Chapter 14
Using Isoscapes to Trace the Movements and Foraging Behavior of Top Predators in Oceanic Ecosystems

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14.1 Introduction

The inability to directly observe the long distant movements of marine predators and the vast extent of their pelagic habitat has hindered our understanding of their movements, distribution, and foraging behavior. Recently these challenges have spurred the development of new methods to examine animal movements remotely, including advancements in electronic tags (Holland et al. 1990; Stewart and DeLong 1995; Lutcavage et al. 1999; Biuw et al. 2007). Electronic tagging is generally limited to studying individual movements of a relatively small number of large individuals. However, the launch of extensive tagging campaigns (e.g., Block et al. 2005) and advancements in tag-to-tag communication could circumvent the

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difficulties of interpreting population-level movement patterns based on only a small number of individuals.

The stable isotope composition of animal tissues can provide intrinsic tags to study the foraging and migratory ecology of elusive or highly migratory species, such as top marine predators (Hobson 1999; Hobson et al. this volume). This method can be applied to track the movements of juvenile stages of marine vertebrates that are not amenable to current electronic tagging technologies. In addition, stable isotope analysis can provide retrospective information on the movement patterns and foraging ecology in both modern (Hobson et al. 1997; Burton and Koch 1999) and prehistoric marine predators (e.g., Burton et al. 2001; Newsome et al. 2007a, b). While foraging in specific environments, individuals acquire the isotopic composition of their local prey. By comparing the isotope composition of the animal to its local prey or the local environmental isotope composition (i.e., local primary producer isotopic composition), information can be gained on residency and movements patterns. In other words, an animal's isotopic composition can be used as a natural "tag" to track their movements through isotopically distinct habitats.

There are several requirements for applying this approach to study the movements and habitat use of top predators in the open ocean. First, the isotopic turnover rates for tissues of interest must be determined for each predator, because these rates provide a temporal framework in which to interpret predator stable isotope compositions. Turnover rates have been determined for carbon and nitrogen isotope ($\delta^{13}C$ and $\delta^{15}N$) values in different tissues for a variety of marine top predators, including seabirds, seals, penguins, tropical tuna, and sharks (Hobson et al. 1996; Bearhop et al. 2002; Kurle 2002; Cherel et al. 2005; Kim et al. 2008; Graham et al. in review). A second critical requirement is to construct maps of the geographical distribution of isotope values in the environment on temporal and spatial scales that are ecologically relevant to movements of the animal of interest. This is especially challenging for isotopic studies examining the movements of highly-mobile, marine predators because of their potentially vast foraging ranges. One approach has been to generate isotopic mapst (i.e., isoscapes) based either on sources that integrate marine production at the base of the food web (e.g., annually integrated phytoplankton, zooplankton, the organic matter in surface sediments), or control taxa at the same trophic level, but with known migratory and habitat preferences. Both approaches require intensive sampling to establish spatial and temporal isotopic patterns, and both necessitate assumptions about food web structure, animal physiology, and animal behavior that should be supported by independent datasets. Given these assumptions, however, if an individual has a similar isotopic value as the local isotopic baseline, then the predator is a resident, whereas if the individual and baseline isotopic values are distinctly different, the predator is an immigrant from another, isotopically distinct region.

14.1.1 Mechanisms That Shape the Isotopic Baseline

The carbon isotope compositions of open ocean consumers reflect those of algae at the base of the food web. At the most general level, higher $\delta^{13}C$ values are associated

with rapid growth rates whereas lower values are associated with slow growth rates (Goericke and Fry 1994; Popp et al. 1998). At relatively small scales within oceanic basins $\delta^{13}C$ values track productivity, with higher values in productive nearshore regions, such as upwelling zones, compared to less productive offshore regions. Because of the preferential uptake of ^{12}C by phytoplankton during photosynthesis, nutrient-driven phytoplankton blooms in upwelling zones increase the $\delta^{13}C$ value of aqueous CO_2 by a few per mil as they draw down its concentration. Low aqueous [CO_2] can itself lead to lower isotopic discrimination during photosynthesis. In offshore regions, especially equatorial regions where the water column is strongly stratified, low nutrient levels lead to low growth rates, so [CO_2] is less of a factor and $\delta^{13}C$ values in primary producers are lower. The gradient in $\delta^{13}C$ values between primary producers in nearshore versus offshore pelagic ecosystems has other, additive causes, including the effects of phytoplankton size and geometry, and taxonomic differences on isotopic fractionation (Bidigare et al. 1997; Pancost et al. 1997; Popp et al. 1998; Rau et al. 2001). Finally, macroscopic marine plants, such as kelp and sea grass, have substantially higher $\delta^{13}C$ values than phytoplankton. Using data compiled from the literature, Clementz and Koch (2001) showed that major marine and marginal marine habitat types have distinct $\delta^{13}C$ values (i.e., seagrass habitat > kelp forest > nearshore marine > offshore marine).

The $\delta^{13}C$ values of primary producers also vary predictably among ocean basins. High-latitude pelagic ecosystems typically have much lower $\delta^{13}C$ values than pelagic ecosystems at lower latitudes. In colder regions, aqueous [CO_2] is high due to seasonally low photosynthetic rates caused by light and trace metal limitation, vertical mixing of a weakly stratified water column, and the greater solubility of CO_2. Under high aqueous [CO_2], the fractionation associated with photosynthetic uptake of CO_2 is strongly expressed, leading to low $\delta^{13}C$ values. The converse applies in the warm, well lit, stratified waters of temperate and tropical latitudes. Finally, taxon-specific biological variables and local environmental conditions must be important, since meridional gradients in particulate organic matter (POM) $\delta^{13}C$ values are significantly different in oceans in the southern versus northern hemisphere (Goericke and Fry 1994).

Nitrogen isotope compositions of primary producers set the $\delta^{15}N$ value at the base of the food web and are dependent upon the $\delta^{15}N$ values of their nutrient source (e.g., nitrate, ammonium, N_2), subsequent biological transformations (e.g., N_2-fixation in subtropical gyres and denitrification in oxygen minimum zones), isotopic fractionation associated with nitrogen assimilation, nutrient pool size, and the degree to which primary producers drawdown the nitrogen pool (see reviews by Sigman and Casciotti 2001; Montoya 2007). N_2-fixation by cyanobacteria is an important source of new nitrogen to oligotrophic high-nutrient, low-chlorophyll regions such as the North Pacific Subtropical Gyre. N_2-fixation generates organic matter with low $\delta^{15}N$ values (−3 to 3‰), because the $\delta^{15}N$ value of dissolved N_2 is near 0‰ and there is little isotopic fractionation associated with its biological uptake by phytoplankton (Dore et al. 2002; Montoya 2007). The relative importance of N_2-fixation fluctuates seasonally. In the winter to spring, the erosion of the thermocline promotes the entrainment of nitrate into the euphotic zone, whereas in the summer to early fall the surface ocean tends to stratify and N_2 fixation dominates new nitrogen and influences the $\delta^{15}N$ value of the primary producers (Montoya 2007).

In most oceanic regions, however, marine primary production is based on nitrate (NO_3^-) supply. The $\delta^{15}N$ values of phytoplankton in these regions reflects two major factors: (1) the $\delta^{15}N$ value of NO_3^- supplied to the euphotic zone, especially via upwelling of nitrate-rich deep water, and (2) the degree of NO_3^- uptake by phytoplankton. Where NO_3^- uptake is complete (the predominant case), the annually integrated $\delta^{15}N$ value of primary production equals the $\delta^{15}N$ value of inputs (*sensu* Eppley and Peterson 1979). The vast sub-surface NO_3^- pool that mixes and is entrained into the euphotic zone averages ~5–7‰ in most regions (Sigman and Casciotti 2001). However below highly productive regions, deep water can become suboxic to anoxic, such as in the Eastern Tropical Pacific oxygen minimum zone. In the absence of adequate O_2, bacteria turn to nitrate to respire organic matter (denitrification), which preferentially removes ^{15}N-depleted NO_3^- and leaves residual nitrate strongly ^{15}N-enriched (+15 to +20‰; Voss et al. 2001). Geographic differences in upwelling intensity and the extent of sub-surface denitrification contribute to large-scale spatial differences in the $\delta^{15}N$ value of phytoplankton. Finally, if the pool of NO_3^- is large and uptake of nitrate is incomplete (e.g., Southern Ocean), then phytoplankton will have lower $\delta^{15}N$ values, because they preferentially assimilate ^{14}N-depleted nitrate. However, as uptake continues and the NO_3^- pool is drawn down, the $\delta^{15}N$ value of phytoplankton will increase, approaching the $\delta^{15}N$ value of the source NO_3^- pool.

14.1.2 Marine Isoscapes in the Pacific and Atlantic Ocean Basins

These differences among and within oceanic regions in nutrient cycling at the base of food web produce geographical gradients in the carbon and nitrogen isotope composition. Both surface POM and deep-sea sediments are proxies for the base of the food web, and their $\delta^{15}N$ values show large isotopic variation and coherent geographical patterns in the Pacific Ocean. For example, a 9‰ variation was observed in the $\delta^{15}N$ values of deep-sea sediments in the eastern equatorial Pacific (Farrell et al. 1995) and a 16‰ variation was observed in the $\delta^{15}N$ values of surface POM along a north-south transect in the central equatorial Pacific (Altabet 2001). In the northeast Pacific Ocean there is approximately a 2–3‰ decrease in baseline $\delta^{13}C$ and $\delta^{15}N$ values from temperate (~30–35° N) to high-latitude (~50° N) pelagic ecosystems (Saino and Hattori 1987; Goericke and Fry 1994; Aurioles et al. 2006). Higher temperatures and extensive upwelling lead to higher phytoplankton growth rates (and higher $\delta^{13}C$ values) in the California Current (CC) relative to the Gulf of Alaska. Higher productivity in coastal systems along the entire eastern Pacific and southern Bering Sea leads to higher ecosystem $\delta^{13}C$ values than in offshore systems. Nitrogen isotope values are also higher at lower latitudes in the eastern north Pacific because intermediate waters in the CC are sourced from the eastern tropical Pacific Ocean, where there is substantial denitrification at depth (Altabet et al. 1999; Voss et al. 2001). This ^{15}N-enriched nitrate is carried northward at depth via

the California Undercurrent and is an important source of nitrogen to surface waters in the CC. Finally, both $\delta^{13}C$ and $\delta^{15}N$ values decrease from east to west in the southeastern Bering Sea (Schell et al. 1998). These isotopic gradients are most likely due to differences in the extent of vertical mixing and the degree of utilization of nutrients in the western Bering Sea.

Constructing maps of isotope values at the base of the food web that are relevant to the movements of marine predators is challenging because in many cases it must be completed on a basin-wide scale. McMahon et al. (in review) generated a baseline isoscape for the Atlantic Ocean based on a meta-analysis of published plankton $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 14.1). The broad spatial patterns observed in these plankton and zooplankton isoscapes reflect the processes described in Section 14.1. For example, in the subtropical gyres, zooplankton $\delta^{15}N$ values are low and reflect the incorporation of fixed-N_2 into the food web. The low $\delta^{15}N$ and $\delta^{13}C$ values observed at high latitudes relate to the utilization rate of NO_3^- by phytoplankton and the high aqueous [CO_2], respectively. These geographical variations in stable isotope values (or isoscapes) provide a means to track the foraging and migration of top marine predators within and between regions on an ocean-basin scale. This approach has recently been used to describe the foraging behavior and movements of a wide variety of marine predators, such as marine mammals, diving seabirds, procellariforms, and tropical tunas (e.g., Lee et al. 2005; Newsome et al. 2007b; Cherel and

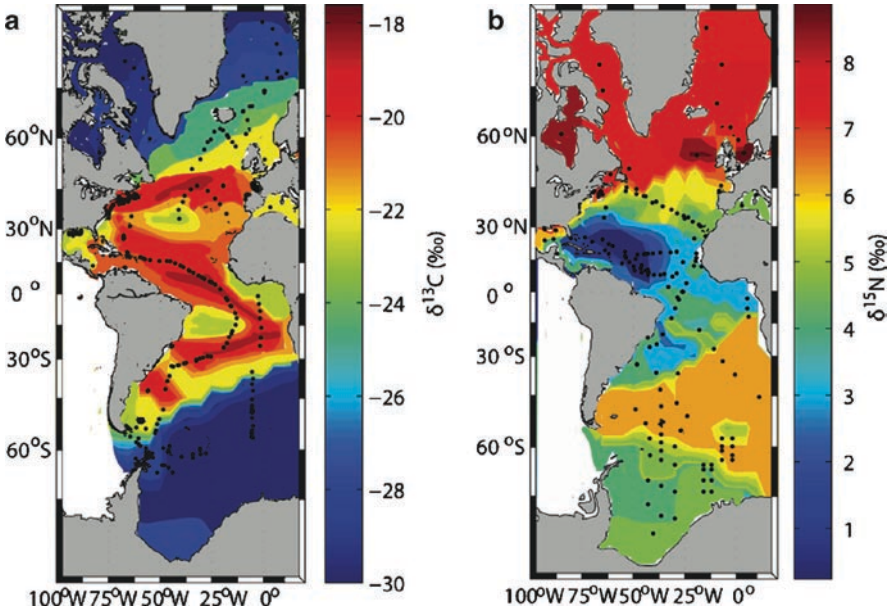

Fig. 14.1 Contour plots of isotope values in the Atlantic Ocean from a meta-analysis of published data. (**a**) $\delta^{13}C$ values of plankton from the upper ocean (0–500 m; n = 425) and (**b**) $\delta^{15}N$ values of zooplankton, primarily calanoid copepods, from the upper ocean (0–500 m; n = 198). *Black dots* indicate sample locations (Data are from McMahon et al. (in review)). Fig. 14.1, see Appendix 1, Color Section

Hobson 2007; Menard et al. 2007; Olson et al. unpublished; Graham et al. 2009). Here we broadly review case studies on two groups of top predators, pinnipeds and tropical tunas.

14.2 Case Studies – Marine Isoscapes and Top Predator Movements

14.2.1 Marine Mammals

Migration and habitat use by marine mammals have been studied extensively and are reviewed in Newsome et al. (in press). Schell et al.'s (1989) pioneering work on bowhead whales (*Balaena mysticetus*) demonstrated that large $\delta^{13}C$ and $\delta^{15}N$ gradients in high-latitude food webs could be exploited to study seasonal migratory patterns between the Bering and Beaufort Seas. Rau et al. (1992) conducted another study examining diet and residence patterns in a range of taxa, including several species of seals, in the Weddell Sea. Hobson et al. (1997) were among the first to suggest that isotopic differences between marine mammal species, in this case harbor seals (*Phoca vitulina*) and Steller sea lions (*Eumetopias jubatus*), were due to coastal/benthic versus offshore/pelagic foraging. Most marine mammal studies have relied on gradients in carbon and nitrogen isotopes, though Stewart et al. (2003) and Outridge et al. (2003) have done elegant work on the movement patterns of walruses (*Odobenus rosmarus*) using patterns of lead isotope variation in different tissues. Here, we will focus on case studies exploring modern and archaeological pinniped populations in the northeastern Pacific Ocean.

Do the isotopic patterns described above for the northeastern Pacific Ocean cascade up to label top consumers in a reliable way, or do differences in trophic level and physiology, as well as prey migration, obscure these basic patterns? We used data from Burton and Koch (1999), Burton et al. (2001), and Newsome et al. (2007a, b) to investigate this issue by studying the isotopic composition of extant pinnipeds with well-understood and geographically-distinct foraging habitats. The key "control" species are harbor seals and northern fur seals (*Callorhinus ursinus*). Harbor seals are relatively sedentary, living along rocky coasts and sloughs from Baja California to the Aleutian Islands. They undertake short, shallow dives and feed nearshore. Northern fur seals, by contrast, forage offshore at the shelf-slope break or beyond. Males and females from the small rookery on San Miguel Island (SMI), California, forage offshore in the CC system, whereas males from the large Pribilof Island rookeries forage in the Bering Sea and Gulf of Alaska. Females from the Pribilof rookeries are highly migratory, and thus not useful as "buoys" to sample any one oceanographic region.

Figure 14.2 presents means (±1 standard deviation) of the $\delta^{13}C$ and $\delta^{15}N$ values for bone collagen or tooth dentin from harbor seals and northern fur seals, separated by geographic region (Alaska vs. California). Bone collagen is a bulk tissue with a

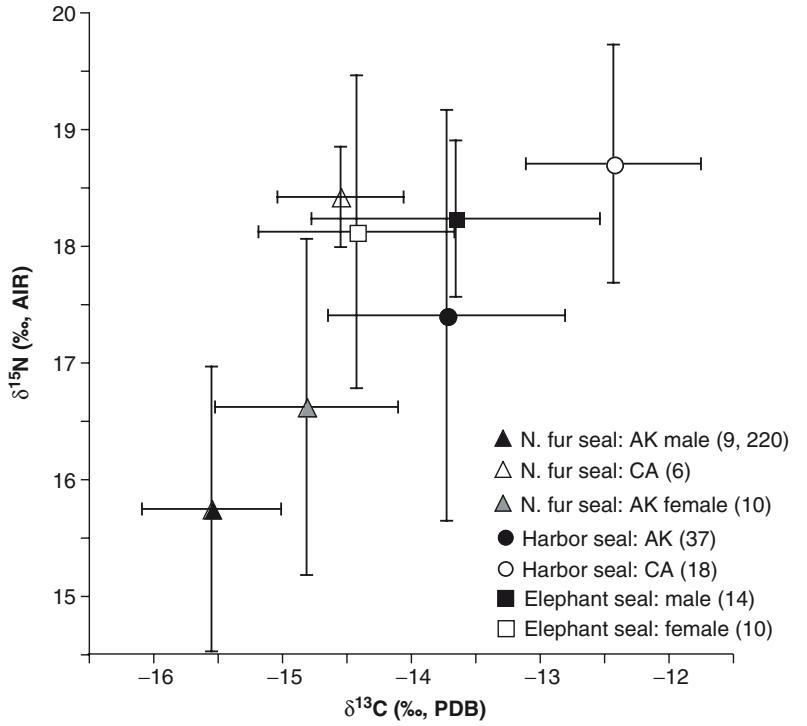

Fig. 14.2 Bivariate plot of collagen carbon and nitrogen isotope values (means ± 1 standard deviation) for three modern pinniped species that breed and feed at different locations in the northeastern Pacific. Number of samples analyzed is indicated in parentheses. For N. fur seal: AK male, the first number is number of bone samples, the second is number of dentin samples; for all other samples only bone was analyzed (Data are from Burton and Koch (1999), Burton et al. (2001), and Newsome et al. (2007b))

slow turnover rate that integrates animal diet over several years. Tooth dentin, which was measured for a large suite of male northern fur seals from the Pribilof Islands, grows by accretion and has conspicuous growth bands. It can be sub-sampled to yield more discrete time periods in an animal's life. For the study by Newsome et al. (2007b), the source of our tooth dentin data, dentin accreted in the third year of life was milled from each tooth.

In both Alaska and California, nearshore-foraging harbor seals had higher $\delta^{13}C$ values than offshore-foraging northern fur seals, as expected. The $\delta^{15}N$ values were not significantly different between nearshore and offshore foragers, which supports the conclusion that animals are feeding at roughly the same trophic level and that $\delta^{15}N$ values do not differ predictably between coastal and pelagic ecosystems in this region. Intra-specific comparisons reveal that high latitude populations in Alaskan waters have lower $\delta^{13}C$ and $\delta^{15}N$ values than temperate latitude populations from California. Thus, isotopic patterns in higher trophic level foragers mirror those observed in plankton and organic matter at the base of the food web. Harbor seals

were not available from sites further west along the Aleutians, so it could not be determined if the large isotopic shifts across the island chain are transmitted up the food web in modern taxa.

With increased confidence that isotopic values from marine mammal tissues track variations in the marine isoscape, we will discuss several case studies that have examined foraging zone or migration in extant northeastern Pacific pinnipeds. First, as noted earlier, female northern fur seals from the Pribilof rookeries are highly migratory (Ream et al. 2005). During the 4-month breeding season females feed in the Bering Sea, as they need to remain near the rookery to nurse their pups. For the 8 months they are off the rookery at sea, many females migrate southward, crossing the Gulf of Alaska to forage as far south as the shelf-slope break from British Columbia to southern California. Other females forage in the open ocean at highly productive sites associated with the transition from subarctic-subtropical waters (35–40° N, 140–180° W; North Pacific Convergence Zone). Not surprisingly, northern fur seal females from the Pribilofs have $\delta^{13}C$ and $\delta^{15}N$ values intermediate between those for males from Alaska and conspecifics feeding off California, consistent with their foraging in both high and middle latitudes during the course of a year (Fig. 14.2; Burton and Koch 1999).

Our other modern case studies focus on northern elephant seals (*Mirounga angustirostris*). These seals breed on islands or isolated mainland beaches from central Baja to northern California, with one outlying rookery on Vancouver Island. The smaller females (~600 kg) are on land for approximately 1 month in winter to give birth and nurse, and for 1 month in summer to molt. The larger males (~2,000 kg) are on land for three winter months to breed, and again for approximately one summer month to molt. Animals fast while breeding and molting. Both sexes are highly migratory when off their rookeries. Satellite tracking data from animals at rookeries on SMI and Point Año Nuevo (PAN), CA, show that the animals undertake long migrations between foraging locations and breeding and molting grounds (Stewart and DeLong 1995; LeBoeuf et al. 2000). At both PAN and SMI, males migrate rapidly to the north, where they feed on benthic prey on the continental shelf from Oregon to the western Aleutians. Females exhibit a greater range of migratory and foraging behaviors. Many females from SMI forage in pelagic waters at the northern edge of the subarctic-subtropical transition (45–50° N, 130–180° W); others forage on benthic prey on the continental shelf from California to Washington. Some PAN females show similar movement patterns, but others forage benthically further north (like males) or in pelagic sub-arctic waters north of the subarctic-subtropical transition. While individuals from the same rookery may have very different migratory patterns, the limited data available from multiple years suggest that individuals return to the same locations each year.

Bone collagen isotope data from males and females at PAN lead to interpretations of foraging and migratory behavior entirely consistent with tracking data. Males from PAN have values similar to harbor seals from Alaska, who also forage benthically at high latitude (Fig. 14.2). Female northern elephant seals from PAN have isotopic values indistinguishable from northern fur seals from California, who also forage pelagically, chiefly in or south of the transition zone to subarctic waters.

We note that these isotopic interpretations of elephant seal migratory behavior for PAN were reached by Burton and Koch (1999) before extensive tracking data were available (LeBoeuf et al. 2000). High-resolution satellite tracking data have since offered independent confirmation of interpretations based on marine isoscapes, albeit interpretations informed by earlier, less extensive tracking and observational data on elephant seal movements.

Aurioles et al. (2006) present another study of foraging location in northern elephant seals. While a great deal is now known about the migratory behavior of animals from the PAN and SMI rookeries, the migratory patterns for elephant seals in Mexico, such as those from the San Benitos Islands (SBI) off Baja California, are largely unknown. To track feeding grounds of SBI elephant seals, Aurioles et al. (2006) measured $\delta^{13}C$ and $\delta^{15}N$ values in hair of recently weaned elephant seal pups at SBI and PAN, assuming that their isotopic values reflect those of mothers' milk and therefore mothers' diets over the preceding few months. Mean $\delta^{13}C$ and $\delta^{15}N$ values (±1 standard deviation) for SBI pups (−16.1 ± 0.9‰ and 17.7 ± 0.9‰, respectively) were significantly higher than those for PAN pups (−17.6 ± 0.4‰ and 15.6 ± 1.0‰, respectively). From data on environmental isotope gradients along the eastern Pacific Rim, Aurioles et al. (2006) estimated that the difference in pup isotope values was consistent with the hypothesis that SBI females foraged, on average, ~8° south of females from PAN.

This hypothesis has gained support from an ongoing study of whiskers from female northern elephant seals at PAN and SBI by Aurioles and Newsome (unpublished data). Whiskers grow continuously, and while the rate of growth is not yet well calibrated for northern elephant seals at this time, and may vary seasonally, it is likely that each whisker represents slightly less than 1 year's growth based on the sinusoidal trends in isotope values along individual whiskers. Considering the average isotopic values for each whisker, mean $\delta^{13}C$ and $\delta^{15}N$ values (± one standard deviation) for SBI females (−15.1 ± 0.5‰ and 17.4 ± 0.8‰, respectively) are indeed higher than those for PAN females ((−15.8 ± 0.2‰ and 15.5 ± 1.0‰, respectively). In Fig. 14.3, every data point from each whisker is plotted for the nine SBI and ten PAN individuals. There is considerable overlap among samples from the two rookeries, but many samples from PAN have lower $\delta^{13}C$ and $\delta^{15}N$ values than observed at SBI, and many samples from SBI have values higher than observed at PAN. From this isotopic pattern, we hypothesize that there are tracks for PAN individuals that extend north of any tracks for SBI individuals, and tracks for individuals from SBI that extend south of any tracks for PAN individuals. This hypothesis is being tested through the collection of tracking data on SBI individuals and further analysis of whiskers collected from both rookeries.

Historical data provide a baseline against which to judge the significance of recent ecological shifts. Burton et al. (2001) and Newsome et al. (2007a) explored the historical ecology of northern fur seals. This species is common in archaeological sites from southern California to the Aleutian Islands, yet today it breeds almost exclusively on offshore islands at high latitudes. In all sites where they co-occur, prehistoric adult female northern fur seals have lower $\delta^{13}C$ values than nearshore-foraging harbor seals (Fig. 14.4), as is the case today (Fig. 14.2), suggesting that the female fur

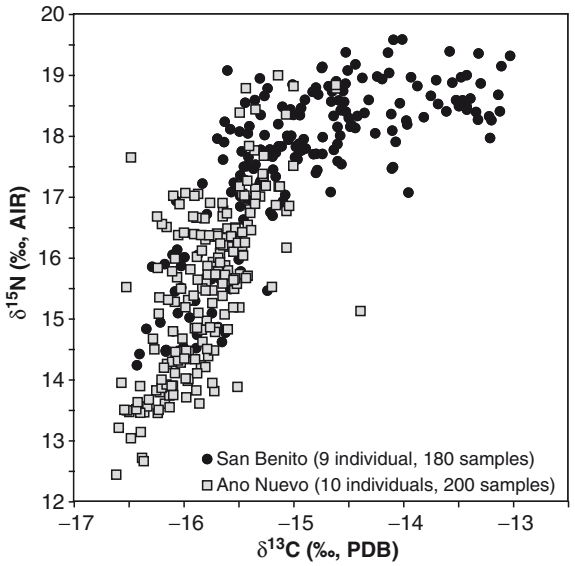

Fig. 14.3 Bivariate plot of whisker carbon and nitrogen isotope values from female northern elephant seals from Pt. Año Nuevo, CA, (ten individuals) and San Benito Island, Baja California, Mexico (nine individuals). Nearly twenty samples were collected from evenly spaced positions along the length of each whisker. Data are from Newsome and Aurioles (unpublished data)

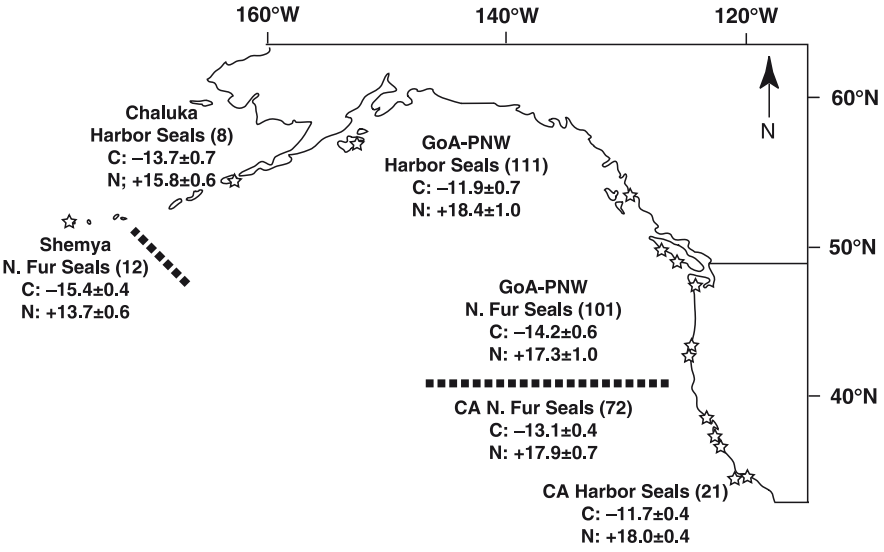

Fig. 14.4 Mean (±1 standard deviation) for $\delta^{13}C$ (*upper numbers*) and $\delta^{15}N$ (*lower numbers*) values for pinniped bone collagen from archaeological sites along the northeast Pacific margin. Number of samples analyzed is indicated in parentheses. Sites from which samples were analyzed are indicated by *star symbols*. *Thick dashed lines* separate sites that combined to calculate values for northern fur seals: Shemya, Gulf of Alaska/Pacific Northwest (GoA/PNW), California. Harbor seals were clustered into the following groups: California, Gulf of Alaska/Pacific Northwest, Chaluka (Data are from Newsome et al. (2007a) as well as Newsome (unpublished) for Chaluka harbor seals)

seals were foraging in deep, offshore waters over their entire range. The availability of fur seals to prehistoric human hunters was not because they foraged close to shore. Furthermore, prehistoric adult female northern fur seals cluster into three geographically-defined groups: a southern group (California) with high $\delta^{13}C$ and $\delta^{15}N$ values, a northern group (eastern Aleutian/Gulf of Alaska/Pacific Northwest) with intermediate values, and a western Aleutian group with very low isotope values (Fig. 14.4). This third group is the first indication in our marine mammal data of the low $\delta^{13}C$ and $\delta^{15}N$ values that characterize the marine isoscape of the western Aleutians. These isotopic distinctions among seals from different regions suggest that ancient northern fur seal females were less migratory than animals from the modern Pribilof rookery, and confirm that prehistoric fur seals from California were not immigrants from northern waters but instead were year-round residents. This conclusion is supported by archaeometric data showing that archaeological sites contain many unweaned pups, confirming the presence of temperate-latitude breeding colonies in California, the Pacific Northwest, and the eastern Aleutian Islands. The relative roles of human hunting versus climatic factors in explaining the loss of these temperature-latitude rookeries are unclear; more paleoclimatic and paleoceanographic data are needed to explore alternative hypotheses for this change in ecosystem state.

14.2.2 Tropical Tunas

Commercial fisheries have removed approximately 50 million tons of tuna from the Pacific Ocean since the 1950s (Sibert et al. 2006). The majority of this exploited biomass has been tropical tunas taken from the equatorial zone (20° N to 20° S). In order to determine population dynamics and develop the most successful fisheries management for tropical tunas, movement patterns of these highly mobile predators must be accurately determined. Tropical tuna form schooling aggregations and some species associate to fixed (e.g., seamounts, fish aggregating devices) or dynamic (e.g., fronts, meso-scale eddies) oceanographic features (Holland et al. 1990, 1999; Polovina et al. 2001). Tuna movements between these sometimes distant oceanic features are not well understood. On a basin-wide scale, there is some evidence from tag and recapture programs of restricted mixing between the eastern Pacific Ocean and the western and central Pacific Ocean. Hence, integrated stock assessments of tropical tunas in the Pacific Ocean are developed for either the entire tropical Pacific basin (Sibert et al. 2006) or for the eastern and western-central management regions (e.g., Hampton 2002; Hoyle and Maunder 2006). If tropical tuna movements are further restricted within these large oceanic regions, where commercial fishing effort is spatially patchy, then current exploitation rates could be locally unsustainable. Stock assessment models can incorporate additional spatial structure, but these models require more observational data on tuna movements to define mixing rates at finer resolutions. The main objective of the following case study was to determine if bulk $\delta^{15}N$ values of tropical tuna could be used as intrinsic tags to examine their habitat use and movements in the equatorial Pacific Ocean.

Marine mammals and seabirds often return annually to specific breeding grounds or rookeries, which provides an opportunity to tag individuals and collect tissue samples. Tropical tuna do not have well-defined spawning regions, but rather, spawn almost continuously in waters near the equator (10° N–10° S), with some individuals spawning in subtropical waters (Itano 2000). With their expansive spawning region and our lack of knowledge on their seasonal or annual movement patterns, sampling tropical tuna must occur opportunistically and the coverage must encompass much of the equatorial and subtropical Pacific Ocean. Commercial fishing of tunas is widespread in the equatorial Pacific and, therefore, can provide a unique sampling platform to collect samples from many individuals over large regions. In the work described below, yellowfin (*Thunnus albacares*) and bigeye (*T. obesus*) tuna were captured by purse-seine and long-line fishing vessels, and were sampled on vessels by fisheries observers from the Inter-American Tropical Tuna Commission and from the national fisheries observer programs in the central and western Pacific. As a result of this international collaboration between scientists, observer programs, and fishers, muscle samples were collected from tuna across much of the equatorial Pacific, allowing for the construction of tuna isoscapes (Graham et al. 2009).

The $\delta^{15}N$ values of yellowfin (YFT) and bigeye (BET) tuna demonstrate highly variable, but spatially coherent structure in the equatorial Pacific Ocean (Fig. 14.5a and b). The overall range in $\delta^{15}N$ values of YFT and BET is 13.7‰ (n = 387) and 12.5‰ (n = 196), respectively. This large isotopic variation could result from geographical variations in (a) their trophic level (TL) or (b) the isotopic baseline value, which is reflected in the tuna $\delta^{15}N$ values. If shifts in the trophic levels of tuna were the primary mechanism producing this 12–14‰ spatial variation, then there would be regional variations of approximately four to five trophic levels. Not only is a TL variation of this magnitude unrealistic in marine ecosystems, which generally have a total of four to five TLs (Fry 1988; Olson and Watters 2003), but stomach content studies conducted in the Pacific Ocean have revealed little foraging specialization in tropical tunas (Reintjes and King 1953; Alverson 1963). It is more likely that these geographical variations in the $\delta^{15}N$ values of tuna reflect differences in nutrient dynamics and subsequent $\delta^{15}N$ values at the base of the marine food web. Popp et al. (2007) used compound-specific nitrogen isotope analysis of individual amino acids from tissues of YFT to test this hypothesis and showed that spatial variations in tuna bulk $\delta^{15}N$ values in the eastern tropical Pacific are controlled by variations in $\delta^{15}N$ values at the base of the food web and not TL. Thus, the $\delta^{15}N$ values of tropical tunas and the resulting isoscapes appear to be driven, in large part, by the geographical variations in nutrient dynamics at the base of the food web (Popp et al. 2007; Menard et al. 2007; Olson et al. unpublished; Graham et al. 2009).

If a predator migrated extensively in the equatorial Pacific, then little geographical isotopic variation would be expected in its tissues because regional differences in baseline $\delta^{15}N$ values would be integrated and homogenized over time. The large isotopic variation observed in YFT and BET throughout the equatorial Pacific suggests these tuna must reside and forage within a region for a long enough period to reflect the baseline $\delta^{15}N$ structure. Tissue turnover rates estimated for juvenile YFT

indicate that the nitrogen in the white muscle represents an accumulated foraging history of approximately 2 months (Graham et al. 2009). Turnover rates are likely slower in larger individuals (Martínez del Rio et al. 2009). Accordingly, the $\delta^{15}N$ values of tuna incorporated into these isoscapes (Fig. 14.5a and b) should represent an integrated foraging history of at least 2–4 months. This intrinsic tag approach reveals that tropical tunas are not 'highly migratory' and suggests a high degree of regional residency on the order of several months in the equatorial Pacific Ocean. These isotope-based conclusions corroborate conventional and electronic tagging studies that reveal restricted movements (e.g., <1,000 km/month) in individual BET tracked in the Coral Sea (Gunn et al. 2005), YFT and BET tracked around the

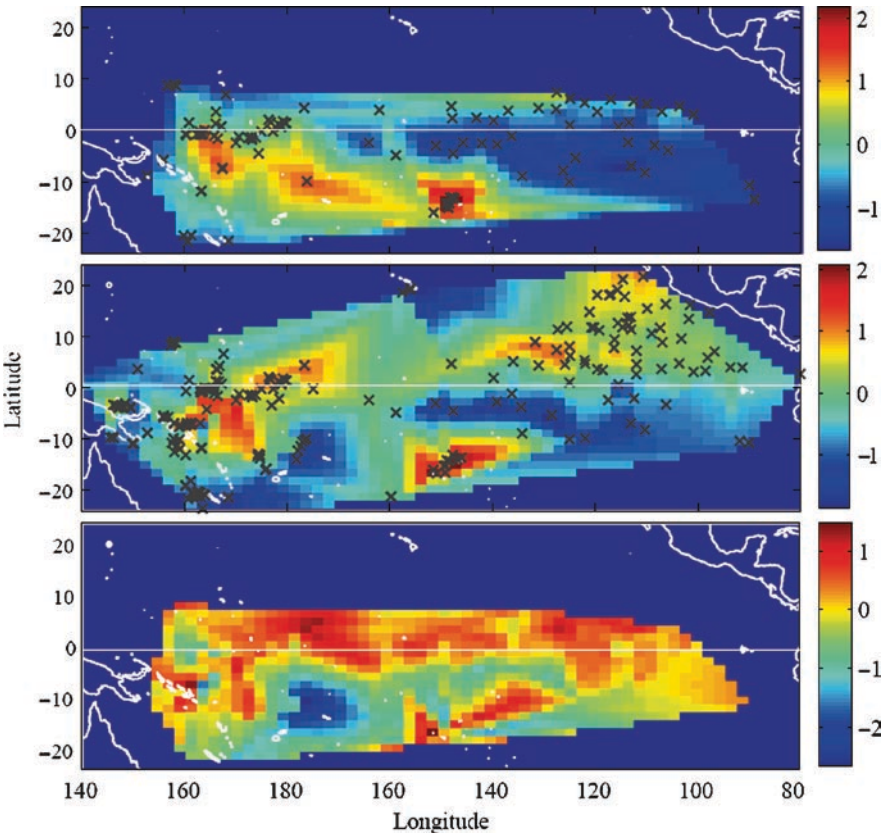

Fig. 14.5 $\delta^{15}N$ isoscapes for (**a**) bigeye (n = 196) and (**b**) yellowfin (n = 387) tuna. *Crosses* indicate sample locations. Samples collected in the eastern tropical Pacific represent a composite of ~five individuals. The $\delta^{15}N$ values for each species were normalized against the average value for that species within the study region. (**c**) A map of the residuals between the interpolated $\delta^{15}N$ values for the two species (i.e., observable difference between the normalized values). Regions with positive residuals represent areas where the $\delta^{15}N$ values of YFT are greater than BET and negative residuals represent areas where the $\delta^{15}N$ values of BET are greater than YFT (Data are from Graham et al. (2009)). Fig. 14.5, see Appendix 1, Color Section

Hawaiian Islands (Adam et al. 2003; Sibert et al. 2003), and YFT tracked near Baja California (Schaefer et al. 2007), but also show that this residency behavior in tuna exists at a population level and over a much larger spatial scale than previously documented. Accordingly, these results suggest that managing tuna fisheries on a basin-wide or sub-basin scale could lead to localized depletions in certain regions because these tuna demonstrate higher site fidelity than previously recognized.

The next step in the study of tuna isoscapes should be to develop a model that quantifies tuna movements. Coupling tissue turnover rates and isoscapes can provide broad constraints on the maximum net directional movements required to maintain the tuna isotopic gradients (Graham et al. 2009). Tuna movements, however, are not simply directed or unidirectional, but include random or diffusive movements. Applying an advection-diffusion reaction model (Sibert and Hampton 2003) to isotopic datasets should better approximate fish movements. Once quantitative estimates of tuna movements can be derived from a synthesis of isotope datasets, these movement rates should be validated with extrinsic tagging datasets and, ultimately, incorporated into stock assessment models to improve the spatial resolution of tuna fisheries management.

Comparing isoscapes of different species over the same geographical range can provide insight into interspecific differences in their resource and habitat utilization. In the equatorial Pacific Ocean, large-scale differences occur in the $\delta^{15}N$ isoscapes of BET and YFT (Fig. 14.5c), however, a significant linear relationship exists between the interpolated (or estimated) $\delta^{15}N$ values of the BET and YFT isoscapes (p-value < 0.01) (Fig. 14.6). This correlation between the two species suggests that although their $\delta^{15}N$ values vary spatially, there is a consistent relationship between their $\delta^{15}N$ values. The interpolated values of the two species of tuna deviate from a direct 1:1 relationship, because at low $\delta^{15}N$ values, YFT have slightly higher $\delta^{15}N$

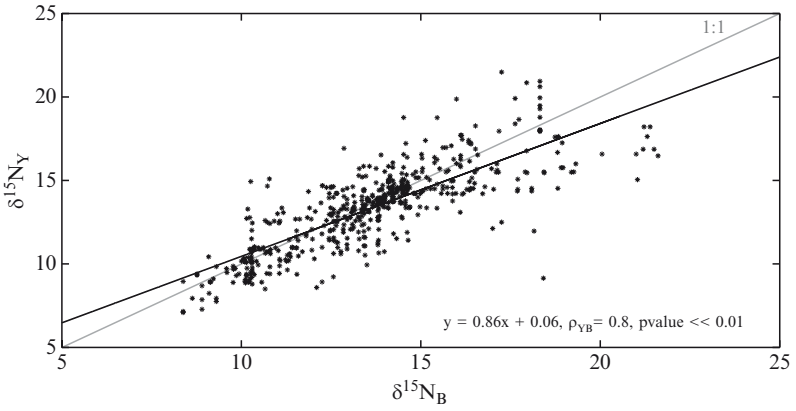

Fig. 14.6 Bivariate plot of the interpolated (estimated) $\delta^{15}N$ values of bigeye ($\delta^{15}N_B$) and yellowfin tuna ($\delta^{15}N_Y$). The *black line* represents the correlation between $\delta^{15}N_Y$ and $\delta^{15}N_B$ values (Pearson correlation coefficient (ρ_{YB})). The *gray line* represents the 1:1 relationship (Data are from Graham et al. (2009))

values than BET, and at high $\delta^{15}N$ values BET have higher values than YFT (Fig. 14.6). We hypothesize that this interspecific pattern relates to differences in their foraging behavior. In the eastern tropical Pacific Ocean, Olson and Watters (2003) assessed trophic levels for upper-trophic level predators with an Ecopath model and estimated the TL to be 5.3 and 4.8 for large BET and YFT, respectively. Large BET generally feed at greater depths than YFT, and while at depth BET can feed on squids and fish species that are at higher trophic levels (e.g., Menard et al. 2006). Small BET and YFT had similar TLs (Olson and Watters 2003). Consequently, small BET and YFT should have similar $\delta^{15}N$ values and large BET should have higher values than larger YFT. We hypothesize that this size-related variation in the trophic dynamics of YFT and BET explains the deviation of the relationship between their $\delta^{15}N$ values from a direct 1:1 relationship. Comparing the interpolated $\delta^{15}N$ values of yellowfin and bigeye tuna suggests that there are components of their foraging behavior that are consistent across the equatorial Pacific Ocean.

In the central and eastern equatorial Pacific Ocean, just a few degrees north of the equator, YFT $\delta^{15}N$ values are higher than BET $\delta^{15}N$ values (Fig. 14.5c). Unless YFT forage at a higher trophic level in this area relative to all other regions, this isotopic difference could represent deviations in BET and YFT habitat utilization. We would predict the baseline $\delta^{15}N$ values to be low at the upwelling area along the equator because of the large pool of NO_3^- and the low rate of utilization by phytoplankton. If BET forage more exclusively in these equatorial waters, then BET $\delta^{15}N$ values would reflect the low baseline values. Additionally, if YFT spent more time foraging at higher latitudes, where there are higher baseline $\delta^{15}N$ values associated to the utilization of nitrate that advects north from the equator, then the $\delta^{15}N$ values of YFT would be higher in these regions. The deviation between YFT and BET $\delta^{15}N$ values at the boundary between low $\delta^{15}N$ values in the equatorial region and higher values at higher latitudes might reflect their relative residency at the equator.

Schaefer et al. (2007) suggested that reproductively mature YFT in the eastern Pacific make seasonal movements to the equator during spawning periods and smaller or non-reproductive individuals remain at higher latitudes. The isotopic difference observed between the YFT and BET isoscapes could result from YFT moving into equatorial regions from subtropical latitudes (higher $\delta^{15}N$ values) to use the warm surface waters for spawning, whereas BET reside and forage within the equatorial region (lower $\delta^{15}N$ values) during spawning and non-spawning periods. Hence, yellowfin and bigeye could exhibit population-level niche separation, where these tunas share habitat along the equator during spawning, but otherwise separate their main foraging regions. Overall, tuna isoscapes provide large-scale, population-level information that then can be tested with high-resolution extrinsic tracking techniques.

14.3 Summary and Future Directions

Over the past two decades, marine ecologists have spent considerable resources developing and deploying electronic and satellite tagging technologies. Recent initiatives such as TOPP (Tagging of Pacific Pelagics, www.topp.org) have amassed

tremendous amounts of high-resolution three-dimensional tracking data that has have given us incredible insight into the movement patterns and foraging strategies of elusive animals difficult to study in their natural environments. Furthermore, tagging programs are beginning to collaborate with biological and physical oceanographers to map the vertical temperature and chemical structure of remote pelagic regions by placing instrumentation on large marine animals (e.g., Biuw et al. 2007). These activities represent a unique opportunity for isotope ecologists to calibrate and expand their tool in marine ecology, specifically in the creation and eventual utilization of $\delta^{13}C$ and $\delta^{15}N$ marine isoscapes. While isoscapes will never achieve the fine-spatial scale details obtained with satellite tags and on-board instrumentation (e.g., time-depth recorders), they provide a cost-effective alternative and may be more suitable for answering population-level questions (i.e., stock discrimination) than tagging technologies or even genetic markers. For example, a typical satellite tag costs ~$4,000, and satellite time costs ~$8/tag per day. With a standard 3-month deployment, researchers invest nearly $5,000 just for the hardware to study the movements of one individual, and these costs do not reflect the personnel and logistical costs associated with the deployment of each tag. By contrast, for $5,000 the $\delta^{13}C$ and $\delta^{15}N$ values of approximately 400 individuals can be determined. Ultimately, research objectives and budget should incorporate the added knowledge gained by the union of extrinsic and intrinsic tagging approaches.

The construction of marine isoscapes from the top-down and bottom-up will take time, as there are numerous factors that must be considered in the accurate interpretation of isotopic time series from behaviorally complex predators (e.g., Wunder, this volume). Briefly, these factors can be categorized into two general types, those that relate to physiological and behavioral changes of the consumer itself, and those that result in temporal and spatial variability in isotope values at the base of the food web (i.e., baseline effects). With respect to the former, physiological condition (i.e., anabolic vs. catabolic state), isotopic turnover/growth rates, trophic enrichment factors between prey and predator, isotopic fractionation among tissues that relate to differences in amino acid composition (i.e., tissue-dependent fractionations), and intra-specific variation in trophic level must be considered as potential sources of isotopic variability when attempting to create spatial and/or temporal isoscapes with data derived from top predators.

Baseline variations result from temporal changes in physical (e.g., temperature), chemical (e.g., nutrient supply), and biological (e.g., algae species composition) variables known to control the isotopic composition of primary producers and consumers in the open ocean. A crucial step in the advancement of using isoscapes to track the movement of ancient and modern predators in oceanic ecosystems retrospectively is to determine the temporal stability of baseline values. As described in detail above, seasonal fluctuations in baseline isotope values depend upon changes in nutrient sources, species composition, biogeochemical cycling rates, and biological productivity. For instance, both annual and decadal variations in $\delta^{13}C$ and $\delta^{15}N$ values have been observed in zooplankton collected from the Gulf of Alaska in the northeast Pacific Ocean (Kline 1999; Kline et al. 2008). Similarly, Hannides et al. (2009) found nearly a 10‰ variation in the bulk $\delta^{15}N$ values of zooplankton

collected over 5 years from a single location in the subtropical Pacific Ocean. To some degree, seasonal isotopic variations at lower trophic levels will be dampened as this primary production signal is transferred up food chains to top predators (Bump et al. 2007), but careful consideration of the nutrient dynamics, temporal lags between the lower and upper trophic levels, and isotopic turnover rates will be essential to interpret baseline and predator isoscapes. We suggest that future work on assessing the isotopic baseline should focus on the development of biogeochemical models that incorporate the mechanistic processes involved in controlling the isotope values at the base of the food web. Eventually, careful consideration of these two types of factors will not only yield a temporally and spatially sensitive isoscape of the ocean, but will also teach us more about the ecology and physiology of top marine consumers.

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