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TROPHIC RELATIONSHIPS AMONG SEABIRDS IN CENTRAL CALIFORNIA: COMBINED STABLE ISOTOPE AND CONVENTIONAL DIETARY APPROACH[1]

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Abstract. We used stable isotope analysis (SIA) and conventional techniques of diet assessment to determine marine trophic relationships in the Gulf of the Farallones, California, with an emphasis on marine birds. Stable-carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes were obtained from 98 tissue samples of 16 species representing primary and secondary consumers in 1993–1994. The values of $\delta^{13}C$ ranged from −20.1‰ in whole euphausiids (krill) to −15.0‰ in muscle of northern sea lions. Values of $\delta^{15}N$ showed step-wise trophic enrichment and ranged from 11.2‰ in euphausiids to 19.8‰ in sea lions. SIA of egg albumen from birds indicated reliance on zooplankton by Cassin's Auklet, Common Murre, and Western Gull, and on fish by Brandt's and Pelagic Cormorants, Rhinoceros Auklets, and Pigeon Guillemots during egg formation (April–May). However, analysis of prey brought to chicks during summer indicated the prevalence of fish in the diet of most seabirds, except Cassin's Auklet which fed primarily on krill. Results suggest a shift in trophic level and diet between spring and summer from krill to fish for Common Murres. $\delta^{13}C$ analysis confirmed that Brandt's Cormorants and northern sea lions feed in neritic habitats, whereas Cassin's and Rhinoceros Auklets foraged in epipelagic offshore waters. Our approach demonstrates the utility of combining both SIA and conventional dietary assessments to understand trophic relationships in dynamic marine ecosystems.

Key words: central California, diet, food-web dynamics, marine birds and mammals, stable isotope analysis, trophic relationships.

INTRODUCTION

Understanding the structure and functioning of marine ecosystems requires information on the trophic relationships of key species (Paine 1988). In coastal food-webs dependent upon upwelling and advection for nutrient input, such as boundary current systems of California, Peru-Chile, Benguela, Canary Islands, and Somalia, only a few taxa often provide key nutritional links between primary producers and secondary or higher-level consumers, including predatory fish, birds and mammals (Cushing 1975). Key species of primary consumers include zooplankton (*Calanus* spp. and *Euphausia* spp.) and several species of epipelagic fish (*Engraulis* spp., *Sardinops/Sardinax* and *Clupea* spp.); these prey are then consumed by secondary predators, including many marine birds and mammals (Vermeer 1981, Briggs et al. 1988, Ainley et al. 1990).

However, evaluation of the structure and dynamics of marine food webs is a complex undertaking because of logistic difficulties which restrict sampling in time and space (Paine 1988). Moreover, indirect methods of dietary assessment, such as stomach, pellet, or fecal analyses, may provide less than satisfactory results if diet composition is biased by differential rates of digestion (reviewed by Duffy and Jackson 1986, Erikstad 1990). Fortunately, the ratios of naturally-occurring isotopes of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) in consumer tissues provide insight into food-web structure that can complement conventional dietary assessments. Stable isotope analysis (SIA) can be a useful complement because stable isotope ratios in consumer tissues reflect those in their diet (DeNiro and Epstein 1978, 1981). Metabolic processes involved in the synthesis of proteins in consumers result in preferential loss of the lighter isotope

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and hence enrichment of the $^{15}N/^{14}N$ ratio in their tissues. In marine ecosystems a step-wise enrichment of ^{15}N typically occurs with each trophic level (Wada et al. 1987, Rau et al. 1992, Hobson et al. 1994). This change in isotope ratios between trophic levels appears to be relatively constant at ~3‰ (‰ = parts per thousand), so measurements of $^{15}N/^{14}N$ ratios in food-web components can be used to infer trophic relationships. Stable-carbon isotope values provide insight into the source of feeding, including inshore vs. offshore foraging in marine habitats (Hobson et al. 1994).

Isotopic studies to date have used primarily whole bodies or specific tissues of consumers. For investigation of avian diets, bird eggs are another potential source of material, since they are formed from nutrients derived from the diet of the laying female (Krapu 1981, Afton and Ankney 1991, Schaffner and Swart 1991). The use of eggs as source material is important because knowledge of marine bird diet during egg formation is scant, yet critical for evaluating hypotheses concerning timing of breeding and other life history traits. In this study, we examine species in the coastal marine food-web of the Gulf of the Farallones, California, using a combination of SIA to infer relative trophic position during the early breeding period, and conventional diet studies to infer chick diets later in the season. We compare and contrast these results and discuss the utility of using both approaches to understanding seabird tropho-dynamics in this coastal food-web. We also compare our results with those of Rau et al. (1983) who used SIA to investigate other portions of the California Current marine ecosystem.

METHODS

PREDATOR SAMPLES

Eggs of Brandt's Cormorants (*Phalacrocorax penicillatus*), Pelagic Cormorants (*P. pelagicus*), Western Gulls (*Larus occidentalis*), Common Murres (*Uria aalge*), Pigeon Guillemots (*Cepphus columba*), Rhinoceros Auklets (*Cerorhinca monocerata*), and Cassin's Auklets (*Ptychoramphus aleuticus*) were collected from Southeast Farallon Island (SEFI; 37°N 123°W) and Año Nuevo Island (ANI, 36°N 122°W) located in waters off central California. Eggs were collected early in the breeding season between April and June 1993 to facilitate relaying by individual pairs. We also obtained muscle tissue samples of northern sea lions (*Eumetopias jubatus*) from dead pups collected at ANI (n = 5, July–October) and SEFI (n = 2), and a few (see below) pectoral muscle samples from seabirds on SEFI (Common Murre, Pigeon Guillemot, Rhinoceros and Cassin's Auklets) salvaged during June–September, 1993.

PREY SAMPLES

Based on previous studies of bird diets in the region (Briggs et al. 1988, Ainley et al. 1990, Croll 1990), we selected the following prey species for SIA: juvenile short-bellied rockfish (*Sebastes jordanii*), northern anchovy (*Engraulis mordax*), juvenile Pacific sardine (*Sardinops sajax*), adult market squid (*Loligo opalescens*), juvenile sablefish (*Anoplopoma fimbria*), juvenile lingcod (*Ophiodon elongatus*), juvenile king salmon (*Oncorhynchus tshawytscha*), and adult krill (*Euphausia pacifica* and *Thysanoessa spinifera*). Prey samples (excluding krill) were obtained by capturing Rhinoceros Auklets as they returned with food at dusk to feed their chicks (see below). Samples were identified and frozen for later SIA analyses. We obtained krill samples from the National Marine Fisheries Service (NMFS) that were collected during rockfish stock recruitment surveys made in the Gulf of the Farallones during February 1994 (n = 5), and one sample from a fresh Western Gull regurgitation collected on SEFI in June 1993.

STABLE ISOTOPE MEASUREMENTS

A minimum of 2 ml of albumen was extracted from each egg, stored frozen in glass scintillation vials and later freeze-dried. Lateral muscle tissue from fish and marine mammals also was freeze-dried, powdered and subjected to lipid extraction using a Soxhlet apparatus with chloroform solvent. Krill samples were similarly treated, but also were soaked with 1 N HCL to remove carbonates before isotopic analysis. We loaded samples for $^{13}C/^{12}C$ and $^{15}N/^{14}N$ analysis in Vycor tubes with wire-form CuO, silver foil, and elemental Cu, then sealed tubes under vacuum and combusted the material at 800°C for at least 6 hr. Carbon dioxide and nitrogen gas was separated cryogenically and analyzed using a VG OPTIMA isotope-ratio mass-spectrometer at the National Hydrology Research Institute, Saskatoon, Saskatchewan. Stable isotope concentrations are expressed in delta (δ) notation as parts per thousand according to the following:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1{,}000$$

where X is ^{15}N or ^{13}C and R is the corresponding ratio $^{15}N/^{14}N$ or $^{13}C/^{12}C$. $R_{standard}$ for ^{15}N and ^{13}C are atmospheric N_2 (AIR) and the PDB standard, respectively. Based on numerous measurements of organic standards, the analytical precision of these measurements is estimated to be ± 0.1‰ and ± 0.3‰ for carbon and nitrogen, respectively.

CONVENTIONAL TECHNIQUES OF DIET ASSESSMENT

To quantify food habits of seabirds, we observed adults feeding chicks. Common Murres and Pigeon Guillemots carry single prey items in their beaks to provision chicks, and diet items can be identified, often to species, by trained observers situated in blinds near breeding colonies. We conducted observations on approximately 100 pairs of murres and 50 pairs of guillemots throughout the chick-rearing period (murres: late May through early July; guillemots: late June through mid-August). To quantify food habits of Rhinoceros Auklets, we collected food items from adults captured at SEFI in mist nets opened near dusk, monitored continuously (~1.5 hr.), and closed just after night fall. We conducted at least three capture sessions at each of three locations on the Farallones from 15 June to 30 August. Brandt's Cormorant diet was determined from analyses of remains in pellets (fish otoliths, squid beaks) collected from nesting areas. A total of 133 pellets from 108 breeding pairs (1–3 pellets per nest) was collected during August–September. Pellets were soaked in water, otoliths were extracted from organic material, dried, and sorted. Otoliths were identified and measured using a dissection microscope and the reference collection of identified otoliths maintained at Point Reyes Bird Observatory (PRBO) or the Museum of Vertebrate Zoology, University of California, Berkeley. Diet of Cassin's Auklets was based on about 100 regurgitations collected each year from parents returning to feed chicks at night. About 10 collections were made every 10 days throughout chick-rearing, mid-May through July. Each regurgitation was weighed and frozen for analysis. During analysis, otoliths, squid beaks, and whole bodies of crustaceans were separated and counted. To aid identifications we used collections maintained at PRBO, Southwest Fisheries Science Center (La Jolla, California) or Moss Landing Marine Laboratory (Moss Landing, California).

RESULTS

TROPHIC POSITION

$\delta^{15}N$ measurements. $\delta^{15}N$ values (mean ± SD) ranged from 11.2 ± 0.5‰ in krill to 19.8 ± 0.6‰ in northern sea lions (Table 1, Fig. 1); overall, species differences were significant (ANOVA: $F_{15,82} = 70.9$, $P < 0.001$). Krill was significantly different from fish, except for lingcod, sardine, sablefish, and squid (Fig. 1, Bonferroni inequality, $P < 0.001$). Among fish, lingcod showed the lowest $\delta^{15}N$ values and northern anchovy the highest. We found the following statistically significant differences among fish: (1) values for lingcod were lower than those for salmon, anchovy, and short-bellied rockfish, (2) those for sablefish and squid were lower than for anchovy and short-bellied rockfish, and (3) those for sablefish were lower than salmon (Bonferroni inequality, all $P < 0.02$). Among birds, two distinct groups were evident (Table 1, Fig. 1). $\delta^{15}N$ values derived from eggs of Brandt's and Pelagic Cormorant, Pigeon Guillemot, and Rhinoceros Auklet were similar, but, in turn were different from the second group composed of Cassin's Auklet, Common Murre, and Western Gull (Bonferonni inequality, all $P < 0.001$). The $\delta^{15}N$ value for northern sea lion muscle was significantly greater than for birds (Bonferroni inequality, all $P < 0.001$). The $\delta^{15}N$ values measured for seabird pectoral muscle were: Cassin's Auklet: 14.0 ± 1.2‰ ($n = 4$), Common Murre: 17.3 ± 0.7‰ ($n = 3$), Pigeon Guillemot: 15.2‰ ($n = 2$), and Rhinoceros Auklet: 17.8‰ ($n = 2$).

Trophic levels were approximated from our nitrogen isotope data by applying a trophic enrichment factor throughout the food-web after assuming that krill occupied trophic level 2.5 (Sanger 1987). The isotopic fractionation factor of 3.1‰ was determined previously by Hobson (1995) and corresponds to changes expected between diet and egg albumen. This value is similar to trophic enrichment factors derived for other components of marine food-webs off California and elsewhere (Rau et al. 1983, 1992, Hobson and Welch 1992). We therefore applied it throughout the seabird food-web of the Gulf of the Farallones (independent of tissue type) as follows:

TABLE 1. Stable-carbon and nitrogen isotope abundance ($\bar{x}$ ± SD) of components of the Gulf of the Farallones food web. Source material includes egg albumen for birds, muscle tissue for fish and northern sea lions, and whole bodies for krill.

Species	n	$\delta^{13}C$(‰)	$\delta^{15}N$(‰)	Trophic level[a]
Crustaceans				
Krill	5	−20.2 ± 0.3	11.2 ± 0.5	2.5
Cephalopods				
Market squid	5	−17.1 ± 0.2	12.3 ± 0.4	2.9
Fishes				
Lingcod	6	−18.3 ± 0.5	12.5 ± 0.3	2.9
Sablefish	5	−17.3 ± 0.2	12.8 ± 0.7	3.5
Pacific sardine	3	−17.0 ± 0.3	12.9 ± 0.1	3.1
Shortbelly rockfish	5	−17.1 ± 0.3	13.8 ± 0.2	3.3
King salmon	4	−17.5 ± 0.2	13.8 ± 0.2	3.3
Northern anchovy	4	−16.8 ± 0.4	13.9 ± 0.8	3.4
Planktivorous Birds				
Cassin's Auklet	7	−18.2 ± 0.5	13.9 ± 1.0	3.4
Western Gull	5	−16.4 ± 0.3	14.4 ± 1.1	3.5
Common Murre	3	−16.9 ± 0.5	14.8 ± 0.9	3.7
Piscivorous Birds				
Pelagic Cormorant	5	−17.7 ± 0.2	16.7 ± 0.5	4.3
Rhinoceros Auklet	6	−17.7 ± 0.7	16.9 ± 0.5	4.3
Pigeon Guillemot	13	−17.7 ± 0.2	16.9 ± 0.5	4.3
Brandt's Cormorant	7	−15.9 ± 0.3	17.3 ± 0.2	4.5
Mammals				
Northern sea lion	5	−15.2 ± 0.5	19.8 ± 0.6	5.3

[a] See text for derivation of trophic level estimates.

$$TL = 2.5 + (\delta^{15}N - 11.2)/3.1$$

where TL is the trophic level of an organism and $\delta^{15}N$ is its stable-nitrogen value in ‰. Estimates of trophic level for each species are presented in Table 1.

$\delta^{13}C$ measurements. $\delta^{13}C$ values ranged from −20.2 ± 0.3‰ in krill to 15.2 ± 0.5‰ in northern sea lions (Table 1, Fig. 1); overall, species differences were significant (ANOVA: $F_{15,82}$ = 52.2, $P < 0.001$). The $\delta^{13}C$ value for krill was significantly less than that for fish (Bonferroni inequality, all $P < 0.001$). Among fish, lingcod showed the lowest $\delta^{13}C$ value and northern anchovy the highest. The value for lingcod was significantly lower than those for other fish. The value for salmon was significantly lower than for anchovy and short-bellied rockfish (Bonferroni inequality, all $P < 0.015$). Among birds, two distinct results emerged: (1) Brandt's Cormorant showed significantly higher $\delta^{13}C$ values than other birds, except Western Gull, and (2) Pigeon Guillemot, Rhinoceros and Cassin's Auklet, and Pelagic Cormorant were all similar, yet different from Common Murre and Western Gull (Bonferroni inequality, all $P < 0.01$). The $\delta^{13}C$ value for northern sea lion was significantly greater than for birds, except Brandt's Cormorant (Bonferroni inequality, all $P < 0.003$). Muscle tissue $\delta^{13}C$ values for seabirds were: Cassin's Auklet: −18.3 ± 0.4‰ (n = 4), Common Murre: −16.6 ± 0.5‰ (n = 3), Pigeon Guillemot: −16.2‰ (n = 2), and Rhinoceros Auklet: −17.1‰ (n = 2).

CHICK DIET COMPOSITION

Brandt's Cormorant. Fifty-six of 108 samples contained a total of 1,108 otoliths from at least 16 identified species. A small number (1.6%) of the otoliths could not be identified, primarily due to wear or fragmentation. The number of otoliths per sample ranged from 1 to 96, and number of species per sample ranged from 1 to 6. The diet composition was diverse, including 13 families of fish (Table 2). Scorpaeniids (rockfish; presumably mostly *Sebastes jordani*) comprised over 57% of the diet by number; bothids and pleuronectids (flatfish) comprised ~20%. Batrachoidids (midshipman) and engraulids (anchovies) comprised an additional 16%. Carangids,

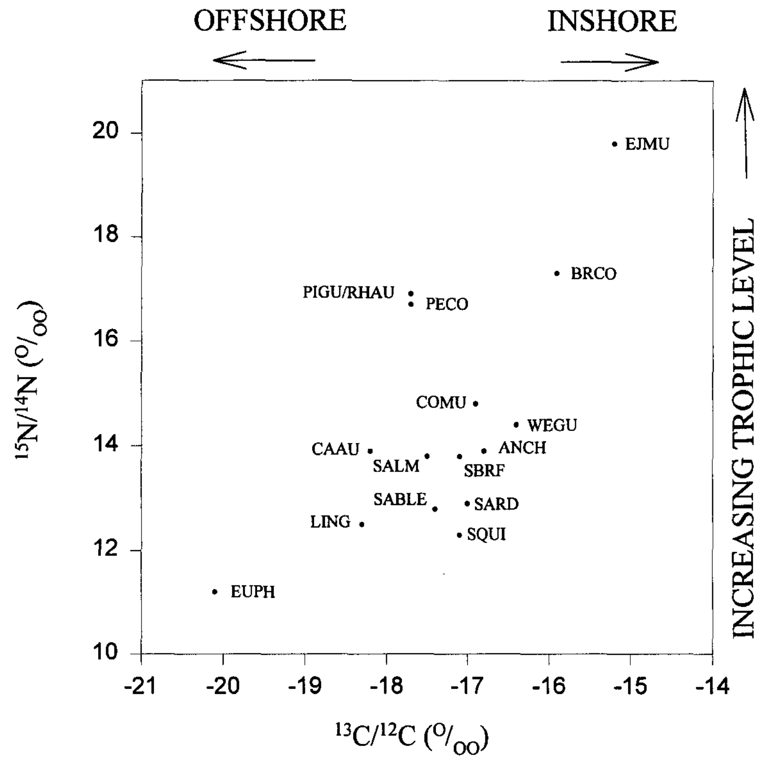

FIGURE 1. Trophic structure in the Gulf of the Farallones based on seabird egg albumen, sea lion and fish muscle tissue, and whole bodies of krill (see Table 1 for statistical details). Abbreviations: EUPH (krill = euphausiids), LING (lingcod), SABLE (sablefish), SQUI (squid), SARD (sardine), SALM (salmon), SBRF (short-bellied rockfish), ANCH (anchovy), CAAU (Cassin's Auklet), WEGU (Western Gull), COMU (Common Murre), PIGU (Pigeon Guillemot), RHAU (Rhinoceros Auklet), PECO (Pelagic Cormorant), BRCO (Brandt's Cormorant), EJMU (northern sea lion).

cottids, and ophiids also were taken, but in relatively low numbers.

Cassin's Auklet. The diet of Cassin's Auklet chicks was composed of crustaceans, principally two species, *Euphausia pacifica* and *Thysanoessa spinifera* (Table 3). Mysids (*Acanthomysis columbiae*) and another euphausiid crustacean, *Nyctyphanes simplex,* comprised ~20% of the diet. Amphipods, decapods, and fish comprised small amounts of the diet.

Common Murre. Principle diet items of Common Murre chicks included juvenile rockfish, mainly *Sebastes jordani,* and northern anchovy (*Engraulis mordax*) (Table 4). Salmon (*Onchorhynchus tshawytscha*), butterfish (*Peprillus simillimus*), night smelt (*Spirinchus starksi*), and cephalopods (*Loligo opalescens*) each made up < 5% of the diet. Flatfish (bothids and pleuronectids) and other species were consumed in relatively low numbers. Adult murres did not feed crustaceans to their chicks.

Pigeon Guillemot. We were unable to document the use of prey to the species-level; thus, much of the compositional analysis of Pigeon Guillemot chick diet is restricted taxonomically to the family-level. The diet composition of Pigeon Guillemot chicks was more diverse than that of Common Murre chicks (Table 5). Rockfish (scorpaenids) and sculpins (cottids) were eaten most frequently, together comprising ~90% of the diet. Flatfish (bothids and pleuronectids) comprised ~5% of the chick diet. Other prey eaten included pholids and stichaeids (gunnels and warbonnets), clinids and blenniids (kelpfish and blennies), ophidiids/liparids (cuskeels and snailfish), and cephalopods (squid, but especially octopus).

Rhinoceros Auklet. The diet of Rhinoceros

TABLE 2. Brandt's Cormorant diet composition in 1993 based on numerical occurrence. The percent contribution of total identified individuals (n = 1,090) is shown.

Prey[a]	% Numerical occurrence
Osteichthyes	
Batrachoididae	
Poricthys notatus	9.2
Bothidae	
Citharichthys sordidus	6.5
Citharichthys stigmaeus	4.3
Carnangidae	
Trachurus symmetricus	2.0
Cottidae	1.5
Embiotocidae	
Cymatogaster aggregata	0.1
Engraulidae	
Engraulis mordax	7.1
Gobiidae	0.1
Merluccidae	0.1
Ophiidae	
Chilara taylori	1.1
Osmeridae (unidentified)	0.1
Pleuronectidae (unidentified)	2.8
Glyptocephalus zachirus	1.7
Lepidopsetta bilineata	2.9
Sciaenidae	
Genyonemus lineatus	1.4
Scorpaenidae	
Sebastes spp.	57.2

[a] Known prey not represented in 1993 include *Microgadus proximus* (Gadidae), Hexagrammidae, *Parophyrs vetulus* (Pleuronectidae), Stomateidae, Zaniolepididae, and *Loligo opalescens* and *Octopus rubescens* (Cephalopoda).

TABLE 3. Cassin's Auklet diet composition in 1993 based on numerical occurrence. Percent of total identified individuals (n = 3,487) is shown. Sample is based upon regurgitations (n = 62) collected throughout the chick-rearing season, May–July.

Prey[a]	% Numerical occurrence
Crustaceans (subtotal)	99.2
Amphipods (subtotal)	>0.1
Decapods	1.1
Euphausiids (subtotal)	83.4
Euphausia pacifica	48.3
Nyctyphanes simplex	7.6
Thysanoessa spinifera	27.5
Mysids	14.6
Osteichthyes (subtotal)	<0.2
Bothidae	<0.1
Citharichthys sordidus	<0.1
Scorpaenidae	<0.1

[a]Known prey not represented in 1993 include Cephalopoda, Gastropoda, Gammarids, Hyperiids, and Cypriids, and *Nematocelis difficilis* (Euphausiidae).

TABLE 4. Common Murre diet composition in 1993 based on numerical occurrence. Percent of total identified individuals (n = 1,985) is shown.

Prey	% Numerical occurrence
Osteichthyes	
Bothidae/Pleuronectidae	1.0
Engraulidae	
Engraulis mordax	62.8
Osmeridae	
Spirinchus starksi	3.0
Salmonidae	1.0
Scorpaenidae (subtotal)	31.2
Sebastes jordani	30.0
Sebastes spp.	1.2
Stomateidae	
Peprillus simillimus	1.0
Other[a]	1.2
Cephalopoda	
Loligo opalescens	1.0

[a] Includes: *Clupea harengus, Cololabris saira, Oxyjulis californica,* and *Octopus rufescens.*

Auklet chicks was dominated by northern anchovy (*Engraulis mordax*), short-belly rockfish (*Sebastes jordani*), and sardines (*Sardinops sajax*); together, these species comprised ~80% of the diet (Table 6). An additional 7 families of fish and cephalopods were taken in low frequencies. Predation on sardines by this species in 1992–1993 represents the first report of this prey in seabird diets since the recent recovery of the

TABLE 5. Pigeon Guillemot diet composition in 1993 based on numerical occurrence. Percent of total identified individuals (n = 4,268) is shown.

Prey[a]	% Numerical occurrence
Osteichthyes	
Bothidae/Pleuronectidae	5.3
Brotulidae	0.1
Clinidae/Blennidae	1.1
Cottidae	28.7
Ophidiidae/Liparidae	1.2
Pholidae/Stichaeidae	0.9
Scorpaenidae (subtotal)	61.5
Sebastes jordani	38.7
Sebastes spp.	22.8
Cephalopoda	
Loligo opalescens	0.1
Octopus rufescens	0.3
Polychaetes (subtotal)	0.1

[a] Known prey not represented in 1993 include Ammodytidae, Batrachoididae, Engraulidae, Gobiidae, Labridae, Merluccidae, and Scomberesocidae.

TABLE 6. Rhinoceros Auklet diet composition in 1993 based on numerical occurrence. Percent of total identified individuals (n = 348) is shown.

Prey[a]	% Numerical occurrence
Osteichthyes	
Ammodytidae	
Ammodytes hexapterus	1.0
Anoplopomatidae	
Anoplopoma fimbria	1.7
Clupeidae	
Sardinops sajax	18.1
Cottidae	
Scorpaenichthys marmoratus	1.0
Engraulidae	
Engraulis mordax	37.4
Hexagrammidae	
Ophiodon elongatus	6.0
Merluccidae	
Merluccius productus	1.0
Salmonidae	
Oncorhynchus tshawytscha	3.2
Scorpaenidae (subtotal)	29.6
Sebastes jordani	25.0
Sebastes spp.	4.6
Stromateidae	
Peprillus simillimus	<1.0
Cephalopoda	
Loligo opalescens	<1.0
Octopus rufescens	<1.0
Other[b]	1.0

[a] Known prey not represented in 1993 includes *Cololabris saira* (Scomberesocidae).
[b] Includes: *Clupea harengus, Oxyjulis californica, Lampetra tridentata, Lestidium ringens*, and Myctophiidae.

sardine population in central California (Barnes et al. 1992).

DISCUSSION

TROPHIC STRUCTURE

Using our isotopic model to calculate average trophic level, we determined that the marine food-web in the Gulf of the Farallones is composed of approximately five trophic levels with marine birds occupying levels 3.4 to 4.5, and northern sea lions occupying the fifth trophic level (Table 1, Fig. 1). However, isotopic analyses of egg albumen reflects a narrow window of dietary integration when compared with muscle or other hard tissues (Hobson 1995). For Farallon Island seabirds in 1993, the period of egg-laying included the months of April–June (Sydeman and Eddy 1995). Although this represents typical timing of breeding for these birds (Ainley and Boekelheide 1990, Sydeman et al. 1991) and our sampling included many food-web components, our conclusions are limited to late spring and early summer. It is unknown how well this food-web structure would apply to other seasons, but we suspect many similarities would be found.

Rau et al. (1983) studied the pelagic food web of the southern California Bight and concluded that this food-web contained five trophic levels between "netted plankton" (composed primarily of zooplankton) and an apex predator, the great white shark (*Carcharodon carcharius*). Rau et al. (1983) based their food web structure on $\delta^{13}C$ values, whereas we based our food web on $\delta^{15}N$ values. In central California, great white sharks are known to extensively feed upon seals and sea lions (Ainley et al. 1985), indicating an "apex" trophic level in the Gulf of the Farallones food-web. The Gulf of the Farallones and southern California Bight are separated by approximately 300 km of coastline and are influenced, to a certain extent, by different oceanographic processes. However, many components of these food-webs are similar, including large populations of Western Gulls, Brandt's and Pelagic Cormorants, Pigeon Guillemots, and Cassin's Auklets, and a reliance on zooplankton (krill), anchovies and rockfish by breeding seabirds in both systems (Anderson et al. 1982, Sydeman et al. 1991, Ainley et al. 1995).

TEMPORAL CHANGES IN DIET AND FORAGING DISTRIBUTION

With the exception of Common Murres, chick diet and trophic position of adults based on the isotopic analysis of egg albumen were concordant. SIA indicated that Common Murres, Western Gulls and Cassin's Auklets were planktivorous during the period of egg formation, whereas Brandt's and Pelagic Cormorants, Rhinoceros Auklets, and Pigeon Guillemots were piscivorous. The diet of seabird chicks in the summer provides corroborating evidence for the piscivorous diets of both cormorants, Rhinoceros Auklets and Pigeon Guillemots, and the planktivorous diet of Cassin's Auklet. In addition, Ainley et al. (1990) found a varied diet of Western Gull chicks, including marine arthropods mostly composed of euphausiids.

Common Murres occupied a lower trophic level (TL = 3.7) consistent with a diet of krill during the egg formation period. Other evidence from the colony on the Farallon Islands and Gulf of the Farallones also suggests that these birds feed on invertebrates during spring (Boekelheide et al. 1990; PRBO, unpubl. data). Isotopic analyses of our small sample of muscle tissue from murres indicates a higher trophic level (TL = 4.5) later in the season corresponding to a piscivorous diet. Although our sample size of murre muscle tissue is small, these data indicate a switch in trophic level between spring and summer for Common Murre adults in the Gulf of the Farallones. A switch in the diet and trophic level for Western Gulls also may occur as this species feeds extensively on fish later during chick-rearing (Sydeman et al. 1991); thus, further isotopic investigations on these species would be informative.

Our findings suggest that some marine birds may have the ability to track the most abundant and/or energetically profitable prey on relatively short time scales. In marine ecosystems characterized by extensive changes in physical oceanographic processes, such as upwelling and coastal advection in the California system, food-web development may be temporarily delayed and spatially variable. In turn, this could have substantial effects on seabird demography. Species able to respond to rapidly changing foraging conditions, or those able to use prey occupying different trophic levels, may have an advantage in being able to maintain relatively constant energy budgets. In variable marine environments, seabirds capable of trophic-level switching may therefore have a greater chance of successful reproduction under unfavorable conditions. Indeed, if we consider interannual variation in the reproductive performance of Common Murres, Cassin's Auklets, and Western Gulls with that of Brandt's and Pelagic Cormorants and Pigeon Guillemots on SEFI, the latter group shows considerably more annual variability (Ainley et al. 1995). Although differences in reproductive effort (clutch size) and foraging range (nearshore vs. pelagic) explain much of these patterns, questions remain concerning which foraging characteristics allow species to follow different reproductive options. Trophic-level switching may provide a mechanism for opportunistic species to cope with limited or uncertain forage reserves.

Results of SIA also are compatible with information on the at-sea foraging habitat of seabirds in the Gulf of the Farallones. In general, organisms which foraged in benthic or nearshore waters of the Gulf of the Farallones were more enriched in $\delta^{13}C$ than offshore or pelagic feeders, a pattern found in other marine food webs (Hobson and Welch 1992, Hobson et al. 1994). Notably, the two species of krill are primarily pelagic in their distribution and showed the lowest $\delta^{13}C$ values. Among birds, Cassin's Auklet, a pelagic feeder, showed the most depleted $\delta^{13}C$ values, whereas Brandt's Cormorant, which feeds in nearshore waters of the Gulf of the Farallones and in coastal estuaries (Ainley et al. 1981, 1990), was most enriched. Common Murres and Western Gulls, which feed in both pelagic and neritic habitats (Ainley et al. 1990, Allen 1994), had intermediate $\delta^{13}C$ values. Thus, SIA also accurately reflected the at-sea foraging habitat of seabirds and their prey in the Gulf of the Farallones.

CONCLUSIONS

Our study of egg albumen and pectoral muscle tissue illustrates the dynamic nature of seabird trophic relationships in the Gulf of the Farallones, California. In doing so, we have demonstrated the power of conducting SIA on several tissues from a single species to infer temporal and spatial variation in trophic relationships and the utility of the stable-isotope approach in delineating trophic relationships. This study adds to the growing number of reports (Hobson and Welch 1992, Rau et al. 1992, Hobson et al. 1994) affirming the importance of this technique in determining marine food-web structure and foraging dynamics. However, conventional diet studies are the only means of establishing details of the types and amounts of prey taken. Thus, whereas SIA provides information on trophic relationships and structure, and conventional dietary assessments provide details of prey utilization patterns, both techniques, when used together, provide a powerful means of detecting patterns in marine ecosystems. Notably, both techniques indicate that the seabird food-web of the central California Current ecosystem is dynamic. This fundamental result suggests that food-web models based on static trophic relationships would inadequately describe the California Current marine ecosystem.

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