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ABSTRACT: We investigated relationships between oceanographic processes, prey availability, diet and the reproductive success of the marbled murrelet *Brachyramphus marmoratus* (Alcidae), a federally threatened seabird. We predicted that cooler ocean conditions (which increase primary productivity in this eastern boundary upwelling system) should result in heightened prey availability and hence higher reproductive success for the murrelet. We also expected that murrelet diets should reflect those potential prey species that are most abundant during any given season or year. Oceanographic conditions were considered at 2 spatial scales: synoptic (Northern Oscillation Index, NOI; Pacific Decadal Oscillation Index, PDO; the North Pacific Index, NPI), and local (upwelling index, UI; sea surface temperature, SST; strength of the spring turnover). To infer seasonal and annual variation in murrelet diets in central California, we used stable isotope analyses of $\delta^{15}N$ and $\delta^{13}C$ in murrelet feathers and prey tissues during the pre- and postbreeding seasons of 1998 to 2002. Isotopic signatures of 10 species of potential prey clustered into 3 distinct groups (low, mid and high trophic level seabird prey). During 1999 to 2001, when more krill (low trophic level prey) were available, murrelet $\delta^{15}N$ and trophic level were lower prior to breeding than after breeding, whereas pre- and postbreeding diets were similar during 1998 and 2002 when fewer krill were available. $\delta^{13}C$ was always lower in prebreeding than postbreeding diets, which tracked availability of ^{13}C enriched juvenile rockfish and market squid. Diet did not differ by sex for either isotope. Murrelet productivity (juvenile:adult ratios) was positively correlated with both rockfish and krill abundance. PDO, NOI, UI, spring turnover strength and NPI indices were unrelated to murrelet productivity and to prey abundances. Murrelet productivity was also positively related to the proportion of mid trophic level prey in postbreeding diets, and thus negatively related to the proportion of low and high trophic level prey consumed. Furthermore, productivity was markedly higher following the apparent 1998 to 1999 PDO regime shift to cooler conditions. These data suggest that cooler local temperatures support increased availability of krill and juvenile rockfish to murrelets, and that this improves murrelet reproductive success.

KEY WORDS: Stable isotope · Marbled murrelet · Seabird · Diet shift · *Brachyramphus marmoratus*

INTRODUCTION

Reproductive success in birds is mediated by a variety of factors including food availability, predation, competition, nest site availability, and disease. Of these forces, food availability is often most sensitive to seasonal, annual and decadal variation in climate (Sæther

2000). Thus, climatic variation can be a dominant force structuring avian populations and communities (Sillett et al. 2000). Many species initiate their reproductive activities to coincide with periods of peak prey availability and climatic variation can induce mismatches between the timing of breeding and prey availability, thereby reducing reproductive success (Thomas et al.

2001). Birds that take prey over large spatial scales, like seabirds, act as environmental samplers, providing information on food web composition, location of prey, and relative abundance of prey among years in relation to changing climatic (oceanographic) conditions (Sydeman et al. 2001).

In marine ecosystems, prey availability for seabirds is affected by oceanographic conditions at both basin-wide and local spatial scales (Parrish & Zador 2003), with local conditions generally being influenced by large-scale processes. In the NE Pacific, and the California Current System (CCS) in particular, basin-scale conditions are dominated by 2 to 7 yr recurrences of warm water El Niño-Southern Oscillation (ENSO) and cool water La Niña events. Basin-scale variation, as measured by Southern Oscillation Index (SOI), Northern Oscillation Index (NOI) and North Pacific Index (NPI), affects both predator and prey species in the CCS. For example, both rockfishes and seabirds exhibit above average reproductive success during cool La Niña years (Ainley et al. 1995, Brodeur et al. 2003). Local-scale conditions, such as sea surface temperature (SST), strength of the spring turnover to cool water conditions, currents, eddies, fronts, vertical mixing and coastal upwelling, occur within the context of these basin-wide patterns. Local-scale conditions typically create regions of increased prey density through physical aggregation or local nutrient enhancement where seabirds can efficiently find adequate prey (Bakun 1996, Becker & Beissinger 2003). For example, warmer ENSO years often exhibit decreased upwelling and/or upwelling of nutrient poor equatorial waters (Castro et al. 2001), while non-ENSO (cool) years exhibit an increase in upwelling and primary productivity (Chavez et al. 2002). Indices of basin-wide and local-scale conditions typically vary annually with moderate to little interannual autocorrelation.

Larger-scale and longer-term oceanographic variation in the NE Pacific occurs in cycles known as the Pacific Decadal Oscillation (i.e. 'regime shifts'). Unlike local and basin indices, PDO is a highly autocorrelated index, showing 20 to 30 yr periods of persistent positive or negative temperature anomalies. 'Cool' states of the PDO favor seabirds and other marine predators in the CCS (Sydeman et al. 2001). Because of its persistent state, PDO shifts may result in a numerical response (i.e. predator populations increase) due to the bottom–up effects of increasing primary and secondary productivity through nutrient enhancement (Hare & Mantua 2000). Long-term PDO cycles create long-term shifts in community composition of plankton, prey fishes, predatory fishes, seabirds and marine mammals (Hare & Mantua 2000). For example, sardine and anchovy populations alternate in dominance with PDO regimes (Chavez et al. 2003). Numerical responses to

PDO appear to occur more rapidly at lower trophic levels, presumably because these organisms have shorter generation times and can respond more rapidly to changes in environmental conditions. Because non-ENSO and cool PDO events increase primary productivity in the CCS, they are also correlated with the abundance of microzooplankton (Hare & Mantua 2000), which are eaten by small fishes and meso- and macrozooplankton. Thus, PDO cycling also affects nutrient delivery to the photic zone and may be viewed as long-term ENSO or non-ENSO conditions.

We investigated the effects of oceanographic variability on prey availability, diet, and reproductive indicators of a federally threatened (USA designation) and state endangered (California) seabird, the marbled murrelet: *Brachyramphus marmoratus* (Alcidae). The murrelet occurs in the NE Pacific coastal zone from the Bering Sea to central California in both upwelling (California Current) and downwelling (Alaska Current) systems. In central California, the murrelet forages in nearshore waters generally less than 25 m deep and within 2 km of shore (Becker & Beissinger 2003). Murrelet populations have been subjected to severe loss of nesting habitat and subsequent population declines over the past century. In addition, murrelet reproductive success is limited by prey availability in some years (Peery et al. 2004b). Thus, both reproductive success and diet should vary with ocean conditions and subsequent prey availability, as with many other seabirds in this region (Sydeman et al. 1997, Miller & Sydeman 2004).

Previous studies indicate that murrelets are somewhat euryphagous, taking a wide variety of prey items potentially impacted by seasonal, interannual and interdecadal climatic variation, including mysid shrimp (*Mysis* spp.), krill *Thysanoessa spinifera and Euphausia pacifica*, northern anchovy *Engraulis mordax*, sand lance *Ammodytes hexapterus*, market squid *Loligo opalescens*, juvenile rockfishes *Sebastes* spp., Pacific sardines *Sardinops sagax*, Pacific herring *Clupea harengus* and smelt Osmeridae (Sealy 1975, Carter 1984, Burkett 1995). Stable isotope analysis of nitrogen ($\delta^{15}N$) conducted on marbled murrelet pectoral muscle collected in British Columbia, Canada, suggested that murrelets have an intermediate trophic level among alcids, primarily eating fish, and to a lesser extent, zooplankton (Hobson 1990). However, numerous observations of murrelets holding fish and squid on the water (Carter 1984) and its long, narrow bill imply that murrelets are primarily piscivores and that lower trophic level invertebrates, such as krill, may be only a minor component of their diet. Nestlings are primarily fed fishes and occasionally squid, but are not known to consume krill (Nelson & Peck 1995).

Here we investigate how marbled murrelet diet and productivity reflect basin and local-scale oceanographic processes. We construct a local food web using known and potential murrelet prey species, examine annual fluctuation in food availability, and determine how the diet and trophic position of murrelets varies seasonally and annually using stable isotope analyses. Finally, we relate indices of basin- and local-scale conditions (basin-scale SOI, NOI, PDO and NPI; and local-scale upwelling, SSTs and spring turnover) to murrelet prey availability, diet composition, and productivity. While this study is primarily an exploratory analysis of these environment–diet–reproduction relationships, we do predict that cooler ocean conditions (which increase primary productivity in this eastern boundary upwelling system) should result in heightened prey availability and hence higher reproductive success for the murrelet.

MATERIALS AND METHODS

From 1998 to 2002, we studied the diet and reproductive parameters of a semi-isolated population of approximately 487 to 637 marbled murrelets (Peery et al. 2004a). This population nests in the Santa Cruz Mountains, about 30 km north of Monterey Bay in central California, USA. Population size appears to have been stable since 1996 but may be sustained by immigration from northern populations (Peery et al. 2006).

We used stable isotope analysis of feathers to infer variation in the diet and trophic level of murrelets. We collected whole breast feathers and the tip of a 5th secondary feather from 215 marbled murrelets (n = 370 feather samples) caught in Año Nuevo Bay (37.1° N, 122.3° W) from 1998 to 2002. Breast feathers are regrown during both the prebreeding and postbreeding molts, while secondaries are only replaced during the pre-basic molt (Carter & Stein 1995). Thus, brown-tipped breast feathers represent the prebreeding diet (March to April), and both secondaries and all-white breast feathers represent the postbreeding diet (August to September). For example, secondaries collected in the spring of 1998 represent diet during the 1997 postbreeding molt. Most birds were sexed via microsatellite DNA extracted from blood samples (Peery et al. 2004b).

Prey samples. We obtained potential murrelet prey items for isotopic analysis from 2 sources: shipboard undulating midwater trawls in Año Nuevo Bay, California, and Monterey Bay, California during 2001 and 2002 (courtesy of Moss Landing Marine Laboratories) and from rhinoceros auklets *Cerorhinca monocerata* bringing prey to chicks at a colony by Año Nuevo Bay during 1996 to 2000 (courtesy of PRBO Conservation

Science). Potential prey obtained included night smelt *Spirinchus starskii*, northern anchovy, sand lance, market squid, juvenile shortbelly, widow and blue rockfish *Sebastes* spp., Pacific sardines, krill *Euphausia pacifica* and *Thysanoessa spinifera*, white croaker *Genyonemus lineatus*, mysid shrimp, and Pacific herring. Obtaining stomach samples directly from murrelets would require sacrificing birds or discharging their stomach contents, neither of which were feasible. Collecting samples at nests would only produce prey carried inland and fed to nestlings, and nests are generally inaccessible.

Isotope values for prey species were pooled across years for statistical analyses because we did not have adequate samples of each prey species for all years. However, we did have multiple years of data for northern anchovy (1997 to 2000) and market squid (1997, 2000) and could test for interannual variation for these species.

Laboratory analyses. We subsampled lateral muscle tissue from all fishes, mantles from squid, and whole bodies of the krill and mysids for stable isotope analysis. Prey samples were freeze-dried, subjected to lipid extraction with a methanol:chloroform:water (50:25:20 v:v) solution for at least 24 h, rinsed with distilled water, and redried (Thompson & Furness 1995). To remove carbonates, krill were also soaked in 1 N HCl until bubbling stopped (Thompson & Furness 1995).

Feathers were cleaned with a methanol:chloroform: water rinse, rinsed with distilled water, and air-dried. Approximately 1.2 mg of dried feather was loaded into tin capsules and analyzed for $\delta^{15}N$ and $\delta^{13}C$ with a Europa 20/20 continuous-flow isotope-ratio mass spectrometer at the University of California Berkeley Center for Stable Isotope Biogeochemistry. Peach leaves (45% C, 10.6% N: National Institute of Standards and Technology, NIST, No. 1577b) and bovine liver (45% C, 2.96% N, NIST No. 1547) were used as standards for C and N, respectively. Standards were analyzed between every 8 feather samples and a least-squares nonlinear model was used to correct any drift during the analysis. Analytical precision (SD) of analyses was always less than ± 0.25‰ for $\delta^{15}N$ and ± 0.10‰ for $\delta^{13}C$. Isotopic ratios are expressed in the del notation (parts per thousand, ‰) relative to atmospheric nitrogen (for $\delta^{15}N$) or Pee Dee belemnite (for $\delta^{13}C$).

Inspection of histograms and probability plots indicated that isotope data were normally distributed, so parametric statistics were used. To facilitate meaningful interpretation of isotope data (Phillips et al. 2005), we used *k*-means clustering to group the potential prey items by reducing within group sums of squares (SPSS 1998). This resulted in 3 groups with statistically similar $\delta^{13}C$ and $\delta^{15}N$ values labeled as low, mid, and high trophic level seabird prey groups. Isotope values

for all prey species were pooled across years for comparison with murrelet diets.

The krill, *Euphausia pacifica* and *Thysanoessa spinifera*, have identical values for $\delta^{13}C$ and $\delta^{15}N$ (Sydeman et al. 1997), so we assumed that any results indicating feeding on *E. pacifica* could equally be *T. spinifera*. This is especially important since the former species is generally oceanic (occurring beyond the shelf-break) and the latter is associated with coastal (over the shelf) upwelling and surface swarming (Smith & Adams 1988, Ainley et al. 1996a, Adams et al. 2004). Murrelets are confined to the nearshore coastal shelf, and the appearance of *T. spinifera* in the spring is related to the onset of breeding and reproductive success in Cassin's auklets (Ainley et al. 1996a). We, therefore, assumed that *T. spinifera* is a more likely euphausiid prey item for murrelets than *E. pacifica*.

To estimate the proportion of prey items from each trophic level grouping that murrelets fed upon, we used a diet–feather fractionation value of 3.7‰ for $\delta^{15}N$ and 1.0‰ for $\delta^{13}C$. This was based on the diet-feather fractionation in common murres (Becker & Beissinger unpubl. data) and is similar to values published for other seabirds (Thompson & Furness 1995, Vanderklift & Ponsard 2003). We used the IsoError dual-isotope, 3-source mixing model (Phillips & Gregg 2001) to estimate the proportion of low, mid and high trophic level prey (see results for prey species comprising each group) consumed by murrelets during each pre- and postbreeding molt from 1998 to 2002. Because all prey items and bird feathers had similar C:N ratios (~15:1) we did not use concentration dependent models.

Prey abundance, energetics and oceanography. Results from the National Marine Fisheries Service annual spring rockfish stock assessment cruises were collected for each year from 1995 to 2003 (Brodeur et al. 2003). There were generally 75 to 100 systematically placed trawls done annually during the onset of the murrelet nesting season in May to June at a range of water column depths (5 to 100 m) between Monterey Bay (36°N) and Point Reyes, CA (38°N) (Data courtesy S. Ralston, NMFS, Santa Cruz). Trawls were as close as 2 km to shore and ranged to the continental slope (up to 30 km from shore). A literature search provided energetic content for potential prey items. We also obtained mean monthly Bakun upwelling indices (Bakun 1996) at 36°N, 122°W, monthly NOI, SOI 3.4, NPI, PDO, and SSTs at SE Farallon Island (www.pfeg.noaa. gov) to search for correlations between oceanographic variation, prey abundance, marbled murrelet diet, and indicators of reproduction. ENSO conditions are measured via the Southern Oscillation Index (SOI), which is the normalized difference in sea level pressure (SLP) between Tahiti and Darwin, Australia. Similarly, the

Northern Oscillation Index (NOI) is a function of the difference in SLP between the NE Pacific and Darwin, Australia. Thus, SOI is a measure of equatorial forces traveling poleward up the west coast of North America, and NOI is a measure of how strongly this effect manifests itself locally in the NE Pacific (Schwing et al. 2002). Because basin-scale oceanographic indicators (SOI and NOI) were highly correlated (r = 0.65, p < 0.05) throughout the study period, we only used NOI in subsequent analyses, as it provides a more locally derived index of basin-scale conditions. The North Pacific Index (NPI) is another large-scale index that summarizes sea level pressure over the North Pacific. We used the annual and mean values of the first 4 months of each year for these indices, as this period is most important to the onset of reproduction in seabirds due to effects of upwelling on prey abundance (Ainley et al. 1996a,b). Strength of the spring turnover was calculated as the difference in mean daily SSTs between the January to March and April to May periods.

Statistical analyses. We tested for correlations between annual indicators of murrelet productivity (juvenile:adult ratios) (Peery et al. 2004b, in press) with diet and oceanographic variables (SOI, NOI, NPI, PDO, SST, turnover strength and upwelling). Estimates of annual reproductive success were measured as hatch-year to after-hatch-year ratios (HY:AHY) and were obtained from at-sea surveys during the breeding season (Peery et al. in press). Tests of the assumptions for using juvenile ratios indicated that they are appropriate measures for estimating annual variability in productivity and relating productivity to environmental conditions (Peery et al. in press). Statistical tests were done using Systat 8.0 (SPSS 1998) and we considered p < 0.05 to be statistically significant. However, because these tests use annual estimates with only 5 to 9 yr of samples, in a few instances we discuss results that approach significance (0.05 < p < 0.10) and allow the reader to judge their importance. Results are presented as means ± 1 standard error or deviation, as indicated.

RESULTS

Prey species composition, abundance and energetics

Potential prey isotopic signatures clustered strongly by species and trophic level (Fig. 1A, Table 1). *k*-means clustering grouped 3 distinct trophic groups on the basis of $\delta^{15}N$ and $\delta^{13}C$ values of potential prey (overall clustering model $\chi^2_{20} = 146.2$, p < 0.001; see Table 1 for classification success). Such *a priori* grouping of dietary sources is useful in dual-isotope models
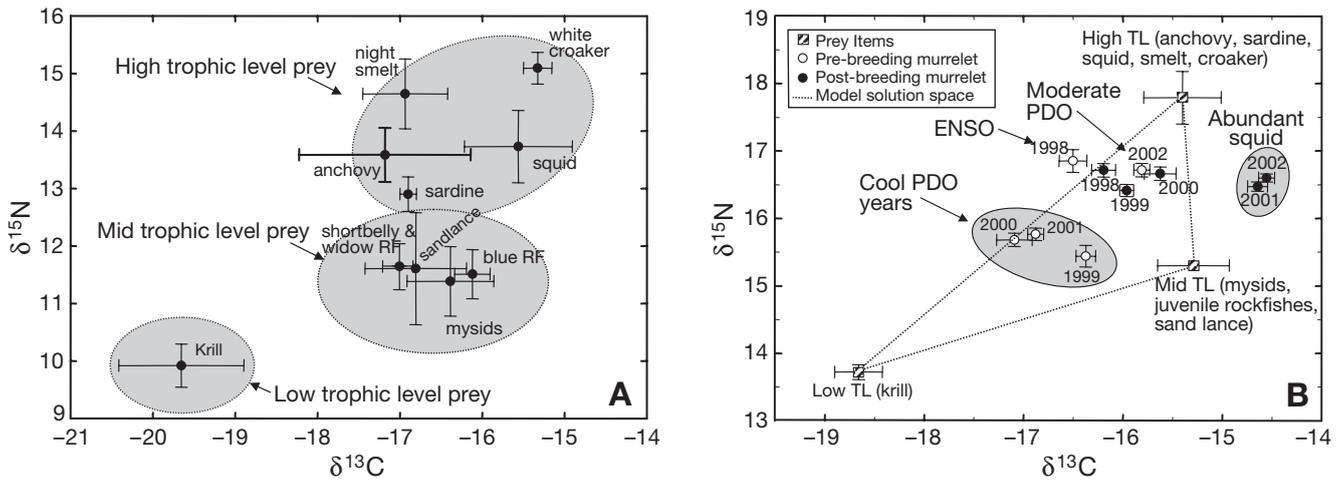
Fig. 1. (A) δ^{15}N and δ^{13}C values for potential prey items (of murrelet *Brachyramphus marmoratus*) collected in central California; low, mid and high trophic levels (TL) based on *k*-means clustering assignments (Table 1). (B) Prey groupings and pre- and post-breeding marbled murrelet diets from 1998 to 2002. Prey items have been corrected for consumer-prey fractionation (δ^{15}N = 3.7‰, δ^{13}C = 1.0‰); area within the dotted line connecting the means of high, mid and low trophic level prey items represents the 3-source isotope mixing model solution space. RF: rockfish. Error bars are SEs

Table 1. *Brachyramphus marmoratus*. Stable isotope ratios for marbled murrelets and their potential prey items (TL: trophic level). Superscripts indicate statistically similar values within columns (Bonferroni inequality, all p > 0.35) but only indicate groupings of either predators or prey. *k* represents classification success: all 3 rockfish species were tested as a group, we thus report 60% classification success for each species

Species	n	δ^{15}N (‰)	δ^{13}C (‰)	*k* (%)
Krill *Euphausia pacifica*	**10**	**9.9 ± 0.4[a]**	**−19.7 ± 0.8[a]**	90
Lower TL fishes and crustacean				
Mysid shrimp	9	11.4 ± 0.6[b]	−16.4 ± 0.5[b]	100
Blue rockfish	3	11.5 ± 0.4[b]	−16.1 ± 0.2[b]	60
Sand lance	7	11.6 ± 1.0[b]	−16.8 ± 0.6[b]	71
Shortbelly rockfish	10	11.6 ± 0.6[b]	−17.1 ± 0.3[ab]	60
Widow rockfish	2	11.7 ± 0.4[b]	−17.0 ± 0.1[b]	60
Group mean	**5**	**11.5 ± 0.1**	**−16.3 ± 0.8**	
Higher TL fishes and cephalopod				
Pacific sardine[1]	3	12.9 ± 0.1[c]	−17.0 ± 0.3[a]	100
Northern anchovy	27	13.6 ± 0.5[d]	−17.2 ± 1.0[a]	74
Market squid	21	13.7 ± 0.6[d]	−15.6 ± 0.7[b]	100
Night smelt	11	14.6 ± 0.6[e]	−16.9 ± 0.5[c]	100
White croaker	10	15.1 ± 0.3[e]	−15.3 ± 0.2[b]	100
Group mean	**5**	**14.0 ± 0.9**	**−16.4 ± 0.9**	
Marbled murrelets				
1997 post-breed	5	17.2 ± 0.3[a]	−15.8 ± 0.8[a]	–
1998 pre-breed	13	16.9 ± 0.6[a]	−16.5 ± 0.5[ad]	–
post-breed	25	16.7 ± 0.5[a]	−16.2 ± 0.6[abd]	–
1999 pre-breed	35	15.4 ± 1.0[b]	−16.4 ± 0.6[ad]	–
post-breed	62	16.4 ± 0.7[a]	−16.0 ± 0.6[abd]	–
2000 pre-breed	42	15.7 ± 0.6[b]	−17.1 ± 1.2[d]	–
post-breed	30	16.7 ± 0.5[a]	−15.6 ± 0.9[ab]	–
2001 pre-breed	36	15.8 ± 0.6[b]	−16.9 ± 0.8[d]	–
post-breed	40	16.5 ± 0.5[a]	−14.6 ± 0.6[c]	–
2002 pre-breed	20	16.7 ± 0.7[a]	−15.8 ± 0.5[abd]	–
post-breed	20	16.6 ± 0.3[a]	−14.6 ± 0.3[c]	–

[1]From Sydeman et al. (1997)

with greater than 3 potential sources to generate interpretable results (Phillips et al. 2005). These 3 groupings (Fig. 1A) were (1) low trophic level prey comprised of 2 species of krill; (2) mid-trophic level prey comprised of mysid shrimp, sand lance, and young-of-the-year rockfishes (comprising blue, widow and shortbelly rockfishes); and (3) high trophic level prey comprising sardine, anchovy, night smelt, white croaker, and market squid. The mid trophic level group exhibited little interspecific variation in δ^{15}N, and averaged 2.6‰ less than high trophic level prey. δ^{13}C means, on the other hand, did not differ between the mid and high groups. Variation in isotopic signature was greatest among prey in the high trophic level group. Nevertheless, assignments to trophic levels were robust for all species (Table 1).

Pooling of species across years also appeared to be robust. Although, northern anchovy δ^{15}N values did vary by year ($F_{3, 23}$ = 7.8, p < 0.001), this effect was entirely due to 1998 (ENSO) being 0.6‰ lower than 1997, 1999, and 2000 (Bonferroni inequality, p < 0.001). Market squid showed no δ^{15}N difference between 1997 and 2000 (Student's *t* = −1.5, df = 18, p > 0.14). There was also no correlation between anchovy length

and $\delta^{15}N$ (r = 0.133, df = 13, p > 0.99) or $\delta^{13}C$ (r = 0.524, df = 13, p > 0.19). Further evidence of limited interannual variation in prey species comes from comparison of our results with Sydeman et al. (1997) who also sampled prey items from the same region during 1994 and 1995. Mean differences among our samples and those reported in Sydeman et al. (1997), for $\delta^{15}N$ and $\delta^{13}C$, respectively, were anchovy 0.3 and 0.4‰; krill 1.3 and 0.5‰, and squid 1.4 and 1.5‰. Furthermore, more recent isotope values of sardines indicate that our values are in agreement with those currently found in California current (R. Vetter & D. Field pers. comm.).

Abundance of potential prey species differed greatly by trophic level (Fig. 2) and appeared to be affected by oceanographic variation (Table 2). Krill, the most

Fig. 2. Log-transformed mean counts from trawls for potential seabird prey items off the coast of central California during late May and early June, 1995 to 2003 (Raw data courtesy of the National Marine Fisheries Service, Santa Cruz, California)

abundant prey, were least abundant during the warm PDO years of 1998 and 2002. Sardine and anchovy abundance was less variable throughout the study period, but anchovies peaked during the 1999 La Niña and declined thereafter. The limited number of years of study precluded robust correlations of prey abundance with oceanographic conditions (Table 2). Nevertheless, basin-scale NOI approached significance with rockfish abundance (p < 0.1), but regional PDO and local UI indices were not associated with prey abundance. Similar patterns of prey abundance by year were reported by Brodeur et al. (2003) for the same region.

Energetic value varied greatly among potential prey species of murrelets, but in general, higher trophic level species had greater per capita caloric value (Table 3). Pacific sardines contained the greatest caloric value, and krill were the least valuable. Juvenile rockfish and market squid had about one-third to one-fourth the energetic value of a sardine prey item, while kJ per food item was 60% less for anchovies. To gain the same energetic value as eating an anchovy, a murrelet would need to consume ~45 low trophic level prey items and ~2–12 mid-trophic level items (Table 3). Similarly, for the even more energy rich sardine, this ratio increases to ~74–80 krill and ~3–20 mid-trophic level prey items. Encounter rates and handling times would have to differ greatly among species to overcome trophic level differences in profitability caused by energetic values.

Annual and seasonal changes in the diet and productivity of marbled murrelets

Murrelet diet composition generally fell within the boundaries imposed by potential diet sources (Fig. 1B)

Table 2. Pearson correlations between mean January to April oceanographic variables, spring prey abundance, and marbled murrelet *Brachyramphus marmoratus* productivity for the years 1995 to 2003 (n = 9). NOI = Northern Oscillation Index, PDO = Pacific Decadal Oscillation, NPI = North Pacific Index, UI = Upwelling Index, SST_4 = sea surface temperature during January to April, SST_{AMJ} = sea surface temperature during April to June, Spring turnover = strength of the spring turnover. * p < 0.05

	NOI_4	PDO_4	NPI_4	UI_4	SST_4	SST_{AMJ}	Spring turnover	An-chovy	Sar-dine	Squid	Rock-fish	Krill
PDO_4	−0.62	−										
NPI_4	0.74*	−0.76*	−									
UI_4	0.61	−0.15	0.32	−								
SST_4	−0.94*	0.77*	−0.73*	−0.75*	−							
SST_{AMJ}	−0.86*	0.68*	−0.77*	−0.49	0.89*	−						
Spring turnover	−0.60	0.60	−0.31	−0.62	0.65	0.26	−					
Anchovy	−0.33	0.08	−0.22	0.20	0.20	0.10	0.38	−				
Sardine	−0.40	0.24	−0.56	0.35	0.29	0.48	0.02	0.61	−			
Squid	0.24	−0.39	0.45	0.24	−0.33	−0.23	−0.23	0.13	−0.17	−		
Rockfish	0.61	−0.47	0.66	0.07	−0.53	−0.45	−0.46	−0.61	−0.67*	0.64	−	
Krill	0.48	−0.32	0.15	0.21	−0.56	−0.57	−0.29	−0.26	−0.41	0.31	0.47	−
Murrelet productivity	0.60	−0.34	0.49	0.24	−0.61	−0.56	−0.37	−0.63	−0.59	0.46	0.79*	0.73*

Table 3. Energetic values for average-sized potential prey items of murrelet *Brachyramphus marmoratus*. The anchovy equivalent column represents the number of average-sized prey items that would equal the energetic content of an average-sized anchovy. Mean prey sizes from Carter (1984) and Sealy (1975), length–mass regression equations from Spear (1993) and D. G. Ainley (unpubl.)

Trophic level	Species	Location	kJ g^{-1} (dry)	kJ g^{-1} (wet)	Length (mm)	Wet mass (g)	kJ/item	Anchovy equivalent
Low	*Euphausia superba*[a]	Scotland	20.8	4.7	16–20	0.11[e]	0.52	48.2
	Thysanoessa spp.[b]	North Atlantic	23.8	–	24	0.12[e]	0.56	44.8
Mid	Shortbelly rockfish	Farallones, CA	21.8	4.9	60	2.51	12.30	2.0
	Sand lance[c]	Alaska	22.0	–	60	–	2.00	12.5
High	Market squid	Farallones, CA	20.9	4.1	40	2.44	10.02	2.5
	Night smelt	Farallones, CA	19.8	4.3	60	1.84	7.91	3.2
	Northern anchovy	Farallones, CA	26.7	9.6	60	2.61	25.07	1.0
	Pacific sardine[d]	California	–	15.8	60	–	41.36	0.6

[a]Clarke & Prince (1980)
[b]Martensson et al. (1994)
[c]Piatt (1990)
[d]Sardine value = 65% more kJ g^{-1} (wet) than anchovy (Sidwell 1981)
[e]Krill wet masses for adult *Euphausia pacifica* and *Thysanoessa spinifera* from California. Source: Adams et al. (2004)

except for 3 of the 10 season–year periods, which fell slightly outside the potential dietary solution area. This is reasonable to expect because extensive feeding on a single species that was particularly enriched in ^{13}C (e.g. squid) within the mid or high trophic level groups could skew predator isotope values away from the mean value of each of the 3 prey groups we used for the calculations. Although it is also possible that murrelets fed on prey not represented in our model, most models found tenable solutions which suggests this was not the case. $\delta^{13}C$ in postbreeding murrelet diets was highest during 2001 and 2002 (Fig. 1B), which was concurrent with high squid abundance during the postbreeding period in these years (Fig. 2). For the 3 periods that fell outside the diet source boundaries (spring 1998, fall 2001, and fall 2002), we normalized the remaining 2 positive diet proportions to 1.

Isotopic composition varied greatly between seasons and among years but showed 2 important patterns. During cool water years, murrelet $\delta^{15}N$ was typically at a lower trophic level during the prebreeding period and at a higher trophic level during the postbreeding period (Fig. 3A). The warmer PDO years of 1998 and 2002 were exceptions to this pattern, with similar pre- and postbreeding diets. $\delta^{13}C$ always shifted higher during the postbreeding season, although this was more pronounced from 2000 to 2002 (Fig. 3B). An ANOVA model including the subset of feather samples from birds that were sexed (n = 134) during 1998 to 2001 found that season and the Season × Year interaction had significant effects on $\delta^{15}N$, while Year was marginally significant (Table 4). Carbon isotope ratios also varied by season, year, and the interaction (Table 4). Diet did not differ by sex for either isotope. Results
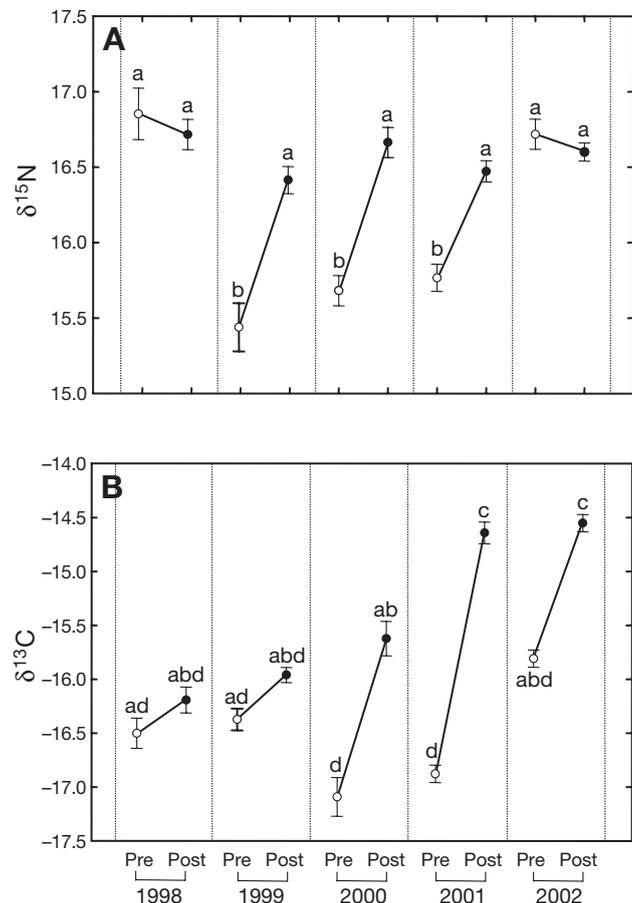
Fig. 3. *Brachyramphus marmoratus*. Marbled murrelet feather isotope values for (A) $\delta^{15}N$ and (B) $\delta^{13}C$ during the pre- (spring) and post- (fall) breeding seasons from 1998 to 2002. Different letters in each panel indicate statistically different values (see Table 1)

Table 4. *Brachyramphus marmoratus*. ANOVA testing effects of sex, season, year, and interactions on murrelet isotope ratios. **Bold**: $p < 0.05$

Factor	SS	df	MS	F	p<
$\delta^{15}N$ ($r^2 = 0.34$)					
Sex	0.50	1	0.51	1.36	0.244
Season	**3.20**	**1**	**3.20**	**8.65**	**0.004**
Year	3.00	4	0.74	2.01	0.094
Season × Year	**4.43**	**4**	**1.11**	**3.00**	**0.020**
Season × Sex	0.04	1	0.04	0.11	0.736
Year × Sex	3.00	4	0.75	2.02	0.092
Season × Sex × Year	2.32	4	0.58	1.57	0.185
Error	82.20	222	0.37		
$\delta^{13}C$ ($r^2 = 0.57$)					
Sex	0.64	1	0.64	1.05	0.306
Season	**28.14**	**1**	**28.14**	**46.64**	**0.001**
Year	**23.10**	**4**	**5.77**	**9.57**	**0.001**
Season ×Year	**31.37**	**4**	**7.84**	**13.00**	**0.001**
Season ×Sex	0.53	1	0.53	0.88	0.349
Year ×Sex	2.92	4	0.73	1.21	0.308
Season ×Sex ×Year	1.35	4	0.34	0.56	0.692
Error	133.92	222	0.60		

from the dual-isotope, 3-source mixing model supported these trends and indicated that the relative consumption of trophic levels by murrelets varied greatly both annually and seasonally. High trophic level prey was always consumed, but in some years either low or mid trophic level prey disappeared completely from the diet (Fig. 4).

Diet and productivity of murrelets were related. In years when krill were more abundant, prebreeding $\delta^{15}N$ tended to be lower (Fig. 5A). Similarly, when the ^{13}C enriched juvenile rockfish and squid were
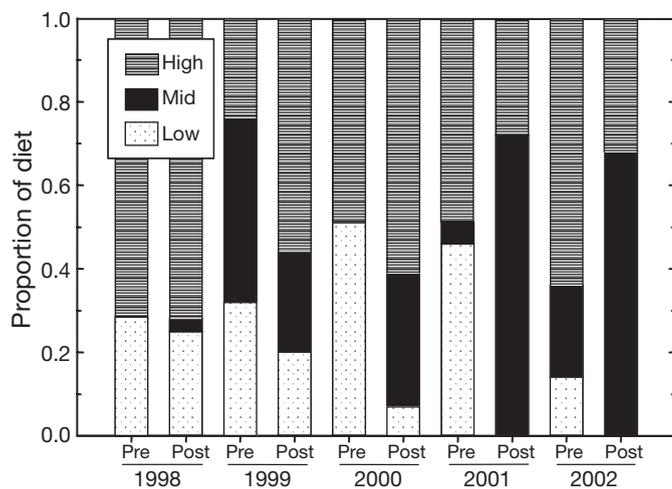
Fig. 4. *Brachyramphus marmoratus*. Results of dual-isotope, 3-source mixing model specifying average murrelet dietary inputs from low, mid and high trophic level prey during pre- and postbreeding seasons from 1998 to 2002. SEs were all between 0.03 and 0.09

more abundant, murrelet postbreeding $\delta^{13}C$ increased (Fig. 5B,C). Murrelet productivity tended to be positively related with both basin-scale NOI and cooler local SST, and was higher during cool water years, although this relationship was not significant ($p < 0.09$; Table 2, Fig. 6A). Furthermore, productivity was positively correlated with both krill and rockfish abundance (Fig. 6B,C). Finally, murrelet productivity was positively related to the proportion of mid-trophic level prey in postbreeding diets, and was negatively related to the proportion of both low and high trophic level prey consumed (Fig. 6D). The only prey items related to ocean conditions, were juvenile rockfishes, which were marginally associated with both cool NOI and NPI conditions ($p < 0.10$; Table 2).

DISCUSSION

Diet and trophic level

Isotopic signatures suggest marbled murrelets in central California consume low and mid-trophic level prey items (i.e. krill, juvenile rockfish, sand lance, and mysids), as well as high trophic prey level items (i.e. anchovy, sardine, squid, croaker, and smelt). While these results compare well with Hobson's (1990) placement of murrelets as a mid-trophic level predator, we also found significant seasonal and annual variation in diet. Furthermore, similar to common murres in the California Current (Ainley et al. 1995, 1996b, Miller & Sydeman 2004), murrelet diets tracked prey availability mediated by climatic forcing. During cool water years when krill were more abundant (1999–2001), murrelets fed at a lower trophic level prior to breeding compared to after the breeding season (Figs. 1B & 3). However, pre- and postbreeding diets were similar during the warm water year of 1998 and the cool year of 2002. In 1998, krill were less abundant, as were squid and juvenile rockfish, while higher trophic level sardines and anchovies were relatively more common. Similarly, in 2002, krill numbers were also depressed and murrelet spring trophic level failed to show the low trophic level diet signature. Then, in the fall of both 2001 and 2002, when squid were at their greatest abundance during the study period, murrelet diets reflected this with an increase in $\delta^{13}C$ that would be expected if they had fed greatly on squid. Thus, we conclude that murrelets are robust environmental samplers whose diet reflects changes in prey availability in the California Current under a wide variety of ocean conditions and seasons.

Isotope values reported here appear to be robust measures of murrelet diet and were not due to oceanographic effects on baseline isotope values or physio-
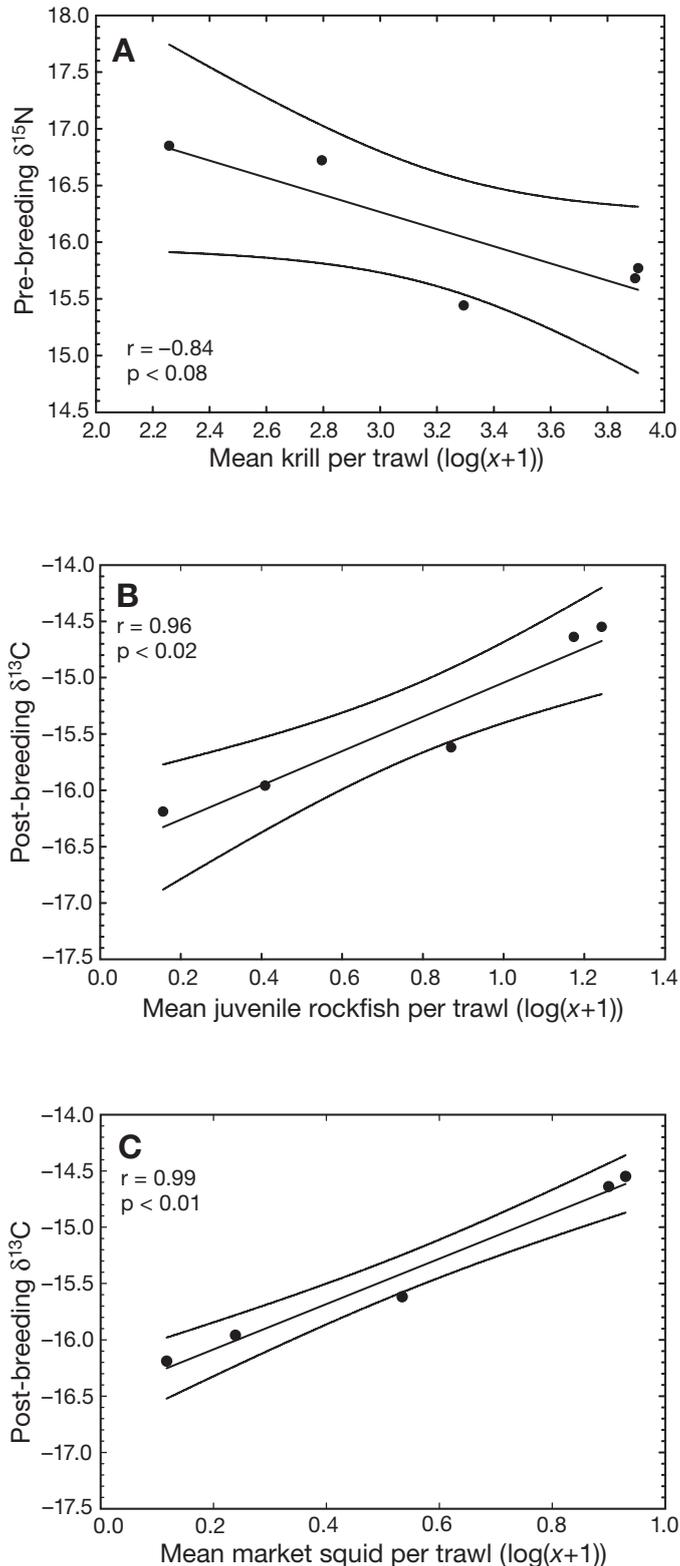
Fig. 5. *Brachyramphus marmoratus*. Relationship between (A) krill abundance and murrelet prebreeding $\delta^{15}N$, (B) juvenile rockfish abundance and postbreeding $\delta^{13}C$, and (C) squid abundance and postbreeding $\delta^{13}C$. Regression lines and 95% confidence intervals are shown

logical variation in the birds (Rau et al. 2003, Vanderklift & Ponsard 2003). $\delta^{15}N$ in zooplankton changed little from 1951 to 2001 in the Monterey Bay region (Rau et al. 2003), although there were small, temporary increases (~1‰) during the strong ENSO years of 1958, 1983, and 1998. Rau et al. (2003) found a similar (~1‰ $\delta^{15}N$) PDO effect on 2 species of chaetognath (arrow worm) zooplankton during the 1979 to 1998 warm PDO regime, compared to the preceding and following cool regimes. Annual variation in $\delta^{15}N$ enrichment could affect both pre- and postbreeding diets. However, postbreeding diets showed remarkably little annual change in $\delta^{15}N$, suggesting both stability in background isotope values and a reduction in low trophic level prey consumed after breeding constraints were relaxed. Furthermore, while fasting could increase $\delta^{15}N$, there is no evidence that murrelets fast prior to or during the molt. In fact, they typically gain mass during the fall molt (M. Z. Peery unpubl. data). Thus, isotopic signals revealed in this study are likely to represent actual variation in diet composition.

The ~1 to 2‰ lower $\delta^{13}C$ values recorded during the springs of 1999 to 2001 suggest that krill had been ingested in significant amounts. To produce the observed isotopic signatures had murrelets been feeding solely on mid- and high trophic level items, $\delta^{13}C$ fractionation in feathers would have to be between 0 and −1‰, which is highly unlikely (Hobson et al. 1994). The presence of krill (as evidenced by the low $\delta^{15}N$ and $\delta^{13}C$ values) in murrelet prebreeding diets during 1999 to 2001 was somewhat surprising because krill are generally described as inhabiting deep water (~100 m) during the day (Marinovic et al. 2002) and to surface at night when murrelets do not forage (M. Z. Peery et al. unpubl. data). During spring, however, krill, especially *Thysanoessa spinifera*, often form surface swarms that are exploited by seabirds during the day (Smith & Adams 1988, Ainley et al. 1996a). Coincidently, surface swarms of krill (*Euphausia pacifica*) were found within 1.5 km of shore in Año Nuevo Bay during June 2003 (D. G. Ainley pers. comm.), which is where most of the birds in this paper were captured and foraged. Furthermore, krill are routinely caught at trawl stations over the continental shelf at both 2 and 5 km from shore in moderate quantities in central California (S. Ralston unpubl. data). Thus, there appears to be ample opportunity for murrelets to capture krill, and the onset of krill swarming coincides with the prebreeding signature of krill found in murrelet diets (Fig. 1B).

A variety of species comprised mid-trophic level prey for murrelets. Juvenile rockfish, which are important to breeding seabirds on the Farallon Islands, California, also may be important to reproduction for the nearshore feeding marbled murrelet (Fig. 1B). Juvenile rockfish and squid should be available to murrelets

since they occur nearshore in densities comparable to the Farallones (Brodeur et al. 2003), and are especially aggregated at nearshore fronts (Bjorkstedt et al. 2002). Mysid shrimp may also comprise a significant portion of the murrelet diet during cool water years and they were present in Año Nuevo Bay where murrelets foraged (Henkel & Harvey 2006). However, due to the absence of time series data for mysids, changes in their abundance cannot be examined in relation to changes in murrelet isotopic signatures and productivity. Similarly, sandlance use these nearshore sandy habitats and may be an important mid-trophic level component of the murrelet's diet. Alternatively, the relationship between mid-trophic level prey and murrelet reproduction may simply be due to favorable conditions for both. However, since we show a sequential relationship between prey availability, diet, and reproductive success, we suspect the relationship is mechanistic and not spurious.

Juvenile rockfishes in murrelet postbreeding diets also closely followed those found in common murre *Uria*

aalge prey delivered to chicks on the Farallon Islands during 1998 to 2002 (Miller & Sydeman 2004). Common murre chick meals had low percentages of juvenile rockfishes during 1998 to 2000 (<10%), but rapidly increased to ~50–75% during 2001 and 2002. However, Common Murres did not increase delivery of squid to chicks in 2001 and 2002 (Miller & Sydeman 2004), when this signal appeared in murrelet diets (Fig. 4). Thus, while we suggest that enriched $\delta^{13}C$ was an indication of a diet rich in squid during the postbreeding seasons of 2001 and 2002, this interpretation could be erroneous.

Whatever the exact species of mid-trophic level prey that murrelets were taking, it appears that mid-trophic level prey are an important food item for successful reproduction. Murrelet reproductive success was strongly correlated with mid-trophic level prey abundance (Fig. 6C) and with their prevalence in the murrelet's postbreeding diet (Fig. 6D). This relationship may have emerged because mid-trophic level prey (1) sustain adults while they tend nests, (2) are fed directly to nestlings, or (3) are eaten by young after they fledge.
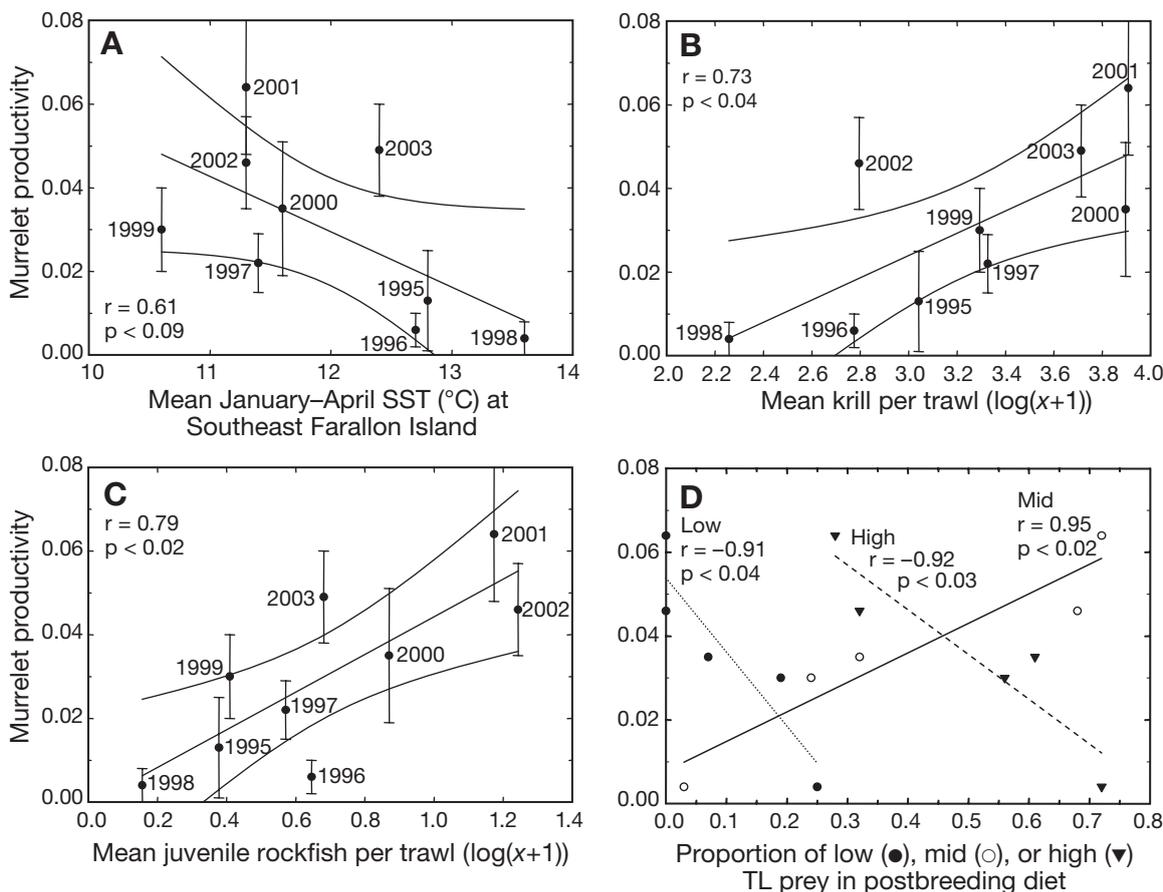
Fig. 6. *Brachyramphus marmoratus*. Relationship between annual reproductive success or productivity (mean date-corrected ratio of juveniles to after-hatch-year birds) and (A) the SSTs at Southeast Farallon Island, (B) krill abundance during 1995 to 2003, (C) young-of-the-year juvenile rockfish abundance from 1995 to 2003, and (D) low, mid and high trophic level prey in postbreeding murrelet diets. Krill and rockfish values are from spring shipboard trawls off central California. Regression lines are shown in all panels, with 95% confidence intervals in (A) to (C)

Moreover, both prebreeding and postbreeding prey availability and diet composition appear to be important to murrelets for successful reproduction (Fig. 6).

Mid-trophic level species and krill and were important components of murrelet prebreeding diets despite overfishing of several species of rockfishes in central California (Leet et al. 2001, Starr et al. 2002) and an apparent decline in zooplankton in the CCS over the past 50 yr (McGowan et al. 1998, Lavaniegos & Ohman 2003). The relationships between mid-trophic level prey dynamics and murrelet diets and reproduction, and the representation of low trophic level prey in murrelet diets could both be due to the concurrent decline in the availability of higher trophic level prey, such as sardines and anchovies due to fishing pressure (Leet et al. 2001) and to natural ecosystem variability such as PDO cycles (Chavez et al. 2003). Contemporary marine food webs around the world and in the California Current are highly modified compared to food webs prior to heavy fishing pressure (Jackson et al. 2001). The relative contributions of natural and anthropogenic factors on marbled murrelet prey are currently unclear. Nevertheless, modern murrelets feed at a lower trophic level during the prebreeding season than they did a century ago (Becker & Beissinger 2006).

Oceanographic effects on trophic level and reproductive success

Seabirds commonly track and consume the most abundant or energetically valuable prey items as they vary seasonally and annually due to oceanographic forcing (Ainley et al. 1995, 1996a,b, Litzow et al. 2002). Our results indicate that a similar pattern occurs for the nearshore-foraging marbled murrelet, however, the direct correlations with climate were weaker. Nevertheless, climatic variability still appeared to affect prey availability, murrelet dietary composition and, as a result, murrelet reproductive success. These relationships, while correlative, are strongly linked by the isotopic evidence showing murrelets do shift their diets in response to availability. Thus, murrelets appear to act as robust environmental samplers that track the availability of prey nearshore, which fluctuates in the CCS primarily due to the influences of climate.

Contrary to our predictions, neither basin nor local-scale conditions (NOI and SST, respectively) appeared to dominate murrelet prey availability, even though correlations approached significance with rockfish counts, and both cool NOI and SST were nearly significantly related to higher murrelet reproductive success. Local-scale conditions are driven by basin-scale processes, but basin-scale conditions may manifest themselves differently at local scales each year. For example, a true ENSO event in the equatorial Pacific is characterized by a low SOI, that generally, but not always, produces a low NOI value in the NE Pacific. This in turn generally leads to above average SSTs and reduced upwelling in the CCS. However, this basin to local-scale relationship is not ironclad: above average SSTs also occur in the absence of ENSO events. Subsequently, similar to Ainley et al.'s (1995) findings with other species of seabirds in the CCS, we consider basin-scale oceanographic conditions as the driving components of murrelet prey availability, diet, and reproductive success, with local conditions both acting as an artifact of and modulating the influence of large-scale climate. Although PDO and NPI values did not correlate with murrelet ecology in this study, both indices were related to local SSTs, and PDO was also correlated with spring turnover strength. Thus, long-term, large-scale phenomena are likely to affect murrelet biology in complex ways that may have not been detected in this study.

A regime shift to cooler ocean conditions may have occurred following the 1997 to 1998 ENSO event for the California Current (Chavez et al. 2003), although this assessment is debatable since the PDO has not unequivocally shifted to cool conditions (Overland et al. 2004, Rodionov 2004). However, marbled murrelet productivity did markedly improve beginning in 1999, with all years prior to 1995 to 1998 having lower reproductive success than 1999 to 2003 (Figs 6A–C). We suggest that cooler, more productive ocean conditions probably made more mid-trophic level prey available to murrelets, which improved reproductive success between 1999 and 2003.

Our results suggest the potential impacts of a progressively warmer marine climate induced by global climate change, which may enter a 'semi-permanent' warm phase PDO or ENSO-like state (McGowan et al. 1998, Sydeman et al. 2001), would be likely to reduce murrelet reproductive success. When combined with the effects of overfishing on marine food webs and seabird diets (Pauly et al. 1998, Becker & Beissinger 2006), global climate change may further exacerbate deteriorating feeding conditions for marine predators such as marbled murrelets. The destruction and fragmentation of the coastal old growth forests has focused conservation concerns on forest habitats that marbled murrelet use for nesting, with little attention to the affects of marine resources on population dynamics and persistence. Nevertheless, the kinds and degrees of impact of climate change on terrestrial and freshwater food webs and ecological linkages (Winder & Schindler 2004) will probably also be manifested in marine seabirds like the marbled murrelet that must compete with fisheries for prey resources whose abundance and availability are climatically mediated.

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