

Millennial-scale isotope records from a wide-ranging predator show evidence of recent human impact to oceanic food webs

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Human exploitation of marine ecosystems is more recent in oceanic than near shore regions, yet our understanding of human impacts on oceanic food webs is comparatively poor. Few records of species that live beyond the continental shelves date back more than 60 y, and the sheer size of oceanic regions makes their food webs difficult to study, even in modern times. Here, we use stable carbon and nitrogen isotopes to study the foraging history of a generalist, oceanic predator, the Hawaiian petrel (*Pterodroma sandwichensis*), which ranges broadly in the Pacific from the equator to near the Aleutian Islands. Our isotope records from modern and ancient, radiocarbon-dated bones provide evidence of over 3,000 y of dietary stasis followed by a decline of ca. 1.8‰ in $\delta^{15}\text{N}$ over the past 100 y. Fishery-induced trophic decline is the most likely explanation for this sudden shift, which occurs in genetically distinct populations with disparate foraging locations. Our isotope records also show that coincident with the apparent decline in trophic level, foraging segregation among petrel populations decreased markedly. Because variation in the diet of generalist predators can reflect changing availability of their prey, a foraging shift in wide-ranging Hawaiian petrel populations suggests a relatively rapid change in the composition of oceanic food webs in the Northeast Pacific. Understanding and mitigating widespread shifts in prey availability may be a critical step in the conservation of endangered marine predators such as the Hawaiian petrel.

fishing | seabird | stable isotope

Historical baselines are a prerequisite to understanding the extent of human impact on a species or ecosystem. In coastal marine environments, retrospective studies show that habitat destruction and harvest of marine organisms have caused severe modifications, including trophic cascades and the regional loss of entire ecosystems (1, 2). It is difficult to assess the extent to which such impacts extend beyond continental shelves to the oceanic zone, because few chronological data are available for regions far out at sea, and the vast size of these ecosystems makes their food webs difficult to study, even in the present.

In the oceanic Northeast Pacific, significant human presence began with the colonization of the Hawaiian Islands, less than 1,000 y ago (3, 4). For centuries afterward, anthropogenic impacts, such as harvesting of marine organisms, were concentrated near the Islands; only in the 20th century, with the advent of industrialized fishing, have a wide variety of oceanic organisms been exploited at a broad spatial scale (5, 6). Our understanding of how human actions such as fishing have affected oceanic food web structure is primarily derived from catch statistics, which show a temporal decline in the abundance of some targeted groups, such as tuna, and in the trophic level of global catch

(6–8). However, catch statistics can be strongly affected by shifting technologies and markets, and reflect only the abundance of species that are harvested. Moreover, catch statistics cannot record information about prehuman conditions, and very few systematically collected catch statistics or scientific surveys predate 1950.

Historical records from generalist predators offer an alternative means of studying marine food webs. Responding to changes in prey availability by shifting their diet or foraging locations, or else declining in abundance, predators such as seabirds can forage over large expanses and are often viewed as sentinels of their food webs (9–11). Here, we present millennial-scale records of foraging ecology from a wide-ranging, generalist predator, the Hawaiian petrel (*Pterodroma sandwichensis*), to provide a unique proxy for the condition of oceanic food webs in the Northeast Pacific Ocean. Shifts in Hawaiian petrel foraging habits have the potential to reflect changes occurring over large portions of the oceanic Pacific given the birds' diverse diet of fish, squid, and crustaceans; the high mobility of individuals (>10,000 km foraging trips); and the species' extensive range from the equator to near the Aleutian Islands (0–50°N, 135–175°W) (12–14).

Hawaiian petrels breed only on the main Hawaiian Islands, where their bones are abundant in paleontological and archaeological sites (Fig. 1). Within those bones, a record of petrel foraging locations and trophic level is preserved by stable carbon and nitrogen isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of the protein collagen (15, 16). We collected isotope data from over 250 individuals, including birds from every known modern and ancient Hawaiian petrel population. Equally extensive genetic studies (based largely on the same set of individuals) show that despite their high mobility, Hawaiian petrels rarely move between islands, and breeding colonies on different islands have diverged into genetically distinct populations (17, 18). Because at least some of those populations also have distinct foraging habits (15), we construct separate isotopic chronologies for each island population. Collectively, our chronologies extend back roughly

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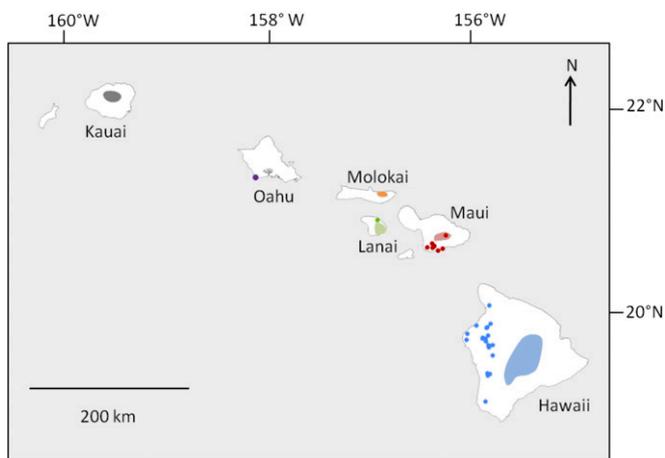


Fig. 1. Collection sites for Hawaiian petrel subfossil bones (dark-colored points), historic breeding distribution for the potentially extirpated population on Molokai, and modern breeding distribution on Kauai, Lanai, Maui, and Hawaii (lighter colored shapes). The distribution on Hawaii includes the saddle region between Mauna Kea and Mauna Loa, where Hawaiian petrel breeding is only documented by indigenous knowledge and bones (46, 58).

4,000 y, to well before human presence in the oceanic Northeast Pacific (3, 4). Our study therefore provides a unique, fishery-independent window into potential anthropogenic alterations of oceanic food webs.

Results and Discussion

We conducted a species-wide study of the Hawaiian petrel based on stable isotope data from six populations and two tissues: collagen and flight feather. Collagen is ideal for constructing long-term isotope chronologies, not only because it is preserved in ancient bones, but because its slow turnover rate in living birds results in an isotopic composition that can reflect foraging over a period of years (19). For the Hawaiian petrel, collagen data also provide spatially integrated dietary signals from individuals that are capable of traveling over large portions of the Northeast Pacific ocean, even within a single season (13). In contrast, flight feathers grow in a month or less during either the breeding season (for hatch-year birds) or nonbreeding season (for adults) (12, 15). Isotope data from flight feathers are therefore more useful for showing the diversity of foraging strategies present among Hawaiian petrels during short periods of time. Here, we study the isotopic composition of modern flight feathers to understand spatial and seasonal variation in petrel foraging habits and to aid in interpretation of our isotope chronologies from collagen.

We found large disparities in feather $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values among populations and age groups, which we interpret as reflecting mainly divergences in foraging locations (Fig. 2, Table S1), as did Wiley et al. (15) in a study of two Hawaiian petrel populations. Our spatial interpretation of feather data is based on well-recognized $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ gradients within the Hawaiian petrel's distribution (Fig. 2A) (15), and is supported by observational studies. In brief, multiple data sets indicate that throughout North Pacific food webs, $\delta^{13}\text{C}$ varies inversely with latitude and $\delta^{15}\text{N}$ values decline precipitously away from an area of elevated $\delta^{15}\text{N}$ values in the southeast portion of Hawaiian petrel distribution, between 4–10° N and 135–140°W (20–24). Thus, petrels that focus their foraging southeast of the Hawaiian Islands are expected to have relatively high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Alternatively, the relatively high $\delta^{15}\text{N}$ values, such as those we observed for Lanai and Hawaii populations, could be due to feeding at a higher trophic level than other petrels. However, Laysan albatross (*Phoebastria immutabilis*) feeding north of the Hawaiian Islands, away from

the region of elevated $\delta^{15}\text{N}$, have relatively low $\delta^{15}\text{N}$ values (12.5‰) (15). Because Hawaiian petrels are unlikely to forage at a higher trophic level than the related and substantially larger Laysan albatross, $\delta^{15}\text{N}$ values greater than 12.5‰ in Hawaiian petrel feathers must result from feeding in a region of elevated $\delta^{15}\text{N}$.

High $\delta^{13}\text{C}$ values among adults are consistent with all adults growing feathers in the southern portion of Hawaiian petrel distribution, with variable $\delta^{15}\text{N}$ indicating that populations rely to different extents on areas of elevated $\delta^{15}\text{N}$ (e.g., in the southeast portion of the species' distribution; Fig. 2A). Relatively low $\delta^{13}\text{C}$ values of Maui and Kauai hatch-year birds are consistent with parental foraging trips near and north of the Hawaiian Islands, as shown by satellite tracks from Maui petrels (Fig. 2). In contrast, petrels from Hawaii likely provision their chicks with prey from southeast of the Hawaiian Islands, based on the elevated $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in the feathers of Hawaii hatch-year birds. Our interpretations of feather data are supported by multiple observational studies. For example, petrels breeding on Hawaii visit their nests more frequently than petrels on Maui, presumably due to shorter foraging trips to different at-sea locations (12, 25). In addition, at-sea observations show that Hawaiian petrels are more concentrated to the southeast of the Hawaiian Islands from October to December (the late breeding season and early nonbreeding season) than during the midbreeding season, consistent with our interpretation that adult petrels move toward this area during the early nonbreeding season (14). Overall, feather data show substantial variation in foraging location, both seasonally and among populations. In contrast, neither $\delta^{15}\text{N}$ nor $\delta^{13}\text{C}$ values of bone collagen vary significantly among modern petrel populations (comparisons of collagen $\delta^{15}\text{N}$ among populations can be found in Table S2; ANOVA for $\delta^{13}\text{C}$, $P = 0.597$, $F = 0.8434$, $df = 11$). Isotopic signals of location are apparently averaged out in modern bone collagen, likely due to the long time period represented by this tissue and the extensive foraging range of individual birds over the course of the breeding and nonbreeding seasons, combined.

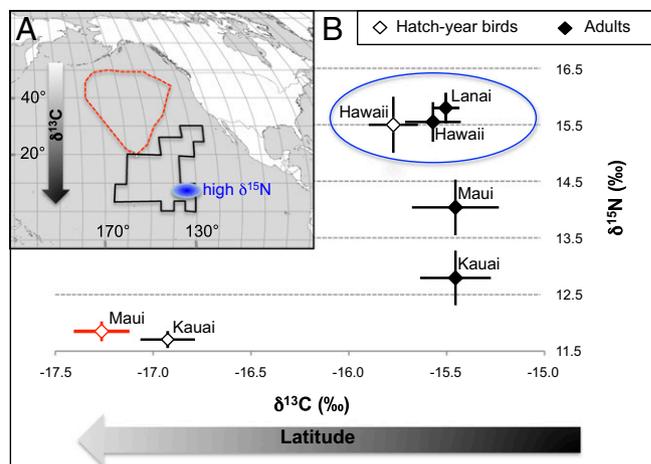


Fig. 2. Flight feather isotope data and at-sea locations of Hawaiian petrels. In A, the black line marks Hawaiian petrel distribution from transect surveys (14). The red dashed line is a typical flight path from a satellite-tracked Maui bird during the breeding season (13). These two regions represent the predominate areas where Hawaiian petrels occur. In A, the blue oval denotes an approximate area where organic matter and consumers have unusually high $\delta^{15}\text{N}$ values within the Hawaiian petrel's range (23, 24). In B, the blue circle identifies petrels that apparently concentrate their foraging in a region with elevated $\delta^{15}\text{N}$. In both panels, arrows emphasize the negative relationship between latitude and $\delta^{13}\text{C}$ of marine organisms (20–22). Hatch-year birds from Maui are outlined in red to associate them with the Maui flight path.

To evaluate temporal trends in foraging, we first grouped collagen samples into island populations: a grouping that allowed separate examination of genetically distinct populations with disparate foraging locations. Next, we divided collagen samples into time bins and compared average isotope values using ANOVA and Tukey honestly significant difference (HSD) post hoc tests (Fig. 3, Table S2). The initial time bins are based on archaeological chronology in the Hawaiian Islands, which were the population center for people fishing within the oceanic range of the Hawaiian petrel until historical times (in contrast, aboriginal people living on continents concentrated their fishing in near-shore environments of the continental shelves) (3, 5). The later time bins reflect the Historic period of Western economic development and whaling in Hawaii and the oceanic eastern North Pacific, followed by the Modern period of industrialized fishing.

Our isotope chronologies show that $\delta^{15}\text{N}$ disparities among populations have decreased through time. Before the Historic period, $\delta^{15}\text{N}$ values of bone collagen differ by as much as 2‰ and show statistically significant separation (Fig. 3, Table S2). In contrast, isotopic segregation is only observable among modern populations over the short time scales represented by flight feathers. This isotopic convergence of populations may be related to a seemingly concurrent, species-wide shift in $\delta^{15}\text{N}$ values.

Between the Prehuman and Modern periods, we observed significant $\delta^{15}\text{N}$ declines for petrel populations on Lanai, Maui, and Hawaii (all of the populations from which modern samples were available) (Fig. 3, Table S2). $\delta^{15}\text{N}$ values from the sample-rich Hawaii chronology did not decline until sometime after the early Expansion period ($P < 0.01$ for Expansion vs. Modern periods, $P = 0.44$ for Prehuman vs. Expansion periods). The 10 most recent Expansion period samples from Hawaii (average age = 204 B.P.) had an average $\delta^{15}\text{N}$ of $16.8 \pm 0.5\text{‰}$, which is similar to the average $\delta^{15}\text{N}$ of the remaining samples in this time period ($16.5 \pm 0.1\text{‰}$) and implies that the $\delta^{15}\text{N}$ decline occurred after ca. 200 B.P. Petrels collected on the island of Molokai in 1914 have an average $\delta^{15}\text{N}$ value that does not differ significantly

from that of any ancient population ($P = 0.072$ for Prehuman Hawaii, $P > 0.76$ for all other comparisons), but is higher than the $\delta^{15}\text{N}$ of modern Maui and Lanai populations (Table S2), suggesting that $\delta^{15}\text{N}$ decline occurred within the past 100 y. Notably, the decline in $\delta^{15}\text{N}$ between ancient and modern petrels is a robust characteristic of our timelines: it is present regardless of the time bins chosen for the ancient samples. Preceding the isotopic decline, a relative stasis in average $\delta^{15}\text{N}$ values is supported by results from the islands of Oahu, Hawaii, and Maui. When the Modern time bin is excluded, there is no decline in $\delta^{15}\text{N}$ for Maui or Hawaii (Table S2). Similarly, before its extirpation around 600 B.P. (615 B.P., youngest date), there is no change in $\delta^{15}\text{N}$ of the Oahu population ($P = 1.00$). Overall, our data support a recent, species-wide shift in $\delta^{15}\text{N}$ that was unprecedented during the last 4,000 y.

We considered whether anthropogenic impact to $\delta^{15}\text{N}$ through a North Pacific-wide input of isotopically unique nitrogen could have influenced our results. However, atmospheric deposition of ^{15}N -depleted anthropogenic nitrogen to the ocean and a possible increase in nitrogen fixation together cannot explain even a 0.2‰ decrease in $\delta^{15}\text{N}$ values (see modeling in SI Text S1). Additionally, we find no evidence that Hawaiian petrel $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values vary with the El Niño Southern Oscillation or longer term climatic perturbations (Materials and Methods) (15). Furthermore, because all modern island populations have lower average $\delta^{15}\text{N}$ values than all ancient populations, migration among islands cannot explain the $\delta^{15}\text{N}$ decline. This conclusion is supported by genetic analyses, which show that migration was very low among islands before human colonization and is currently low among extant populations (17, 18).

We considered whether declining population size in the Hawaiian petrel could be causally linked with the observed isotopic shift. However, the timing of $\delta^{15}\text{N}$ decline argues against this explanation. Our analysis identifies the isotopic shift occurring most likely within the past 100 y. While the population trend over the past century is not well documented, the majority of population

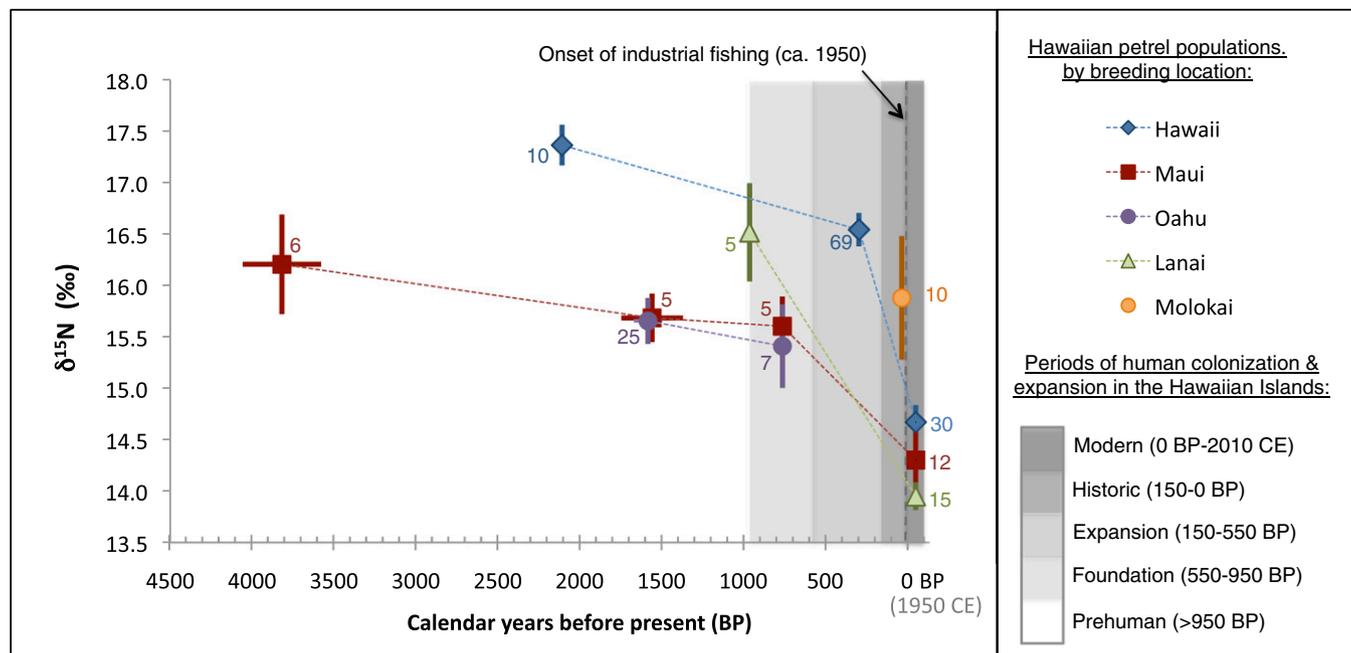


Fig. 3. $\delta^{15}\text{N}$ values of modern and radiocarbon-dated bone collagen for five Hawaiian petrel populations. The average age and isotopic composition of each time bin, \pm SE, is plotted with sample size noted (see Fig. S1 for $\delta^{13}\text{C}$ results and Fig. S2 for confidence intervals of radiocarbon dates). Gray shading indicates time bins. Modern samples were unavailable from Oahu and Molokai due to population extirpation. Stippled lines connecting data points are for visualization purposes; isotopic shifts between time bins may have occurred nonlinearly. CE, Common Era.

Kauai hatch-years ($n = 12$), Maui adults ($n = 13$), Maui hatch-years ($n = 9$), and Lanai adults ($n = 17$).

We sampled 132 subfossil bones from sites across four of the Hawaiian Islands (Fig. 1; see ref. 18 for distinction between archaeological and paleontological sites). The distribution of the paleontological sites helps to record the former breeding range of the Hawaiian petrel, which was more extensive than either the modern or historical range. The Hawaiian petrel was not recorded historically from Oahu, West Molokai, or the leeward slope of Haleakala Volcano on Maui (46). Its subfossil bones, however, are abundant and widespread on the extensive Ewa Plain of southwest Oahu, to near sea level; they also occur near sea level in the dunes of West Molokai, and in lava caves of East Maui, documenting a former breeding range down slope as far as 808 m above sea level (asl) at Lua Lepo Cave (28, 29). On the island of Hawaii, active burrows have been recorded historically only from above 2,500 m asl on Mauna Kea and from above 1,800 m asl on Mauna Loa, although 19th-century interviews record indigenous knowledge of a wider prior breeding range, particularly in the saddle region between Mauna Loa and Mauna Kea (46). However, the species is very common and widespread in paleontological sites that extend past the known historic range, including areas in North Kona from the saddle region down to Kawaihai Bay, in the Puu Waawaa region of Hualalai Volcano, as well as in South Kona to near South Point.

Stable Isotope and Accelerator Mass Spectrometry Radiocarbon Methods. Before stable isotope analysis, feathers were washed in solvent (87:13 chloroform–methanol, v:v), rinsed with ultrapure distilled water (E-Pure, Barnstead), and dried at 25 °C in a vacuum oven. Stable isotope data were obtained from samples representative of the entire feather vanes (47).

Collagen was isolated and purified using a method modified from Stafford et al. (48). Bones were decalcified with quartz-distilled hydrochloric acid (0.2–0.5 M) and soaked in 0.05 M potassium hydroxide overnight to remove humate contaminants. The resulting collagen was gelatinized with 0.05 M hydrochloric acid (110 °C, 1–3 h), passed through a 0.45 μm Millipore HV filter, and lyophilized. One aliquot of gelatinized collagen was used for stable isotope analysis. For ancient samples, a second aliquot of gelatinized collagen was hydrolyzed in hydrochloric acid (6 M, 22 h) and passed through a column containing XAD-2 resin to remove fulvic acids. The resulting hydrolysate was dried, combusted to CO₂, and graphitized for Accelerator Mass Spectrometry (AMS) dating (W. M. Keck Carbon Cycle AMS laboratory, University of California, Irvine). Background contamination from ¹⁴C-depleted and ¹⁴C-enriched carbon during the preparation of each sample set was evaluated by dating hydrolyzed gelatin of known age: ¹⁴C-dead whale (ca. 70,000 y B.P.) and *Bison bison* (mean pooled radiocarbon age, 1,794 ± 5.8 y B.P., $n = 9$).

For 10 ancient samples, collagen was extracted at the Keck facility using techniques modified from Longin 1971, followed by ultrafiltration (49, 50). We demonstrated the comparability of dates obtained using XAD-2 purification versus Longin-ultrafiltration methods. First, we compared dates obtained from the *B. bison* sample (median probabilities of 1,740–1,820 y B.P., $n = 10$, by XAD purification; 1,750–1,785 y B.P., $n = 2$, for Longin-ultrafiltration). Second, we compared dates from Hawaiian petrel bones found in a short-term archaeological site, Fireplow Cave, Hawaii (median probabilities of 459–525 y B.P., $n = 4$, for XAD purification; 473–482 y B.P., $n = 3$, for Longin-ultrafiltration). In both cases, dates for the Longin-ultrafiltration methods fell within the range of those prepared using XAD purification.

We calibrated our conventional radiocarbon ages using the program CALIB 6.0 and applied a marine reservoir correction to account for incorporation of ¹⁴C-depleted marine carbon. Specifically, we included a global model of the marine reservoir effect (Marine09 model), along with a regional correction, or ΔR, of 54 ± 20 y, calculated specifically for the Hawaiian petrel. We calculated our correction for the Hawaiian petrel by comparing radiocarbon dates on Hawaiian petrels and a terrestrial species (Hawaiian goose, *Branta sandvicensis*) in a short-term archaeological site, and also by obtaining radiocarbon dates on known-age museum specimens of the Hawaiian petrel collected in 1914–1917, before the age of atmospheric nuclear bomb testing. All radiocarbon dates referred to in the text are median probabilities, or the average of median probabilities from a group of samples. Similarly, median probability dates were used for all graphing and statistical analysis.

^{δ13C} and ^{δ15N} values of gelatinized collagen (ca. 1.0 mg) were determined using an elemental analyzer (Eurovector) interfaced to an Isoprime mass spectrometer (Elementar). Stable isotope values are expressed in per mil (‰) as: $\delta X = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1,000$, where X is ¹³C or ¹⁵N, R is the corresponding ratio ¹³C/¹²C or ¹⁵N/¹⁴N, and R_{standard} is Vienna-Pee Dee Belemnite and air for ^{δ13C} and ^{δ15N}, respectively. Precision was ≤0.2‰ for both ^{δ13C} and ^{δ15N}.

We corrected for the Suess Effect using an ice-core–based estimate of the rate of ^{δ13C} decrease in the atmosphere: 0.22‰ per decade since 1960, and 0.05‰ per decade between 1860 and 1960 (51, 52). All stable isotope and radiocarbon data from subfossil bones can be found in Table S3. Stable isotope data from modern and historic bones and feathers are in Table S4.

Temporal and Statistical Analysis. Isotope data from gelatinized collagen were binned based on archaeological and historical time periods marking the growth and development of the human population of the Hawaiian Islands, plus one bin covering the modern period of industrial fishing. Based on Hawaiian archaeology and history, the following time bins were used: the Prehuman period (before human colonization; <1000 CE or >950 y B.P.), the Foundation period (time of Polynesian colonization, with small human population size; 1000–1400 CE; 550–950 y B.P.), the Expansion Period (characterized by increasing human population size; 1400–1800 CE; 150–550 y B.P.), the Historic Period (including the period of European colonization and whaling; 1800–1950 CE; 0–150 y B.P.), and the Modern period (a time of industrialized fishing in the North Pacific; 1950–2010 CE) (4, 6, 53). We subdivided the Prehuman time bin for the island of Maui in half along a natural gap in the data of >850 y, due to the exceptionally long period of ca. 3,500 y covered by those samples. We combined all ancient samples (>100 y old) from the island of Lanai into one time bin, due to their relatively narrow range of dates (899–1,088 y B.P.) and our small sample size ($n = 5$).

The effects of island population and time on collagen isotope values were evaluated through multiple ANOVA models. For ^{δ15N} only (where both population and time had significant effects), Tukey HSD post hoc tests were used to make all possible pair-wise comparisons between population–time bin groups. ANOVA and Tukey HSD tests were similarly used to evaluate isotopic variation among modern feathers. Normal quantile–quantile plots and Levene's tests were used to check assumptions of normality and homogeneity of variance. All statistical tests were conducted using R statistical software (version 2.12.1, R Foundation for Statistical Computing, 2010).

Age Classification for Bones. Among subfossil bones in our ancient chronologies, six were identified as hatch-year birds (<1 y in age) based on osteological evidence of incomplete bone formation (using indications such as open sutures, spongy texture, and the presence of small pores and striations; *SI Text S3* and *Fig. S3*): one from Oahu, three from Lanai, and two from Hawaii. For the island of Maui, all modern and ancient hatch-year bones were excluded from analysis due to the isotopic disparities observed between age classes in the modern population for both feather and bone (t test comparing six hatch-year and 10 adult bones: $P = 0.021$ for ^{δ15N} and $P = 0.018$ for ^{δ13C}). We retained hatch-year petrels in our chronology for the island of Hawaii, because no isotopic disparity was observed between age classes for either feathers or bones in the modern population from this island (t test comparing eight hatch-year and 18 adult bones: $P = 0.862$ for ^{δ15N} and $P = 0.690$ for ^{δ13C}), and because the average ^{δ15N} value for the known hatch-year birds in the ancient chronology was the same as the average for all ancient Hawaii birds (16.6‰). While hatch-year birds were included in our ancient sample from Lanai, the modern sample from this island consists entirely of adults. For Lanai, the three ancient hatch-years have lower ^{δ15N} values than the ancient adults, as we would expect based on the foraging pattern of breeding Lanai adults, which appears to be similar to that of Maui birds (13, 54). The inclusion of hatch-year petrels in the Lanai chronology will tend to lower the average ^{δ15N} value for our ancient Lanai time bin, perhaps causing us to underestimate any ^{δ15N} decline through time.

Effects of Climate on Hawaiian Petrel ^{δ15N} Values. We used a measure of El Niño Southern Oscillation (ENSO), the Southern Oscillation Index (SOI), to evaluate potential impacts of climatic variation on ^{δ15N} of modern Hawaiian petrel flight feathers. SOI values, standardized according to the methods of Trenberth 1984 (www.cgd.ucar.edu/cas/catalog/climind/soi.html) (55), were averaged over the months surrounding flight feather growth (September–December for hatch-year birds; November–March for adults, with SOI averages offset by 1 mo for all Maui petrels to account for their earlier breeding cycle; SOI values used in statistical analyses can be found in Table S4). We used an analysis of covariance (ANCOVA) to test for an effect of SOI while accounting for the variance associated with age class (adult vs. hatch-year) and population. Based on data from all of the flight feathers where year of collection was known ($n = 82$; Table S4), SOI had a statistically insignificant effect on ^{δ15N} values (t value = 0.055, $P = 0.9559$). Additionally, we compared ^{δ15N} values from the most data-rich El Niño event (Fall/Winter of 2006) and La Niña event (Fall/Winter of 2007) for petrels nesting on the islands of Lanai and Hawaii (all data combined, as the ^{δ15N} values of these age

groups and populations were not significantly different). Because there was unequal variance in $\delta^{15}\text{N}$ among years (F statistic = 0.0039), we performed a Welch t test, which showed no significant difference in $\delta^{15}\text{N}$ between the El Niño and La Niña years ($t = -0.6282$, $P = 0.599$, $n = 18$, $df = 6.928$).

We also did not detect a significant difference in average isotope values between our Prehuman time bins (4,409–955 B.P.) and Foundation time bins (555–914 B.P.) (Fig. 2, Table S1), a time span that encompassed considerable climatic variation around the Pacific basin (e.g., Medieval Warm Period vs. cooling at ca. 1,500 B.P.) (56, 57).

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