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Using stable isotopes to determine seabird trophic relationships

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Summary

1. The stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) were analysed in 22 species of marine birds from coastal waters of the northeast Pacific Ocean. Analyses confirm that stable nitrogen isotopes can predict seabird trophic positions.

2. Based on $\delta^{15}N$ analyses, seabird trophic-level inferences generally agree with those of conventional dietary studies, but suggest that lower trophic-level organisms are more important to several seabirds than was recognized previously.

3. Stable-carbon isotope analysis may be a good indicator of inshore vs. offshore feeding preference.

4. In general, stable-isotope analysis to determine trophic level offers many advantages over conventional dietary approaches since trophic inferences are based on time-integrated estimates of assimilated and not just ingested foods, and isotopic abundance represents a continuous variable that is amenable to statistical analysis.

Key-words: carbon-13, nitrogen-15, seabird community, stable-isotope analysis, trophic levels.

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Introduction

In many areas, diets of breeding seabirds are often overwhelmingly influenced by prey from single trophic levels such as small pelagic fishes or zooplankton. For example, capelin *Mallotus villosus* (Müller, 1777) is of major importance to alcids in the North Atlantic (Bradstreet & Brown 1985; Piatt 1987); pilchards *Sardinops ocellata* (Pappe, 1853) and anchovies *Engraulis ringens* (Cuvier, 1817) dominate seabird diet off South Africa and Peru (Nelson 1978; Furness 1982) and krill *Euphausia* sp. dominates the diets of several seabirds and marine mammals in the Antarctic (Croxall & Prince 1987). In such systems, certain seabird natural history traits reflect directly the dynamics of prey populations (Cairns 1987; Hunt, Piatt & Erikstad 1991). Seabird diets thus may be used as convenient indicators of changes in marine ecosystems (Furness 1982; Springer *et al.* 1984; Ainley & Boekelheide 1990; Vader *et al.* 1990).

Dietary analyses based on stomach contents, direct observation or collection of prey remains at colonies, unless sampled regularly over an extended period, reflect short-term diet and are often biased by the more rapid digestion of soft-bodied prey (e.g. crustaceans; Bradstreet 1980; Gaston & Nettleship 1981) and by the retention of hard body parts (e.g. squid beaks; Wilson *et al.* 1985). Recently, however, it has been demonstrated that stable-isotope analysis complements well these conventional techniques (Hobson 1990, 1991, 1993; Hobson & Montevecchi 1991; Rau *et al.* 1992). This analytical approach is based on the fact that stable isotopes of carbon and particularly nitrogen show a step-wise enrichment with trophic level in marine systems (Rau 1982; Wada *et al.* 1987; Fry 1988; Hobson & Welch 1992). Moreover, because the turnover rates of diet-derived stable isotopes in consumer tissues vary according to the metabolic rate of those tissues (Tieszen *et al.* 1983), stable-isotope analysis can integrate dietary information over different time periods (e.g. weeks, months, years; Hobson & Clark 1992). The accurate evaluation of temporal and geographic variation in seabird trophic levels using stable isotopes, thus, represents a significant advance in the use of seabirds as 'bio-indicators' of marine ecosystems.

To date, it has not been clear how broadly applicable the stable-isotope technique may be in various

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ocean systems since isotopic information on food-web components are yet to be available for many marine areas. In this paper, we investigate $\delta^{15}N$ and $\delta^{13}C$ values in tissues of seabirds and their prey from three areas of the northeastern Pacific Ocean; coastal waters of Vancouver and Queen Charlotte islands and the Gulf of Alaska. The study area (Fig. 1) is a productive temperate marine region, where little long-term dietary information exists for most of the seabird species. Our overall objectives were to determine (i) if regular patterns of $\delta^{15}N$ and $\delta^{13}C$ enrichment with trophic level could be detected for seabirds in three geographically distinct marine food webs; and (ii) if dietary inferences emerging from isotope analyses were consistent with those from conventional dietary information in these three areas. During the course of other studies, we obtained samples of seabirds and their prey from the west coast of Vancouver Island, the Queen Charlotte Islands and adjacent mainland coast, and from Kachemak Bay and the Shumagin and Semidi Islands (Fig. 1). Previous investigations in Barkley Sound, British Columbia, provided preliminary evidence that stable isotopes could be used to determine the trophic positions of inshore vs. offshore-feeding alcids (Hobson 1991).

Study area and methods

VANCOUVER ISLAND

The west coast of Vancouver Island supports about 500 000 breeding seabirds (Rodway & Lemon 1990). Samples were obtained primarily from Barkley Sound, an embayment 25 km wide and 20 km long on the Island's southwest coast (see Porter & Sealy 1981; Fig. 1). Seabirds sampled included six Cassin's auklets *Ptychoramphus aleuticus* (Pallas), five pigeon guillemots *Cepphus columba* (Pallas), nine rhinoceros auklets *Cerorhinca monocerata* (Pallas), 19 marbled murrelets *Brachyramphus marmoratus* (Gmelin), five tufted puffins *Fratercula cirrhata* (Pallas) and 12 ancient murrelets *Synthliboramphus antiquus* (Gmelin).

Food web samples were collected in the Barkley Sound region in May–August, 1990. Particulate organic matter (POM) was collected on 24 July using methods similar to those described in Hobson & Welch (1992). Euphausiids (*Euphausia* sp.) were obtained from the stomachs of walleye pollock *Theragra chalcogramma* (Pallas, 1811) caught in early May. Other organisms were obtained through trawls, beach seine or collections at low tide.

QUEEN CHARLOTTE ISLANDS AND HECATE STRAIT

Over 1·5 million seabirds of 12 species breed at almost 200 sites among the Queen Charlotte Islands (Rodway *et al.* 1988). We examined muscle and bone samples primarily from two sites: Lucy Island, located in northern Hecate Strait, between the Charlottes and the mainland, and Hippa Island, on the west coast of the Charlottes (Fig. 1).

Muscle and bone samples were dissected from six fork-tailed storm-petrels *Oceanodroma furcata* (Gmelin), six Leach's storm-petrels *Oceanodroma leucorhoa* (Vieillot) and six Cassin's auklets collected on Hippa Island, 4–5 May 1990. Muscle and bone was obtained also from six rhinoceros auklets collected on Lucy Island on 19 May 1990. Bone samples were salvaged from five surf scoters *Melanitta perspicillata* (L.) and five white-winged scoters *Melanitta fusca* (L.) killed in an oil spill in Hecate Strait in October, 1989. Muscle and bone was obtained from four sooty shearwaters *Puffinus griseus* (Gmelin) collected in Hecate Strait in July 1985.

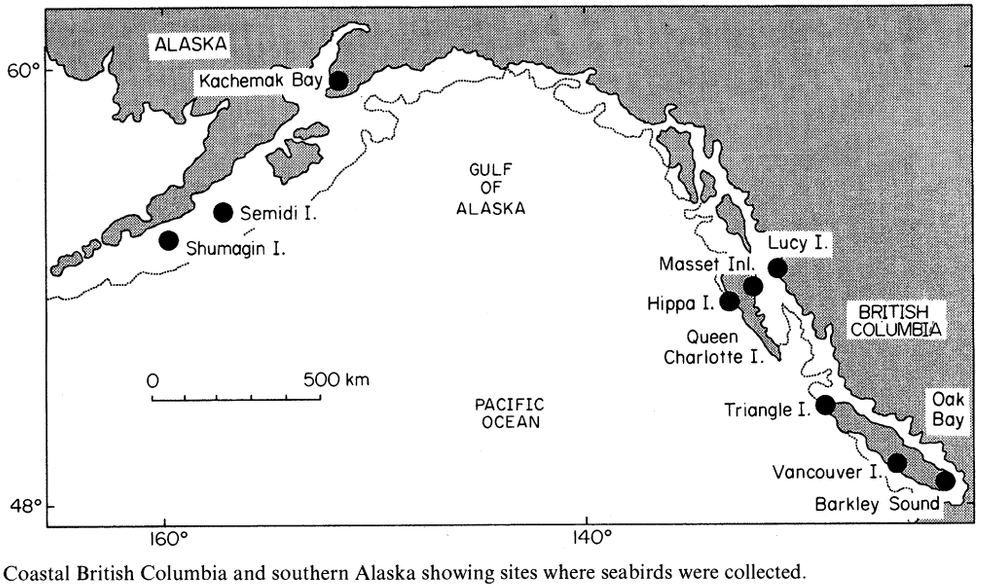

Fig. 1. Coastal British Columbia and southern Alaska showing sites where seabirds were collected.

NORTHERN GULF OF ALASKA

The Semidi and Shumagin islands (Fig. 1) support about 2·8 million breeding marine birds (Sowls, Hatch & Lensink 1978). Pectoral muscle tissue was obtained here from the following species during the breeding season 1990: six crested auklets *Aethia cristatella* (Pallas), seven parakeet auklets *Aethia psittacula* (Pallas), four ancient murrelets, four horned puffins *Fratercula corniculata* (Naumann), five tufted puffins, three rhinoceros auklets, seven Cassin's auklets, four pigeon guillemots, six common murres *Uria aalge* (Pontoppildan), five Leach's storm-petrels, one fork-tailed storm-petrel, six black-legged kittiwakes *Rissa tridactyla* (L.), five glaucous-winged gulls *Larus glaucescens* (Naumann), three mew gulls *Larus canus* (L.), five northern fulmars, four pelagic cormorants *Phalacrocorax pelagicus* (Pallas), and one double-crested cormorant *Phalacrocorax auritus* (Lesson). In addition, muscle tissue was obtained from six Kittlitz's murrelets *Brachyramphus brevirostris* (Vigors) and 10 marbled murrelets collected in Kachemak Bay (Fig. 1). Seabird tissue was also obtained by salvaging material from other studies. For example, 537 seabirds comprising 16 species had been collected by shooting in the Alaska study area, May–June 1990, in a study to assess the ingestion of plastic particles by seabirds. Prey were obtained in the region from seabird stomachs' and by use of variable-size mesh gill nets, and hook and line fishing.

ISOTOPIC ANALYSES

Muscle samples were freeze-dried and powdered using an analytical mill. Bone collagen was extracted as a gelatin according to the methods of Chisholm *et al.* (1983) and then freeze-dried. Lipids were extracted from all tissues using a Soxhlet apparatus with chloroform solvent. Samples for $^{15}N/^{14}N$ analysis were converted to ammonia by Kjeldahl reaction and then to N_2 gas using LiBrOH (Porter & O'Dean 1977). Samples for $^{13}C/^{12}C$ analysis were loaded into Pyrex tubes with 1 g of wire-form CuO and silver foil, sealed under vacuum and combusted at 550°C for at least 6 h. This technique gave similar results to that using Vycor tubes and higher temperature combustion (Swerhone *et al.* 1991). Carbon dioxide and nitrogen gas was analysed using a VG-SIRA 12 and a VG Micromass 602E mass spectrometer, respectively. Stable-isotope concentrations were expressed in δ notation as parts per thousand according to the following:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000 \qquad \text{eqn 1}$$

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. Several hundred replications of a glycine and wheat grain standard indicated a combined measurement error of ± 0.3‰ for nitrogen and ± 0.1‰ for carbon.

ISOTOPIC MODELS

The abundance of stable isotopes in various biochemical components of foods fractionate or change when incorporated into consumer tissues according to the relationship:

$$D_t = D_d + \Delta_{dt} \qquad \text{eqn 2}$$

where D_t is the isotopic abundance in the consumer tissue, D_d the isotopic abundance in the diet, and Δ_{dt} the isotopic fractionation factor between diet and tissue. Once Δ_{dt} is known for a particular trophic relationship, the isotopic signature of the average diet can be inferred from the isotopic abundance measurement of the consumer tissue (e.g. Tieszen *et al.* 1983).

For the simple situation involving two prey that are segregated trophically, an estimate of the relative contributions of each to the diet of a consumer may be estimated according to the following relationship:

$$P_a = D_t - D_b / D_b - D_a \qquad \text{eqn 3}$$

where P_a is the proportion of the diet derived from source a, D_t the isotopic value of the consumer tissue measured, and D_b and D_a are the consumer tissue isotopic values corresponding to exclusive diets of type a and b, respectively. We used this method to estimate the relative contributions of zooplanktivorous fish and euphausiids to seabird diets simplistically assumed to compromise only these two trophic levels.

In marine systems where particulate organic matter (POM) is assumed to be the first trophic level (TL 1), and where the isotopic enrichment factor between trophic levels (ΔTL) is known, the trophic level of a consumer ($TL_{consumer}$) in that food web may be estimated according to the relationship:

$$TL_{consumer} = 1 + (D_{consumer} - D_{POM})/\Delta TL \qquad \text{eqn 4}$$

where $D_{consumer}$ is the isotopic signature of the consumer and D_{POM} is that of POM.

Results

BARKLEY SOUND

Components of the Barkley Sound food web were segregated by their isotopic concentrations (MANOVA: Wilke's Lambda $F_{26,58} = 86{\cdot}1$, $P < 0{\cdot}0001$). Stable-N isotope values ranged from $6{\cdot}8 \pm 0{\cdot}1$‰ in POM to $14{\cdot}4 \pm 0{\cdot}2$‰ for smelts *Thaleichthys pacificus* (Richardson, 1836) and a general pattern of isotopic enrichment from lower to higher trophic positions was

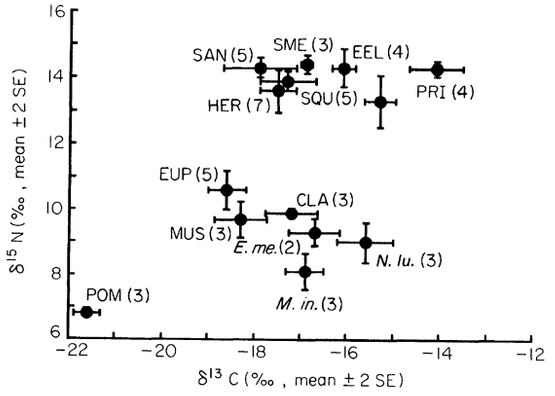

Fig. 2. Stable carbon and nitrogen isotope concentrations in components of the Barkley Sound food web. POM, particulate organic matter; EUP, euphausiids; MUS, mussel; CLA, clams; *E. me., Egregia menziesii* (kelp); *M. in., Macrocystis integrifolia* (kelp); *N. lu., Nereocystis luetkena* (kelp); SAN, sandlance; HER, herring; SME, smelt; SQU, squid; SUR, surfperch; PRI, prickleback; see Appendix 1.

evident (Fig. 2, Appendix 1). Stable-C isotope values were similarly the least enriched for POM ($-21{\cdot}6 \pm 0{\cdot}2$‰) and the most enriched for the benthic black prickleback *Xiphister atropurpureus* (Kittlitz, 1858) ($-14{\cdot}1 \pm 0{\cdot}5$‰). After a large fractionation between POM and heterotrophs, a consistent pattern of trophic enrichment in $\delta^{13}C$ was not obvious in this food web (Fig. 2).

The mean $\delta^{15}N$ value for planktivorous fish and squid (*Loligo opalescens*) of $14{\cdot}0 \pm 0{\cdot}7$‰ contrasted with that of $10{\cdot}6 \pm 0{\cdot}6$‰ for euphausiids (*Euphausia* sp.; Tukey's test, $P < 0{\cdot}05$). Making the assumption of a single trophic level separating fish and euphausiids, these isotopic data suggest a mean $\delta^{15}N$ trophic enrichment factor close to $+3{\cdot}4$‰.

We predicted the relative contributions of fish and euphausiids to the diets of seabirds in this area by applying $\delta^{15}N$ tissue isotopic fractionation values of $+2{\cdot}4$ and $+3{\cdot}9$‰ appropriate for adult seabird muscle and bone (Mizutani, Kabaya & Wada 1991), respectively, and making the assumption that the seabirds sampled fed only on these dietary options (Table 1). Thus, seabirds feeding exclusively on planktivorous fish or squid are expected to have muscle and collagen $\delta^{15}N$ values close to 16·4 and 17·9‰, respectively, and those feeding exclusively on euphausiids, 13·0 and 14·5‰, respectively.

Overall, species had a significant effect on the distribution of both isotopes in the seabird sample (MANOVA: Wilke's Lambda $F_{10,76} = 8{\cdot}6$, $P < 0{\cdot}0001$; Fig. 3, Table 1) reflecting differential residence of seabird species at different trophic levels. Cassin's auklet showed the lowest $\delta^{15}N$ values corresponding approximately to a 60% dietary contribution of euphausiids, whereas pigeon guillemot was the most enriched species indicating an exclusive diet of fish. Tufted puffins, ancient murrelets, marbled murrelets and rhinoceros auklets assumed intermediate values reflecting mixed diets of fish and invertebrates.

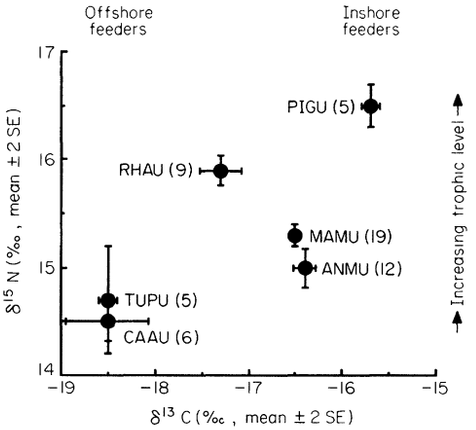

Fig. 3. Stable carbon and nitrogen isotope concentrations in pectoral muscle of seabirds collected from the west coast of Vancouver Island. Sample sizes given in parentheses. Species codes according to Tables 1 and 2.

Table 1. Stable-carbon and nitrogen isotope concentrations (mean ± SD‰) of lipid-extracted pectoral muscle tissues of seabirds from British Columbia and results of one-way ANOVA tests for differences among species for each isotope. Predictions of the relative euphausiid contributions to seabird diets are according to a $\delta^{15}N$ model of the marine food web of Barkley Sound

Spp.*	Location	*n*	$\delta^{13}C$†	$\delta^{15}N$	Mean % euphausiids
CAAU	Barkley Sound	6	$-18{\cdot}5 \pm 0{\cdot}5^{a}$	$14{\cdot}5 \pm 0{\cdot}2^{a}$	56
TUPU	Triangle Island	5	$-18{\cdot}5 \pm 0{\cdot}1^{ab}$	$14{\cdot}7 \pm 0{\cdot}5^{ab}$	50
ANMU	Oak Bay	12	$-16{\cdot}4 \pm 0{\cdot}2^{bc}$	$15{\cdot}0 \pm 0{\cdot}3^{b}$	41
MAMU	Barkley Sound	19	$-16{\cdot}5 \pm 0{\cdot}1^{cd}$	$15{\cdot}3 \pm 0{\cdot}2^{b}$	32
RHAU	Barkley Sound	9	$-17{\cdot}3 \pm 0{\cdot}3^{da}$	$15{\cdot}9 \pm 0{\cdot}2^{c}$	15
PIGU	Barkley Sound	5	$-15{\cdot}7 \pm 0{\cdot}1^{ec}$	$16{\cdot}5 \pm 0{\cdot}2^{d}$	<0
ANOVA			$F_{5,44} = 31{\cdot}7$, $P < 0{\cdot}0001$	$F_{5,44} = 37{\cdot}0$, $P < 0{\cdot}0001$	

*CAAU, Cassin's auklet; TUPU, tufted puffin; ANMU, ancient murrelet; MAMU, marbled murrelet; RHAU, rhinoceros auklet; PIGU, pigeon guillemot.

†Superscripts having at least one letter in common indicate no significant difference between samples (Tukey's multiple comparison test $P > 0{\cdot}05$).

Table 2. Stable nitrogen isotope concentrations (mean ± SD‰) of muscle and bone tissues of seabirds from the Queen Charlotte Islands and Hecate Strait region of the BC coast and predictions of the relative contributions of euphausiids to diets based on the Barkley Sound food-web model

Spp.*	Location	*n*	Collagen δ^{15}N†	Mean % euphausiid	Muscle δ^{15}N	Mean % euphausiid
SUSC	Hecate St.	5	$11{\cdot}8 \pm 1{\cdot}0^{a}$	NA	—	—
WWSC	Hecate St.	5	$12{\cdot}2 \pm 0{\cdot}4^{a}$	NA	—	—
SOSH	Hecate St.	4	$15{\cdot}8 \pm 0{\cdot}4^{bc}$	62	$11{\cdot}7 \pm 0{\cdot}9^{a}$	>100
CAAU	Hippa I.	6	$16{\cdot}4 \pm 0{\cdot}2^{cd}$	44	$12{\cdot}3 \pm 0{\cdot}5^{ab}$	>100
LESP	Hippa I.	6	$17{\cdot}1 \pm 0{\cdot}3^{cd}$	23	$13{\cdot}5 \pm 0{\cdot}9^{b}$	85
COMU	Masset Inlet	6	$17{\cdot}3 \pm 0{\cdot}8^{cd}$	18	$15{\cdot}5 \pm 1{\cdot}3^{c}$	26
RHAU	Lucy I.	6	$17{\cdot}6 \pm 0{\cdot}4^{d}$	9	$15{\cdot}4 \pm 0{\cdot}5^{c}$	29
FTSP	Hippa I.	6	$17{\cdot}9 \pm 0{\cdot}4^{d}$	0	$15{\cdot}9 \pm 0{\cdot}4^{c}$	14
ANOVA			$F_{7,31} = 46{\cdot}9$ $P < 0{\cdot}0001$		$F_{5,24} = 21{\cdot}5$ $P < 0{\cdot}0001$	

*SUSC, surf scoter; WWSC, white-winged scoter; SOSH, sooty shearwater; LESP, leach's storm-petrel; COMU, common murre; FTSP, fork-tailed storm-petrel. See Table 1 for other abbreviations.

†See note to Table 1.

QUEEN CHARLOTTE ISLANDS AND HECATE STRAIT

Bone collagen from surf and white-winged scoters showed the least, and from rhinoceros auklets and fork-tailed storm-petrels the greatest δ^{15}N enrichment (Table 2, Fig. 4). Scoter muscle tissue was unavailable for analysis, but for this tissue, species ranked similarly in δ^{15}N compared to their collagen values with sooty shearwaters having the least and fork-tailed storm-petrels the greatest δ^{15}N concentrations. Similar to the Barkley Sound food web, we established the relative contributions of euphausiids and fish to the diets of these seabirds (Table 2) assuming similar isotopic abundances in prey from the two areas. We excluded scoters from this analysis since their diets are known to consist primarily of bivalves (see below). The >100% dietary contributions predicted for shearwaters and Cassin's auklets suggest that prey with lower than expected mean δ^{15}N were taken by these seabirds.

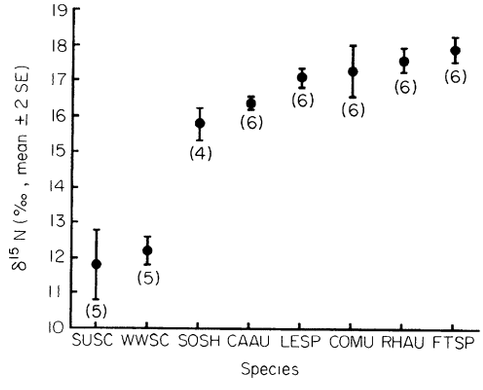

Fig. 4. Stable-nitrogen isotope values for pectoral muscle of seabirds from the Queen Charlotte Islands and Hecate Strait. Sample sizes indicated below error bars. Species codes according to Tables 1 and 2.

OVERALL BRITISH COLUMBIA TROPHIC PATTERN

Combining the results of δ^{15}N analyses for marine food webs in both regions of coastal British Columbia, we constructed a trophic ladder to illustrate possible trophic relationships (Fig. 5). We felt justified in grouping the British Columbia samples and in analysing separately the Gulf of Alaska samples since major changes in oceanography, production regimes and dominant avian communities occur between coastal British Columbia and the northern Gulf of Alaska (Gould & Piatt 1993). Species were deliberately placed in trophic sequence and not in taxonomic order. The gradual enrichment in δ^{15}N between species suggests that the concept of trophic levels, with discrete jumps in trophic position along a food chain, is inappropriate. Co-existing species appear to feed along a continuum of trophic levels, and as the data for Cassin's auklets and rhinoceros auklets indicate, these positions may vary over short geographic distances or between different years.

NORTHERN GULF OF ALASKA

Seabirds from the Shumagin and Semidi islands differed significantly in their muscle tissue δ^{15}N values (Fig. 6), but individual species segregation was generally poor due, in part, to small sample sizes. Least auklets showed the least and double-crested cormorants the greatest δ^{15}N enrichment. As with the British Columbia food web, there was a continuous level of ^{15}N enrichment among the 19 co-existing species of seabirds. Predatory fish occupied similar positions to large, fish-feeding seabirds. Sandlance from the Gulf of Alaska were considerably less enriched in ^{15}N compared to those from Barkley Sound and further sampling is required to determine if this pattern

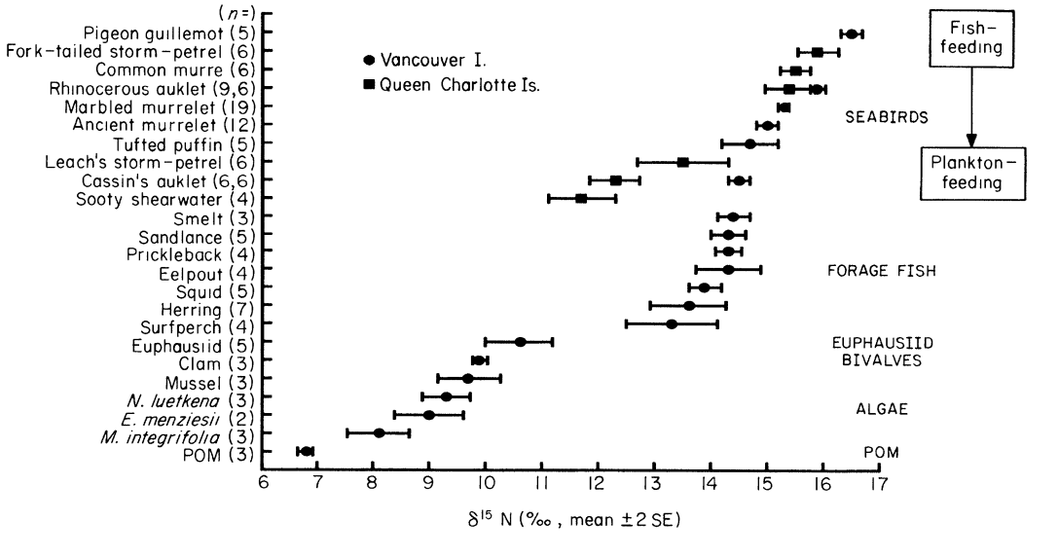

Fig. 5. Stable-nitrogen isotope concentrations in various components of the marine food web in British Columbia. Sample sizes given in parentheses after names of species.

results from dietary differences between these populations.

We were unable to establish a trophic model analogous to that determined for the Barrow Strait–Lancaster Sound system (Hobson & Welch 1992) because the Gulf marine food web is not in a well-confined region and was not sampled extensively (Appendix 2). However, stable-N isotope values were obtained for samples of euphausiids and capelin, and the trophic level of these prey items, together with several others, were estimated previously by Sanger (1987a) in the study region using conventional dietary techniques. Sanger calculated average seabird trophic levels based on published values for prey and an Index of Relative Importance (after Pinkas, Oliphant & Iverson 1971). Combining the isotopic data with Sanger's trophic-level estimates for seabird prey items allowed seabird trophic estimates to be derived from the isotopic data. Sanger's estimates were based on a rigorous approach to seabird stomach data and were the only existing TL information previously available for the Gulf of Alaska. For example, the mean euphausiid isotope value of 11·2‰ corresponded to a trophic level of 2·5, and the mean capelin isotope value of 13·3‰ to a trophic level of 3·2. This suggests a trophic enrichment value of about 3·0‰ between these components of the marine food web, an estimate remarkably close to that found for other marine systems (Schoeninger & DeNiro 1984).

Using the relationship that an adult seabird feeding exclusively on euphausiids would occupy TL 3·5 and have a muscle δ^{15}N value of 13·6‰ (i.e. 11·2 plus a

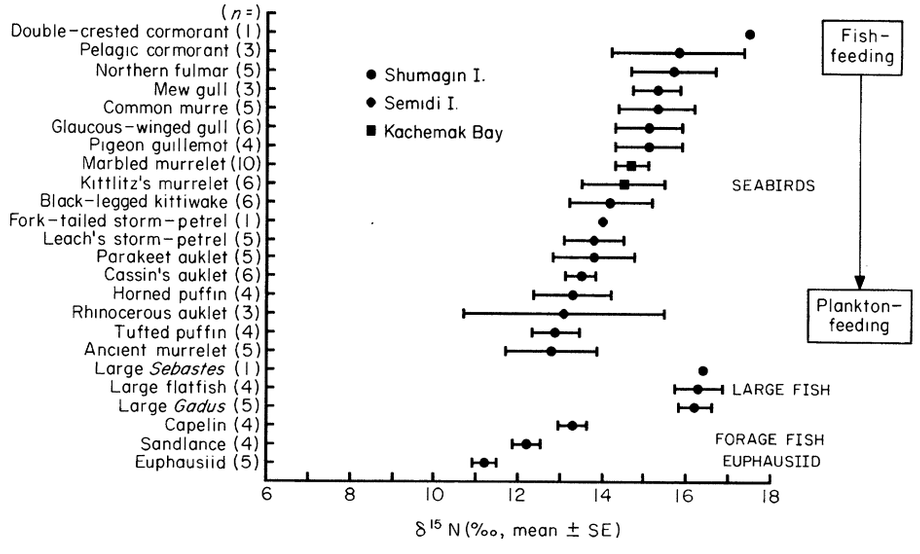

Fig. 6. Stable nitrogen isotope concentrations in the pectoral muscle of tissue of seabirds and some seabird prey from the northern Gulf of Alaska. Sample sizes given in parentheses after species names.

diet-muscle fractionation factor of +2·4‰), we calculated the trophic level of other Alaskan seabirds according to:

$$TL_A = TL_{euph} + (\delta^{15}N_A - \delta^{15}N_{euph})/3 \quad \text{eqn 5}$$

where TL_A is the trophic level of a bird with a hypothetical diet 'A', TL_{euph} is the trophic level of a bird consuming euphausiids only, $\delta^{15}N_A$ is the nitrogen isotope concentration of the muscle tissue of that bird and $\delta^{15}N_{euph}$ is the nitrogen isotope value of the muscle tissue of a bird feeding exclusively on euphausiids. Thus, equation 5 becomes:

$$TL_A = 3{\cdot}5 + (\delta^{15}N_A - 13{\cdot}6)/3. \quad \text{eqn 6}$$

This allowed the direct comparison of TL estimates for our Gulf of Alaska samples with those of Sanger (1987a). This comparison provided a means of contrasting TL estimates using isotopic and conventional techniques. In general, inferences from the two techniques were in reasonable agreement (Table 3). Notable differences were found for horned and tufted puffins, rhinoceros auklets, ancient murrelets and northern fulmars, which had lower TLs using the isotope approach.

Previous isotopic investigations suggested that stable-C isotope values may be useful in tracing pelagic vs. benthic food webs (McConnaughey & McRoy 1979; Hobson 1993). In order to investigate the possibility that muscle $\delta^{13}C$ values of Alaska seabirds might provide information on seabird foraging location (e.g. inshore vs. offshore), we measured also $\delta^{13}C$ in a subsample of 11 species (Fig. 7, Table 3). For those cases where both $\delta^{13}C$ and $\delta^{15}N$ values were available, sig-

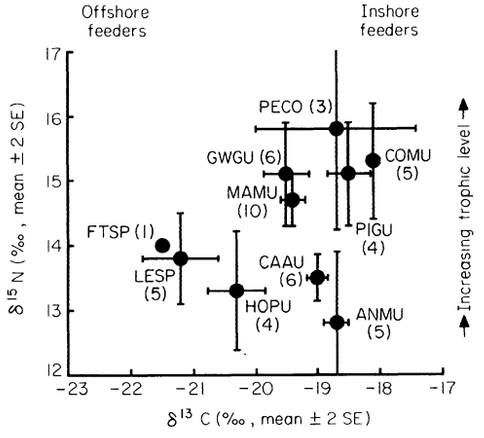

Fig. 7. Stable carbon and nitrogen isotope concentrations in pectoral muscle tissue of Semidi and Shumagin Islands seabirds. Sample sizes are given in parentheses. Species codes are according to Tables 1–3.

Table 3. Stable-carbon and nitrogen isotope values (mean ± SD‰ of pectoral muscle tissue of seabirds collected in the vicinity of the Semidi and Shumagin Islands, Alaska, during July 1990 and their calculated mean trophic levels based on $\delta^{15}N$ results

Spp.*	Location	*n*	$\delta^{13}C$‡	$\delta^{15}N$	Trophic level: This study	Trophic level: Sanger (1987a,b)	Trophic level: diff.
CRAU	Shumagin Islands	6		$12{\cdot}5 \pm 0{\cdot}7^{a}$	3·1		
ANMU	Shumagin Islands	5	$-18{\cdot}7 \pm 0{\cdot}2^{bc}$	$12{\cdot}8 \pm 0{\cdot}6^{a}$	3·2	3·7	−0·5
TUPU	Shumagin Islands	4		$12{\cdot}9 \pm 0{\cdot}5$	3·3	4·1	−0·8
RHAU	Semidi Islands	2		$13{\cdot}1 \pm 1{\cdot}2$	3·3	4·1	−0·8
HOPU	Shumagin Islands	4	$-20{\cdot}3 \pm 0{\cdot}4^{a}$	$13{\cdot}3 \pm 0{\cdot}8^{a}$	3·4	4·0	−0·6
CAAU	Shumagin Islands	6	$-19{\cdot}0 \pm 0{\cdot}2^{bc}$	$13{\cdot}5 \pm 0{\cdot}4^{ab}$	3·5	3·2	+0·3
PAAU	Shumagin Islands	5		$13{\cdot}8 \pm 0{\cdot}4^{ab}$	3·6		
LESP	Semidi Islands	5	$-21{\cdot}2 \pm 0{\cdot}6^{a}$	$13{\cdot}8 \pm 0{\cdot}7^{ab}$	3·6		
FTSP	Semidi Islands	1		14·0	3·6	3·8	−0·2
BLKI	Shumagin Islands	6		$14{\cdot}2 \pm 1{\cdot}1^{ab}$	3·7	4·0	−0·3
KIMU	Kachemak Bay	6		$14{\cdot}5 \pm 1{\cdot}1^{bc}$	3·8	3·8	0
MAMU	Kachemak Bay	10	$-19{\cdot}4 \pm 0{\cdot}3^{b}$	$14{\cdot}7 \pm 0{\cdot}6^{bc}$	3·9	3·8	+0·1
PIGU	Shumagin Islands	4	$-18{\cdot}5 \pm 0{\cdot}3^{c}$	$15{\cdot}1 \pm 0{\cdot}7^{bc}$	4·0	4·1	−0·1
GWGU	Shumagin Islands	6	$-19{\cdot}5 \pm 0{\cdot}4^{b}$	$15{\cdot}1 \pm 0{\cdot}9^{bc}$	4·0	4·0	0
COMU	Shumagin Islands	5	$-18{\cdot}1 \pm 0{\cdot}1^{c}$	$15{\cdot}3 \pm 0{\cdot}9^{bc}$	4·1	4·1	0
MEGU	Shumagin Islands	3		$15{\cdot}3 \pm 0{\cdot}4^{bc}$	4·1		
NOFU	Shumagin Islands	5		$15{\cdot}7 \pm 1{\cdot}0^{bc}$	4·2	5·0	−0·8
PECO	Shumagin Islands	3	$-18{\cdot}7 \pm 0{\cdot}9^{bc}$	$15{\cdot}8 \pm 1{\cdot}1^{bc}$	4·2	3·9	+0·3
DCCO	Shumagin Islands	1		17·5	4·8		
ANOVA†			$F_{7,41} = 23{\cdot}7$ $P < 0{\cdot}001$	$F_{15,68} = 6{\cdot}9$ $P < 0{\cdot}001$			

*CRAU crested auklet; HOPU, horned puffin; BLKI, black-legged kittiwake; NOFU, northern fulmar; PAAU, parakeet auklet; KIMU, Kittlitz's murrelet; GWGU, glaucous-winged gull; MEGU, mew gull; PECO, pelagic cormorant; DCCO, double-crested cormorant. See Tables 1 and 2 for other abbreviations.

†Only samples with $n > 2$ included in ANOVA.

‡Superscripts having at least one letter in common indicate no significant difference between samples (Tukey's multiple comparison test $P > 0{\cdot}05$).

nificant differences among species were found (MANOVA, Wilke's Lambda $F_{18,61} = 7{\cdot}7$, $P < 0{\cdot}001$). Carbon-13 segregated species approximately into two groups with Leach's and fork-tailed storm-petrels, and horned puffins occupying a $\delta^{13}C$ range of $-20{\cdot}3$ to $-21{\cdot}8$‰, and the remaining seven species occupying a range of $-17{\cdot}6$ to $-19{\cdot}7$‰ (Fig. 6).

Discussion

USE OF STABLE ISOTOPES IN TROPHIC STUDIES

Winter diet is an important component of seabird ecology that has been poorly documented. In fact, our conceptions of seabird diet have been heavily biased toward the diets of *breeding* seabirds and these diets have, in turn, been biased toward upper trophic-level prey estimates (Hobson 1993). The transfer of seabirds to different, especially lower, trophic positions within and between seasons, and the determination of factors influencing these shifts presents an important area of seabird research. It is largely unknown, for example, what the roles of prey availability, opportunism, nutrition and the constraints of attachment to breeding site have on the ability of seabirds to switch from specialist to generalist diets. Recently, Ainley, Ribic & Fraser (1992) suggested that the availability of prey, and the means and rate by which prey become available, rather than the type of prey, has a strong bearing on the structure of pelagic seabird faunas. The stable-isotope technique, with its ability to determine time-integrated trophic information, will undoubtedly make a strong contribution to answering these questions in future seabird dietary studies.

Our isotopic survey of marine birds and their prey has demonstrated that ^{15}N enrichment can be used to infer relative and sometimes absolute trophic positions in the northeast Pacific. The approximate $\delta^{15}N$ trophic enrichments of $+3{\cdot}4$‰ in Barkley Sound and $+3{\cdot}0$‰ for the Alaskan food web are similar to estimates of 3–5‰ reported for other marine systems (Schoeninger & DeNiro 1984; Wada *et al.* 1987; Sholto-Douglas *et al.* 1992; Hobson & Welch 1992). Depending on the tissue analysed, TL estimates based on stable-nitrogen isotope measurements represent the integration of dietary information over differing time periods. Hobson & Clark (1992) provide the only estimates for isotopic turnover in birds and suggest that isotopic analyses of muscle tissue represent an integration over 3–4 weeks. Dietary information derived from the isotopic analysis of liver integrates diet over a week and bone collagen over the lifetime of birds. The isotopic measurement of several tissues from the same individual will thus yield information of changes in diet through time (Hobson & Sealy 1991; Hobson 1993). Recent investigations using stable isotope measurements of feathers, blood and eggshells (Mizutani *et al.* 1991; Schaffner & Swart 1991; Hobson & Clark 1993) also yield trophic information over different temporal periods. However, further studies are required to better refine diet-tissue fractionation factors for seabirds and to determine sources of isotopic variation within wild populations (Hobson 1993).

Rather than being a useful indicator of trophic level *per se*, ^{13}C may be more suitable for determining foraging locations of seabirds or their links with benthic food webs in the north-east Pacific. Off the west coast of Vancouver Island, pigeon guillemots showed the greatest $\delta^{13}C$ enrichment, a pattern consistent with their inshore benthic feeding preference where they may have consumed carbon of detrital origin (McConnaughey & McRoy 1979; Dunton *et al.* 1989). Other species showing enriched $\delta^{13}C$ values in that sample were ancient and marbled murrelets, both of which frequent inshore locations. In contrast, the lower $\delta^{13}C$ values for Cassin's auklets and tufted puffins were consistent with their more pelagic feeding, as well as with their lower trophic-level diets (see below). Common murres, pelagic cormorants and pigeon guillemots showed the most enriched $\delta^{13}C$ values of those species examined from the Shumagin and Semidi islands, and this again is consistent with their inshore foraging. Leach's and fork-tailed storm-petrels, the most pelagic of the species examined, showed the most negative $\delta^{13}C$ values.

Stable-carbon isotope values of seabird prey organisms from Vancouver Island also show evidence of an inshore/offshore or benthic/pelagic gradient that would be expected from the above interpretations of seabird foraging distributions. Within the highest trophic feeding group, herring, squid, smelt and sandlance show the least ^{13}C enrichment compared to more benthic or inshore foragers like surfperch and prickleback. Further isotopic investigations in the northeast Pacific and elsewhere are required to establish how patterns of $\delta^{13}C$ abundance in seabird tissues are linked with trophic level and preference for pelagic or inshore feeding, as several different factors may explain the $\delta^{13}C$ gradient shown in seabirds and their prey (McConnaughey & McRoy 1979; Dunton *et al.* 1989; Hobson 1993).

Despite the tremendous potential of the isotope technique in seabird dietary studies, it is important to stress the need to establish isotopic inventories of prey in the appropriate study areas. Many seabirds are also migratory and may move seasonally among ocean systems of differing carbon and nitrogen isotopic signature (e.g. Rau, Takahashi & Des Marais 1989; Saino & Hattori 1985). Such considerations are particularly relevant to studies investigating isotope values in seabird tissues with long rates of carbon and nitrogen turnover (e.g. collagen).

COMPARISON OF CONVENTIONAL AND STABLE-ISOTOPE DIETARY INFORMATION

Comparisons between dietary information based on the stable-isotope approach and conventional dietary

approaches were most readily made for Gulf of Alaska seabirds where the seabird trophic estimates of Sanger (1987a) were available. We were also able to make comparisons between isotopic results and other published information on the diets of seabirds in our study area.

Based on his conventional TL model, Sanger (1987a) noted that, on average, most seabirds in the Gulf of Alaska feed as secondary carnivores. With the assimilation of much additional data this result differed from a previous position that most sub-Arctic Pacific seabirds fed as second- and third-order carnivores (Ainley & Sanger 1979). Our isotopic data from the Semidi Islands generally suggested lower trophic positions for species compared to Sanger's estimates. In the 13 cases where comparisons could be made, the isotope estimate was less than Sanger's value in seven cases, the same in three cases and higher in only three cases (mean difference — 0·2TL). Thus, the isotope data confirm Sanger's (1987a) contention that seabirds rely more heavily on lower TLs than previously thought.

We expected good agreement between isotope and conventional techniques for seabirds with relatively simple or monotonous diets and, during the breeding season, this was the case for true planktivores such as Cassin's and crested auklets (e.g. Payne 1965; Manuwal 1974). Hobson & Montevecchi (1991) similarly found that the planktivorous dovekie *Alle alle* (L.) showed the lowest δ^{15}N values of all seabirds they examined in the North Atlantic.

Amongst the five planktivorous auklets inhabiting the North Pacific, the parakeet auklet has the most general diet consisting of zooplankton, invertebrates and fish (Bedard 1969; Hunt, Burgeson & Sanger 1981). Jellyfish are also an important component in the diet but these are expected to disappear fast in stomachs (Harrison 1990) and so are likely to be underestimated by conventional approaches. Our estimate of TL 3·6 for parakeet auklets is consistent with a mixed diet intermediate between euphausiids and fish, squid or jellyfish.

As with the true planktivores, agreement between stable-isotope and conventional approaches is expected also for piscivorous species. In general, this was the case for common murres, pigeon guillemots, glaucous-winged gulls and cormorants (e.g. Bedard 1969; Krasnow & Sanger 1986; Sanger 1987a). In the north Atlantic, the diet of common murres consists primarily of fish in all seasons (reviewed by Bradstreet & Brown 1985). The species' diet in the Gulf of Alaska is less known, but recent studies indicate that fish are also the principal prey, particularly capelin, juvenile walleye pollock and sandlance (reviewed by Vermeer, Sealy & Sanger 1987).

Greater discrepancies between conventional and isotopic information are likely for species with mixed diets. Since components of higher trophic-level prey are retained longer in gizzards (e.g. squid beaks) compared to soft-bodied prey from lower trophic levels, many stomach analyses that include items from gizzards are expected to overestimate seabird trophic position relative to the isotopic approach. This was observed when comparing isotopic trophic estimates with Sanger's (1987a) estimates for the following species: ancient murrelet, tufted puffin, horned puffin, rhinoceros auklet, black-legged kittiwake and northern fulmar.

Ancient murrelets wintering off southwest Vancouver Island in 1979 had diets consisting of about 40% prey from the euphausiid TL (Gaston, Carter & Sealy 1993). This is consistent with the isotopic analysis of bone collagen of birds from Reef Island that suggested a year-round dietary average of about 32% euphausiids, the rest of the diet being either fish or squid (see also Gaston 1992). However, the Alaska isotope data show that, in some areas or years, this species may rely almost exclusively on invertebrates, likely euphausiids. Sanger (1987a) similarly noted that euphausiids were the single most important prey item for ancient murrelets in the Gulf of Alaska.

Isotopic data for tufted puffins from Triangle Island suggest that prey at the TL of euphausiids made up about 50% of the summer diet. Alaskan birds showed even lower δ^{15}N values corresponding possibly to an exclusive diet of invertebrates. Throughout their range tufted puffins are known to feed their young almost exclusively fish and occasionally squid (Vermeer 1979; Wehle 1982; Baird 1991), but Baird (1987, 1991) noted that non-breeding tufted puffins in Alaska ate more invertebrate prey than breeders.

Based on the observation that the stomachs of 43 northern fulmars contained primarily unidentified squid, Sanger (1987a) assigned a trophic level of 5·0 to this species in the Gulf of Alaska, the highest of all species he examined and substantially higher than our value of 4·2 for this species based on isotopic analyses. The presence of squid beaks in the stomachs of fulmars presents problems of interpretation for conventional dietary studies and we suggest that fulmars in the Gulf of Alaska consume more lower trophic-level prey than previously thought (reviewed by Hatch 1993).

The above comparisons demonstrate how important new information on the ecology of seabirds can be obtained by using both isotopic and conventional dietary techniques. Thus, while the stable-nitrogen isotope approach provides a more powerful means of establishing average seabird trophic position and how these may change through time, details of prey choice obtained through conventional approaches are often essential to the interpretation of isotopic results and vice versa. Isotopically different values between individuals also provide unequivocal evidence for dietary segregation and indicate an important direction for further dietary study.

TROPHIC COMPARISONS OF TAXONOMICALLY RELATED SPECIES

The stable-isotope approach can provide further insight into trophic segregation between closely related species. The two *Brachyramphus* murrelets are endemic to the north Pacific Ocean and overlap in breeding range in Alaska (AOU 1983). Both species generally forage in inshore areas (Sealy 1975; Sowls *et al.* 1978; Vermeer *et al.* 1987; Sanger 1987b) where they feed on both planktivorous fish and invertebrates. In Alaskan waters, marbled murrelets feed mostly on capelin and Pacific sandlance, and in British Columbia on Pacific sandlance and Pacific herring (Vermeer *et al.* 1987). In Barkley Sound, where our sample was derived, marbled murrelets consumed primarily Pacific herring and sandlance (Carter 1984), a result consistent with the isotopic prediction of about 85% planktivorous fish. Assuming that murrelets from Alaska fed exclusively between euphausiid and planktivorous fish endpoints, the isotopic data suggests a mean euphausiid contribution of 44% for Kittlitz's murrelets and 31% for marbled murrelets. Sanger obtained almost exactly the same TL estimates for these species in the Gulf of Alaska. Further investigations to determine if Kittlitz's murrelets depend more on lower-trophic level prey than marbled murrelets may be useful.

Throughout their range in the north Pacific, both white-winged and surf scoters feed primarily on bivalves (Glude 1967; Grosz & Yocom 1972; Vermeer 1981). Vermeer & Bourne (1984) found over 20 species of bivalves in the diets of these birds wintering off the B.C. coast, but crabs, shrimp and barnacles *Balanus glandula* (Cornwall, 1969) were also consumed in smaller amounts. The isotopic data for bone collagen of these scoters wintering in Hecate Strait support dietary inferences of lower trophic-level prey. Furthermore, mean dietary $\delta^{15}N$ values of 7·9 and 8·3‰ for surf scoters and white-winged scoters, respectively, suggest that some trophic segregation between these species occurs.

Fork-tailed and Leach's storm-petrels are small pelagic birds known to feed on small fishes and zooplankton (Ainley, Morrell & Lewis 1975; Watanuki 1985; Vermeer & Devito 1988). These closely related species are sympatric in the northern Pacific Ocean (AOU 1983). The stable-nitrogen isotope data for storm-petrels from Hippa Island indicates species differences in early spring diets. Leach's storm-petrels fed primarily on lower trophic-level invertebrate prey, whereas fork-tailed storm-petrels consumed primarily higher trophic-level prey at that time. Long-term diets were much more similar with both species showing increased use of higher trophic-level prey but, again, fork-tailed storm-petrels showed higher enrichments than Leach's storm-petrels. The myctophid *Stenobrachius leucopsarus* (Eigenmann & Eigenmann, 1890), a species occurring in storm-petrel diets, is known to feed on other fish as well as copepods and euphausiids (Hart 1973). Although we have not measured this myctophid isotopically, we suggest that fork-tailed storm-petrels consumed considerably more myctophids than Leach's storm-petrels and that this difference accounted for higher trophic estimates for fork-tailed storm-petrels.

In recent decades, the determination of ecological isolating mechanisms between members of seabird communities has received considerable attention (Ashmole & Ashmole 1967; Harrison, Hida & Seki 1983; Croxall & Prince 1987). The manner in which the resources of the marine environment are partitioned is one of several important factors that may contribute to ecological segregation in seabird communities and it is in this area of investigation that the stable-isotope approach offers an additional research tool. While similar isotopic values between species or individuals cannot be interpreted as evidence for similar diets, differences between these values do indicate different feeding patterns and provide evidence for trophic segregation. Together with conventional dietary approaches, stable-isotope analysis of seabird communities should thus become a routine method of investigating ecological isolating mechanisms and how these might change seasonally.

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Appendix 1

Stable carbon and nitrogen isotope concentrations (mean ± SD‰) in selected components of the Barkley Sound marine food web May–August 1990 and results of ANOVA and Tukey's tests for each isotope

Sample	*n*	$\delta^{15}N$*	$\delta^{13}C$
POM (particulate organic matter)	3	$6{\cdot}8 \pm 0{\cdot}1^{a}$	$-21{\cdot}6 \pm 0{\cdot}2^{a}$
Kelp			
Macrocystis integrifolia	3	$8{\cdot}1 \pm 0{\cdot}4^{a}$	$-16{\cdot}9 \pm 0{\cdot}3^{b}$
Nereocystis luetkena	3	$9{\cdot}3 \pm 0{\cdot}3^{bc}$	$-16{\cdot}7 \pm 0{\cdot}4^{b}$
Egregia menziesii	2	$9{\cdot}0 \pm 0{\cdot}3^{bc}$	$-15{\cdot}6 \pm 0{\cdot}3^{c}$
Invertebrates			
Mytilis californianus	3	$9{\cdot}7 \pm 0{\cdot}4^{cd}$	$-18{\cdot}3 \pm 0{\cdot}4^{d}$
Mya arenaria	3	$9{\cdot}9 \pm 0{\cdot}1^{cd}$	$-17{\cdot}2 \pm 0{\cdot}4^{b}$
Euphausia sp.	5	$10{\cdot}6 \pm 0{\cdot}6^{d}$	$-18{\cdot}6 \pm 0{\cdot}4^{d}$
Loligo opalescens	5	$13{\cdot}9 \pm 0{\cdot}3^{e}$	$-17{\cdot}3 \pm 0{\cdot}6^{b}$
Fish			
Ammodytes sp.	5	$14{\cdot}3 \pm 0{\cdot}3^{e}$	$-17{\cdot}9 \pm 0{\cdot}8^{d}$
Clupea harengus pallasi	7	$13{\cdot}6 \pm 0{\cdot}8^{e}$	$-17{\cdot}5 \pm 0{\cdot}5^{b}$
Thaleichthys pacificus	3	$14{\cdot}4 \pm 0{\cdot}2^{e}$	$-16{\cdot}9 \pm 0{\cdot}1^{b}$
Lycodopsis pacifica	4	$14{\cdot}3 \pm 0{\cdot}5^{e}$	$-16{\cdot}1 \pm 0{\cdot}4^{e}$
Cymatogaster aggregata	4	$13{\cdot}3 \pm 0{\cdot}7^{e}$	$-15{\cdot}3 \pm 0{\cdot}3^{e}$
Xiphister atropurpureus	4	$14{\cdot}3 \pm 0{\cdot}2^{e}$	$-14{\cdot}1 \pm 0{\cdot}5$
ANOVA		$F_{13,31} = 99{\cdot}8$	$F_{13,31} = 99{\cdot}8$
		$P < 0{\cdot}0001$	$P < 0{\cdot}0001$

*Results of Tukey's multiple comparison test indicated by superscript. Superscripts having at least one letter in common indicate no significant difference between samples ($P > 0{\cdot}05$).

Appendix 2

Stable-nitrogen isotope concentrations (mean ± SD‰) of food items obtained from the stomachs of seabirds and with fishing gear at the Shumagin Islands, Alaska, May–June 1990

Sample*	*n*	$\delta^{15}N$
Invertebrates		
Euphausiid spp.	5	$11{\cdot}2 \pm 0{\cdot}3$
Fish		
Ammodytes hexapterus	4	$12{\cdot}2 \pm 0{\cdot}3$
Mallotus villotus	4	$13{\cdot}3 \pm 0{\cdot}3$
Lepidopsetta bilineata	4	$16{\cdot}3 \pm 0{\cdot}5$
Gadus macrocephalus	5	$16{\cdot}2 \pm 0{\cdot}4$
Sebastes melanops	1	16·4
unidentified (MAMU)		13·9
(COMU)		14·4
(COMU)		13·3
(PECO)		14·8
(PECO)		13·4

*Parentheses refer to seabird species in which unidentified fish were found in stomachs. See Tables 1–3 for abbreviations.