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Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer

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Abstract

Electronic tracking tags have revolutionized our understanding of broad-scale movements and habitat use of highly mobile marine animals but a large gap in our knowledge still remains for a wide range of small species. Here we report the extraordinary transequatorial post-breeding migrations of a small seabird, the sooty shearwater, obtained with miniature archival tags that log data for estimating position, dive depth, and ambient temperature. Tracks (262 ± 23 days) reveal that shearwaters fly across the entire Pacific Ocean in a figure-eight pattern, while traveling 64,037 ± 9,779 km roundtrip – the longest animal migration ever recorded electronically. Each shearwater made a prolonged stopover in one of three discrete regions off Japan, Alaska, or California, before returning to New Zealand through a relatively narrow corridor in the central Pacific Ocean. Transit rates as high as 910 ± 186 km day^{-1} were recorded and shearwaters accessed prey resources in both the northern and southern hemisphere's most productive waters from the surface to 68.2 meters depth. Our results indicate that sooty shearwaters integrate oceanic resources throughout the Pacific Basin on a yearly scale. Sooty shearwater populations are today declining and because they operate on a global scale, they may serve as an important indicator of climate change and ocean health.

Animal migration is widely regarded as a biological phenomenon driven by seasonal cycles in food supply and weather patterns (1). Although migration patterns of a few marine predator species have recently been established using electronic tags (2-5), the spatial and temporal dynamics of individuals is unknown for most species. This is particularly true of oceanic seabirds that spend up to 90% of their lives in the open sea (6).

Sooty shearwaters (*Puffinus griseus*) are small seabirds (*ca*. 800 g) that are currently one of the most abundant species in the world (7). Observations of migrating sooty shearwaters at sea suggest that the population conducts a transequatorial pan-Pacific flight (8, 9). However, without tracking individual birds from a known provenance, it is impossible to determine the exact timing and direction of migratory flyways or the individual spatial and temporal patterns of habitat use once at the designated wintering grounds (3). Sooty shearwaters are major consumers of marine resources (10), and given their large population size, which is estimated to be several million birds (11), their potential impact on resources at the wintering grounds is likely to be significant. However, we know little about their specific foraging and activity patterns. Recent evidence also shows that sooty shearwater populations are declining in the northern and southern hemisphere, purportedly as a result of climate change (12, 13) and fisheries interactions (14). Studying the at-sea behavior and distributions of shearwaters may therefore be critical for understanding the putative causes of their decline.

Here, we report the extraordinary migratory journeys and broad-scale habitat use of sooty shearwaters, using miniature archival geolocating tags. The data reveal that shearwaters traverse the entire Pacific Ocean while integrating oceanic productivity over a global scale.

Results and Discussion

Sooty shearwaters (n = 19) were tracked with geolocating archival tags from two breeding colonies in New Zealand (see Materials and Methods), for an average of 262 days (± 23 days, 222 – 313 days). The Pacific Ocean migration cycle had a figure-eight pattern (Fig. 1) that lasted an average of 198 ± 17 days. Shearwaters made directed movements between both ends of the Pacific basin with prolonged aggregations on the wintering grounds in the North Pacific. All shearwaters (10 females, 4 males, 5 undetermined) used the entire Pacific Ocean (Fig. 1) with latitudinal coverage ranging from Antarctic waters to the Bering Sea and longitudinal coverage ranging from Japan to Chile. No sex-specific behavioral tendencies were observed and each individual from three different breeding pairs dispersed independently of each other (Fig. 1 b, c, d). These extraordinary migration routes (64,037 ± 9,779 km excluding the breeding period) represent the longest recorded of any animal tracked to date. Although new information has been shed on the remarkable flight capabilities and distribution of albatrosses during sabbatical years using electronic tags (2, 3, 15), until now, almost nothing comparable was known about smaller seabird species (< 1 kg) outside their breeding periods. Arctic terns (*Sterna paradisaea*) undertake a similar transequatorial migration as sooty shearwaters (16, 17) but the movements of individual terns have not been studied so the true ranges, distances and rates of travel, habitat usage, and migratory flyways remain equivocal. Cory’s shearwaters (*Calonectris diomedea*), another small seabird (*ca*. 700 g), have also been tracked outside the breeding period using satellite telemetry (18) but the migration tracks were incomplete so the ranges and extent of migration are unknown.

We hypothesize that the figure-eight migration pattern of sooty shearwaters is facilitated by global wind circulation patterns and the Coriolis effect, which influence the long-range trajectories of the birds as they fly rapidly between hemispheres (9). At the start of migration in early April, shearwaters traveled eastward between 40 – 60°S in the direction of prevailing westerly winds at rates of 536 ± 159 km day^{-1}. Once shearwaters began heading north from the Southern Ocean, they appeared to use easterly trade winds to travel northwest across the Pacific. The highest transit rates were achieved during this period (910 ± 186 km day^{-1}) and birds were displaced an average of 38° (± 20°) west of their starting longitude in the southern hemisphere (Fig. 1). Upon arrival into cool oceanic waters above 30°N (14.2 ± 3.0°C, tag temperatures prior to diving, see Fig. 2), shearwaters traveled to one of three wintering grounds, where they resided for the remainder of the migration cycle. On the wintering grounds, shearwater transit rates were significantly reduced (220 ± 37 km day^{-1}) and movements were confined to discrete regions of the North Pacific with no movement between regions. The figure-eight pattern is completed when birds return to New Zealand waters, again purportedly using easterly trade winds in a south-westerly direction, at rapid travel speeds (837 ± 134 km day^{-1}). Remarkably, travel of all birds across the equator is highly synchronized (7 October ± 5 days) and passage is through a narrow corridor (157°W ± 9°).

Very little information exists on the population structure of migrating sooty shearwaters (9, 10). However, we determined that shearwaters from both our study populations, separated by 850 km, overlapped completely within their distributions in both the South and North Pacific Oceans (Fig. 1). Four birds also traveled to the coast of Chile, where a sizeable population of sooty shearwaters breed (19), before migrating northward. This suggests that populations of sooty shearwaters from either side of the Pacific could easily mix within any of the major migration destinations of the North Pacific. Both members of a breeding pair also travel to either different or similar regions of the North Pacific during migration (Fig. 1), suggesting that shearwaters from the same provenance, let alone the same nest, are not geographically constrained. Alternatively each individual could have a specific sector where it winters, because no shearwaters moved between 'over-wintering' regions. It is even possible that some individuals return to the same areas from one year to the next, as it has been observed for albatrosses during sabbatical years (2, 3).

The tracking data reveal that sooty shearwaters experience a perpetual cycle of spring, summer, and autumn from year to year. When shearwaters breed in the austral spring/summer, they predominantly travel to cold Antarctic waters (4.4 ± 2.9°C, tag temperatures prior to diving), where they engage in intense diving activity (Fig. 2), indicative of foraging, to mean depths of 14.2 ± 11.1 meters (max 68.2 meters). Upon completion of breeding in the austral autumn, shearwaters undertake their migration to one of three areas in the western, central, or eastern North Pacific: 1) Kuroshio and Oyashio Currents region off Japan and Kamchatka Peninsula, 2) eastern Aleutian Islands and Gulf of Alaska region, or 3) the California Current region (Fig. 1). The timing of their arrival upon the wintering grounds (4 May ± 13.4 days), occurs when oceanic productivity in the North Pacific exceeds that found in the South Pacific (Fig. 3). The North Pacific wintering grounds are biologically productive due to physical forcing, converging water masses, or coastal upwelling, which promote primary and secondary production attracting fish, squid, and krill consumed by sooty shearwaters (8, 10). Shearwater foraging activity is evident from the propensity of diving activity (Fig. 2; 10.7 ± 8.2 meters, max 51.2 meters) in highly productive waters during prolonged residency periods (150.9 ± 12.4 days). Thus, sooty shearwaters appear to seek out biologically productive areas to 'over-winter' in the northern hemisphere summer and similar regions in the southern hemisphere summer when breeding. Indeed, 95% of all recorded dives (n = 4,370) occurred within these highly productive regions in both hemispheres (Fig. 2). The pursuit of an 'endless summer' by transiting between hemispheres, allows sooty shearwaters to integrate peak oceanic resources on a global scale throughout the year (Fig. 3).

The ability of sooty shearwaters to travel throughout the Pacific Ocean is a key element of their migration strategy that may have evolved as a mechanism to buffer the birds from interannual variability in Pacific-wide biological productivity, in particular during El Niño Southern Oscillation events (20). Importantly, climate change (21) may impact sooty shearwater populations if warming trends influence major ecosystem dynamics of the North Pacific (e.g. 22). Indeed, sooty shearwater populations have declined in recent years both at breeding colonies in New Zealand (23) and at wintering grounds in the eastern North Pacific (12, 13). These trends were associated with concomitant increases in oceanic temperatures, which may have limited regional biological productivity (12, 13, 23). Significant food limitation over the course of a long-distance migration could ultimately lead to increased shearwater mortality, or to an abstention of breeding upon return to the southern hemisphere. Distributional shifts between wintering regions of the North Pacific could also account for the observed declines (12, 13). However, this seems less likely because our study confirms that shearwaters range throughout the North Pacific Rim, without movement between regions, during a given migration cycle. Fisheries interactions also impose a significant risk for sooty shearwaters as birds are caught as bycatch in several driftnet fisheries in the western North Pacific (14). Hence, the capacity of sooty shearwaters to fly and integrate resources over trans-Pacific scales, combined with recent declines in their abundance, implies that they may serve as a sensitive species to monitor the impacts of global climate change and health of oceanic ecosystems.

Materials and Methods

In January-March 2005, we deployed 33 archival tags (Lotek 2400, Lotek Wireless, Canada) on breeding sooty shearwaters at two colonies in New Zealand (Codfish Island/Whenua Hou, 46.8°S, 167.7°E, n = 25 birds and Mana Island, 41.1°S, 174.8°E, n = 8 birds). Breeding begins in late November to early December and ends in April to early May (6). Archival tags recorded the daily activities of each bird during the latter part of breeding, the complete trans-Pacific migration cycle, and for some birds, the prenuptial period prior to the start of the next breeding cycle. All birds were captured in their underground burrows, using methods described elsewhere (24). For most study burrows, only a single partner was equipped with an archival tag; however, we equipped both members of three breeding pairs from Codfish Island/Whenua Hou to determine the dispersion of the pair (Fig. 1 b, c, d). Gender was determined by molecular methods (25).

Geolocations (n = 4,736) based on ambient light levels from each archival tag were recorded, processed, and error-checked according to previous validation studies (26, 27), which yielded mean errors of 184 ± 114 km and 202 ± 171 km, respectively (see Supporting Information). All filtered locations (93% of original locations) were interpolated at 10 minute intervals (28) for subsequent analyses of movement patterns and for estimating dive locations of each bird. In addition, the tags recorded pressure and temperature at 432 s intervals throughout the tracking period, which provided a sub-sample of diving depths and environmental temperatures from activity at sea. The environmental temperatures were used in combination with light-based longitudes to improve or obtain latitude estimates (27, 29) during the equinox periods when light-based geolocation is unreliable (30). All data are presented as mean ± s.d.

Twenty shearwaters (15 at Codfish/Whenua Hou and 5 at Mana) were recaptured at their same breeding burrows, between October 2005 and February 2006. Each shearwater returned with a tag, and with exception of minor callusing on the legs of some birds, all adults were in good physical condition with body masses similar to those of non-equipped shearwaters ($n = 37$; 14 chosen at random for comparison to tracked birds; t-test, $t_{26} = -1.56$, $P = 0.131$). Nineteen of 20 recovered tags provided complete records of tracks during breeding and migration (Fig. 1) and 11 tags provided records of diving depths and environmental temperatures (Fig. 2 a, b). Non-recovered tags could have fallen off at sea, although no equipped shearwaters were recaptured without a tag. Birds may have avoided detection and changed breeding burrows, or potentially they did not survive the postbreeding migration.

Vertically-integrated primary productivity rates for the ocean were calculated for successive 8-day periods from October 1997 to December 2005 (time series analysis only, see below) from measurements of Chlorophyll *a*, temperature, and photosynthetically available radiation (PAR) using the method of Behrenfeld and Falkowski (31). Estimates of Chlorophyll *a* (32) and PAR (33) were derived from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) carried aboard the Orbview-2 spacecraft. Sea surface temperatures were adapted from Reynolds (34), and estimates of daylength were derived from basic celestial mechanics (35). Data were extracted from the resulting global time series for boxes with a spatial extent of 1° longitude and 2° latitude centered at each calculated position and time (2005 only) occupied by the birds (Fig. 2 c). The dimensions of this box were chosen based on the error of the geolocation method (26, 27). To compare the seasonal signal in primary production with the shearwaters' migration patterns, time series (1997 – 2005) were extracted for two large boxes that bounded 85% of all filtered geolocations and 90% of all dive locations (box 1: 35°S – 70°S by 120°E – 140°W in the south; box 2: 30°N – 60°N by 130°E – 120°W in the north). These time series were then used to develop 'climatologies' for each region frequented by the shearwaters (Fig. 3).

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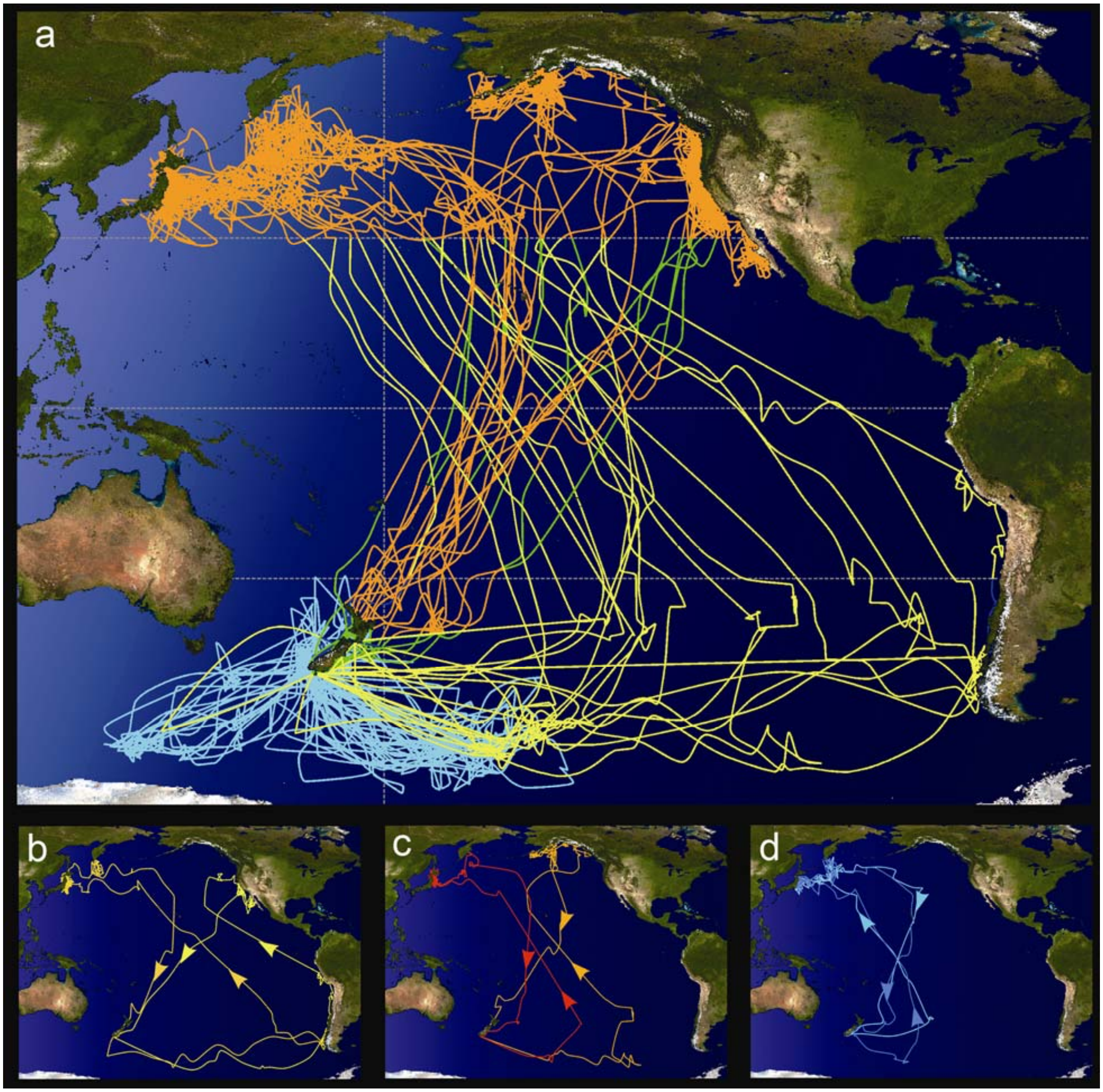
Figure Legends

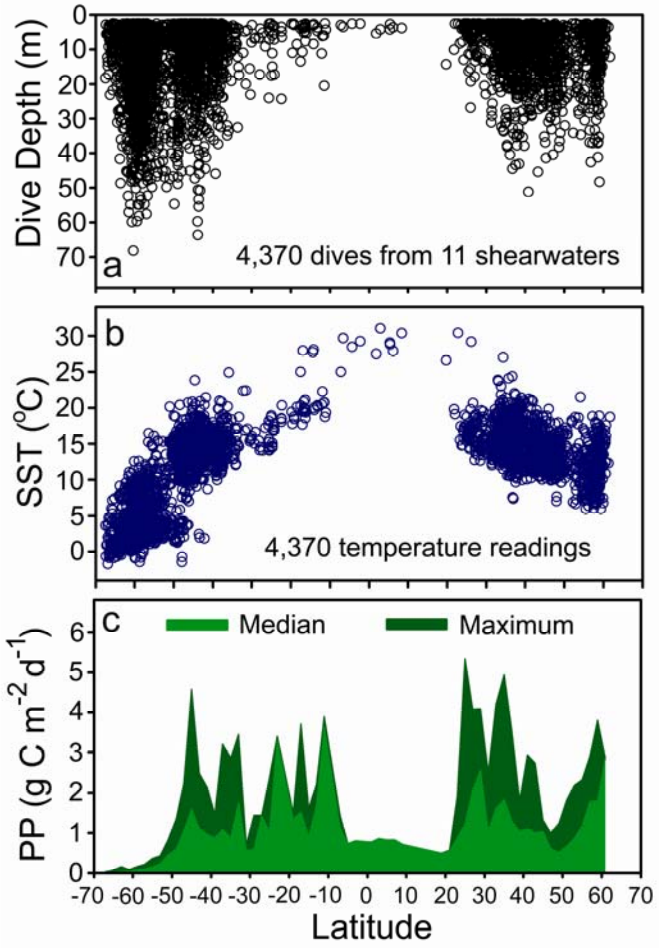
Fig. 1. a) Interpolated geolocation tracks of 19 sooty shearwaters during breeding (light blue) and subsequent migration pathways (yellow – start of migration and northward transit, and orange – wintering grounds and southward transit). Panels' b, c, and d illustrate representative figure-eight movement patterns of individual shearwaters traveling to one of three 'winter' destinations in the North Pacific. These tracks also represent those of three breeding pairs to reveal the dispersion and extent of each pair. The 30° parallels, equator, and International Dateline are indicted by dashed lines. Image created using Blue Marble dataset (36).

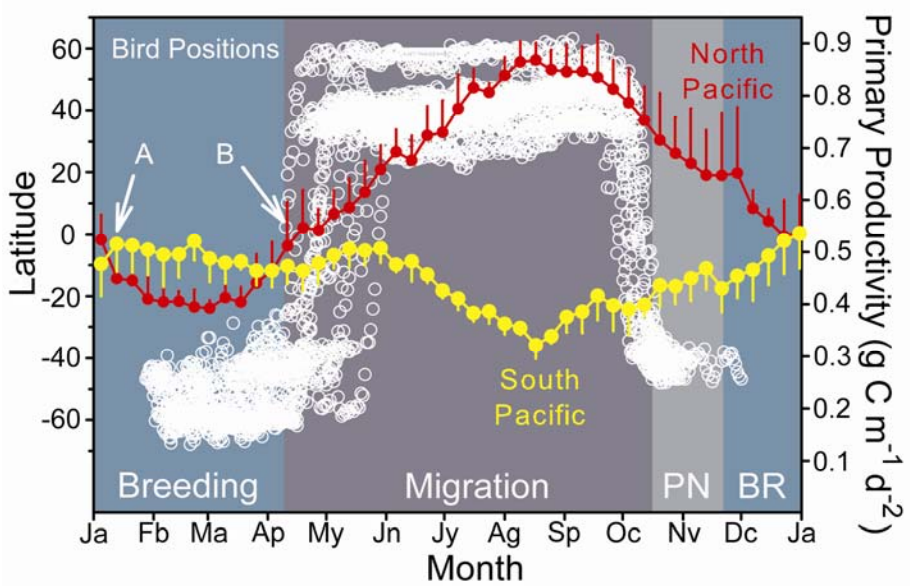
Fig. 2. Sooty shearwater diving depths and frequency (a), sea surface temperatures experienced (b), and primary productivity (c) at each dive location, in relation to latitude. Sea surface temperatures (SST) were recorded by the archival tags on each bird just prior to a dive. Primary productivity (PP) was measured remotely by satellite and overlaid onto the locations of each dive (see Materials and Methods). Note the paucity of dives, warm sea surface temperatures, and low primary productivity at low latitudes of the South and North Pacific when shearwaters cross the equatorial region.

Fig. 3. Sooty shearwater latitudinal movements (white open circles, n = 4,375 filtered locations) and primary productivity in the South (yellow) and North (red) Pacific throughout the year. Primary productivity is represented by the mean (± s.d.) of 8-day productivity from 1997 to 2005

encompassing the geographic regions where sooty shearwaters most frequently occurred (see Materials and Methods). The shaded regions represent the time periods for breeding (BR), migration, and prenuptial (PN) phases. Note that chick-hatching (A) occurs during the austral summer when productivity becomes higher in the South Pacific than in the North Pacific. Upon completion of breeding, the onset of migration coincides with the period when primary productivity becomes higher in the North Pacific (B). Primary productivity in the North Pacific peaks several months before shearwaters return to the South Pacific. Shearwaters conduct the reverse migration in October when productivity is still higher in the North Pacific. However, the timely return is required so adults can court during the prenuptial phase and lay an egg that will hatch (A) when productivity is the highest available at that time (i.e. between A & B).


a
b
c
d


Dive Depth (m)
0
10
20
30
40
50
60
70
a
4,370 dives from 11 shearwaters
SST (°C)
30
25
20
15
10
5
0
b
4,370 temperature readings
PP (g C m-2 d-1)
6
5
4
3
2
1
0
c
Median
Maximum
-70 -60 -50 -40 -30 -20 -10 0 10 20 30 40 50 60 70
Latitude


Bird Positions
North Pacific
South Pacific
A
B
Breeding
Migration
PN
BR
Latitude
60
40
20
0
-20
-40
-60
Primary Productivity (g C m-1 d-2)
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
Ja
Fb
Ma
Ap
My
Jn
Jy
Ag
Sp
Oc
Nv
Dc
Ja
Month