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Contemporary and historical separation of transequatorial migration between two genetically-distinct seabird populations

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Abstract

Pelagic seabirds are highly mobile, reducing the likelihood of allopatric speciation where disruption of gene flow between populations is caused by physically insurmountable, extrinsic barriers. Segregation during the non-breeding season appears to provide an intrinsic barrier to gene flow among seabird populations that otherwise occupy nearby or overlapping regions during breeding, but how this is achieved remains unclear. Here we show that the two genetically distinct populations of Cook's petrel (*Pterodroma cookie*) exhibit transequatorial separation of non-breeding ranges at contemporary (ca. 2-3 yrs) and historical (ca. 100 yrs) time scales. Segregation during the non-breeding season *per se* appears an unlikely barrier gene flow. Instead we provide evidence that habitat specialisation during the non-breeding season is associated with breeding asynchrony which, in conjunction with philopatry, restricts gene flow. Habitat specialisation during breeding and non-breeding likely promotes evolutionary divergence between these two populations via local adaptation.

Introduction

Divergent migratory behaviours to and from breeding sites have led to the disruption of gene flow among populations in many species [1,2], contributing to reproductive isolation under the classic model of allopatric speciation [3]. In terrestrial environments, genetic differentiation among migratory populations is frequently paralleled by extrinsic (e.g. mountain ranges) and intrinsic (e.g. timing of dispersal, inherited migratory direction, host use by parasites) barriers that restrict gene flow and facilitate divergence via genetic drift and/or selection [4-6]. However, the nature of the extrinsic and intrinsic barriers that disrupt gene flow among populations of marine animals have only recently begun to be investigated [7,8] and remain poorly known for many highly mobile taxa [8,9].

Seabirds undertake the longest known migrations on Earth, routinely crossing hemispheres between breeding and non-breeding habitat within ocean basins [10,11]. As a result of this extreme mobility, seabirds experience few apparent physical barriers to dispersal. Thus, seabirds can potentially visit and ultimately breed on islands thousands of kilometres from their natal colony, which may contribute to a lack of genetic structure observed in several species [12-15]. Yet other seabird species show surprisingly high levels of population genetic structure [8,16-18] and intrinsic barriers to gene flow appear to play an important role in the evolution of seabird diversity [4,18-22]. For example given the strong tendency for seabirds to return to their natal site to breed, natal philopatry has been proposed as such a barrier to gene flow [19]. However given that not all seabirds exhibit strong genetic structure it is unlikely to be the sole driver.

A recent meta-analysis suggests that segregation of non-breeding distributions may be a key determinant of genetic structure among seabird populations [8], but how occupying disjunct non-breeding distributions can restrict gene flow remains unclear. Although advances in tracking technology have improved our ability to record the long-distance movements of seabirds at sea [20], few studies have examined the non-breeding segregation amongst seabird populations that occupy nearby or overlapping regions during the breeding season [11,21]. Accordingly, the role of seasonal movements in shaping the genetic structure of seabird populations, and the persistence of these movement patterns at the timescale of generations, remain unknown. Such information is vital for providing insights into behavioural and ecological mechanisms underlying the diversification of highly mobile taxa, including those within oceanic environments.

Pterodroma cookii (Cook's petrel; Procellariiformes: Procellariidae Gray 1843), are pelagic seabirds that breed exclusively on two islands at the northern and southern extremes of their prehistoric range within the New Zealand archipelago [22]: Little Barrier Island (LBI) and Codfish Island (CDF), respectively [23,24]. When breeding, *P. cookii* range within the south-west Pacific and Tasman Sea, with overlapping foraging ranges centred around their respective breeding colonies [25]. Shipboard observations indicate that after breeding, *P. cookii* are trans-equatorial and trans-Pacific migrants, with sightings concentrated in the North Pacific (North-Pacific Convergence and centrally along Baja California) and in the South Pacific (Humboldt Current) Oceans [26]. On the basis of body size and plumage characteristics, in 1929 Murphy [27] distinguished between smaller *P. c. cookii* that were collected in the North Pacific and assigned to the breeding population at LBI, and the larger *P. c. orientalis*, of unknown breeding origin, collected south of the Equator, off the coast of Peru. Subsequently, Falla [28] observed

105 that the plumage and morphological characteristics of *P. cookii orientalis* were
106 consistent with juveniles of *P. cookii cookii* from the breeding population at CDF that
107 was discovered in 1934 [24]. In addition to differences in body size, body mass, and the
108 potential for non-breeding birds to occupy disjunct habitats [5,26,29], birds on LBI and
109 CDF exhibit a one-month asynchrony in breeding phenology [5] and are genetically
110 distinct [6]. These combined observations strongly suggest that gene flow between the
111 two extant *P. cookii* populations is highly restricted. Thus, *P. cookii* is an ideal study
112 species to explicitly examine whether and how occupying disjunct non-breeding
113 distributions can restrict gene flow among seabird populations.
114
115 Here we combined geolocator-based tracking with an isotopic ($\delta^{13}C$ and $\delta^{15}N$) and
116 genetic (mitochondrial cytochrome Oxidase subunit 1) comparison of modern breeding
117 birds, and historical specimens (i.e. museum skins), to test the hypothesis of
118 transequatorial separation of the two *P. cookii* breeding populations at varying temporal
119 scales. Specifically, we tested the predictions that contemporary *P. cookii* populations,
120 tracked over a complete annual cycle, would exhibit divergent non-breeding
121 distributions, habitat use, and foraging patterns; this divergence would be consistent
122 between contemporary cycles (ca. 2-3 years) as revealed by stable isotope analyses; the
123 stable isotope signatures of historical specimens of unknown breeding provenance
124 collected ca. 100 years ago from the two non-breeding oceanic regions used by
125 contemporary populations, would match those of modern samples, and that genetic
126 analysis would clearly assign origin of breeding population for these museum
127 specimens and confirm divergence in transequatorial migration of the *P. cookii*
128 populations over historical timescales. This combination of tracking, museum-based
129 investigation, and elemental and molecular analyses presents a novel opportunity to

evaluate how differences in contemporary and historical migratory behaviour can contribute to the diversification of a highly mobile marine species.

Results

Population movements

Consistent with the prediction that contemporary tracked *P. cookii* would exhibit divergent non-breeding distributions, our analysis reveals that birds tracked between consecutive breeding seasons using light-based geolocation loggers (hereafter called loggers) between 2007 and 2009 from LBI (n = 11: female (♀) = 5, male (♂) = 6) and CDF (n = 11: ♀ = 6, ♂ = 5) exhibited transequatorial separation of their non-breeding habitats within the Pacific Ocean (Fig. 1, Supplementary Fig. S1). This contrasts with previous studies of other transequatorial migrants, including related Procellariiform seabirds, which showed substantial overlaps in space use and mixing during the nonbreeding period of individuals that originated from different breeding populations [10,11,29]. Post-breeding LBI *P. cookii* (tracked for 389 ± 49 SD days) completed an anti-clockwise migration of 48,037 ± 7953 SD km within the North and South Pacific Ocean. Birds tracked from LBI moved east, then north across the equator to reach core non-breeding distributions within the California and North-Pacific currents (approximately 35°N) in 34 ± 8 SD days. Pre-breeding migration returning to New Zealand waters was completed in 20 ± 5 SD days (Fig. 1) on a direct southwest route. In contrast, post-breeding CDF *P. cookii* (tracked for 450 ± 3 SD days) migrated within the South Pacific Ocean (37,813 ± 6920 SD km) moving east then north within the Humboldt Current to reach core non-breeding distributions off the Peruvian Coast (approximately 15° S) in 19 ± 5 SD days. Pre-breeding migration returning to New Zealand was again completed in 20 ± 5 SD days through a south-western corridor, north

of the region traversed during post-breeding movements. Consistent with their breeding timetables, the migration schedule of both *P. cookii* populations was asynchronous; LBI birds commenced post- and pre-breeding migrations approximately 1 month before CDF birds (post-breeding 11 March ± 12 SD days vs. 8 April ± 15 SD days ($t_{(18)}$ = -4.67, $p < 0.0001$) ; pre-breeding 5 Sept ± 10 SD days vs. 20 Oct ± 6 SD days ($t_{(15)}$ = -11.85, $p < 0.0001$)).

During initial migration east towards South America, the routes taken by *P. cookii* from LBI and CDF overlapped, followed a similar direction to those of post-breeding sooty shearwaters (*Puffinus griseus*) [11] and Westland petrels (*Procellaria westlandica*) [30], but not Australasian gannets (*Morus serrator*), departing from New Zealand nesting colonies [31]. Subsequently, LBI birds moved north-west across the equator and eventually returned on south-westerly trajectories to New Zealand along routes that were directionally similar to sooty shearwaters [11], flesh-footed shearwaters (*Puffinus carneipes*) [32] and bar-tailed godwits (*Limosa lapponica baueri*) departing from on or off North America [33]. These observations highlight the existence of an important cross-taxa avian migration corridor within the Pacific Ocean between approximately 170° E and 160° W.

Isotopic and habitat segregation

P. cookii moult during the non-breeding period [26,34], and hence incorporate local isotopic dietary signals in their new plumage [35]. Stable isotope ratios of C ($\delta^{13}C$) and N ($\delta^{15}N$) in particular provide an indication of carbon source (benthic vs. pelagic, inshore vs. offshore, and information on water mass) and trophic level of prey, respectively [35], and comparisons thus can indicate geographic and/or dietary segregation [36,37].

Consistent with the prediction that geographic divergence would be consistent between the *P. cookii* populations at a contemporary timescale (ca. 2-3 years), there was no significant difference in the isotope signatures of *P. cookii* body feathers collected in 2006 and 2008 from LBI (2006 untracked n = 20, 2008 tracked n = 11)(δ^{13}C: Z = 0.83, p = 0.41; δ^{15}N: Z = 1.70, p = 0.10) or CDF (2006 untracked n = 20, 2008 tracked n = 9)(δ^{13}C: Z = 1.34, p = 0.19; δ^{15}N: Z = 1.79, p = 0.07)(Fig. 2) suggesting that, currently, within each breeding population, birds forage within similar oceanic regions and on prey of a similar trophic level in successive years.

In support of the prediction of a match between the stable isotope signatures of historical and contemporary samples sharing the same non-breeding provenance, variation in the δ^{13}C signatures of feathers from modern (LBI: 2006 and 2008 combined; CDF: 2006 and 2008 combined) and historical specimens collected within the core non-breeding habitats of birds tracked from LBI and CDF, respectively (samples collected in 1905 at 22.42°N, 112.67°W, North Pacific Ocean, in the California Current region off Baja California, hereafter called BC, and in 1913 at ca. 11°S, 79°W, South Pacific Ocean, in the Humboldt Current, hereafter called HC; Supplementary Tables S1 and S2) suggest that birds have used population-specific oceanic regions, with similar carbon signatures, at historical time scales (Fig. 1) ($F = 81.32$, $df = 2$, $p < 0.001$). The mean δ^{13}C value of LBI *P. cookii* (-17.18 ± 0.70 SD ‰) was not significantly different from that of historical samples from BC (-16.72 ± 0.51 SD ‰) ($t = 2.085$, $p = 0.250$), but was significantly lower than that of modern samples from CDF (-14.69 ± 0.58 ‰) ($t = 14.92$, $p < 0.01$), and historical samples from HC (-14.79 ± 0.73 ‰) ($t = 9.292$, $p < 0.001$) (Fig. 2). The mean δ^{13}C value of modern CDF samples was not significantly different from that of historical samples collected within

the HC ($t = 0.42$ $p = 1.00$) but was significantly higher than historical samples collected from BC ($t = 8.94$ $p < 0.001$) (Fig. 2). These results suggest consistent differences in carbon isotopic signals between the North Pacific Convergence and South Pacific Humboldt Current systems, and support our initial prediction.

The mean $\delta^{15}N$ value of modern LBI *P. cookii* feathers (15.37 ± 0.95‰) was not significantly different from modern CDF feathers (16.05 ± 1.29‰) ($t = 3.69$, $p = 0.16$) and the only difference in mean $\delta^{15}N$ value between modern and historical feathers was observed in modern samples from LBI (15.37 ± 0.95‰) and historical samples from HC (16.76 ± 1.42‰) ($t = 3.53$, $p < 0.01$) (Fig. 2). The most likely explanation for these results is that modern *P. cookii* feed on prey at similar trophic levels, despite occupying different oceanic regions (as suggested by tracking and carbon isotope data). Accordingly, the environmental characteristics of core non-breeding habitats exploited by modern LBI and CDF *P. cookii* were significantly different, with LBI *P. cookii* foraging over deeper (4930 ± 581 SD m vs. 3330 ± 314 SD m, $Z = -3.97$, $p < 0.0001$), warmer (20.11 ± 1.97 SD °C vs. 17.29 ± 1.59 SD °C, $Z = 3.12$, $p < 0.01$) and less productive waters (0.16 ± 0.10 SD mg Chl *a* m^{-3} vs. 0.73 ± 0.18 SD mg Chl *a* m^{-3}, $Z = -3.91$, $p < 0.0001$) than their CDF conspecifics (Fig. 3). At the intrapopulation level, comparisons of environmental characteristics for presence and absence data indicated that LBI *P. cookii* occupied less productive waters (0.16 ± 0.10 mg Chl *a* m^{-3} vs. 0.28 ± 0.17 mg Chl *a* m^{-3}, $Z = -2.20$, $p = 0.03$) and CDF *P. cookii* more productive waters (0.73 ± 0.18 mg Chl *a* m^{-3} vs. 0.47 ± 0.12 mg Chl *a* m^{-3}, $Z = 2.79$, $p < 0.01$) than those available within their respective non-breeding core habitats (Fig. 3).

Genetic divergence

Consistent with prediction that genetic analysis would confirm divergence in transequatorial migration of the *P. cookii* populations over historical timescales, all nine historical BC *P. cookii* skins had mitochondrial *cytochrome c oxidase subunit 1* (COI) haplotypes that were identical to those of the modern LBI population [38] (Fig. 1). Seven of ten historical HC *P. cookii* skins shared the same haplotype as that of modern CDF *P. cookii* [38] and each of the three remaining skins had a novel haplotype (Fig. 1). We previously identified a single nucleotide polymorphism (SNP; at site 156) that differentiates modern LBI and CDF *P. cookii* [38]. All haplotypes sequenced from historical HC *P. cookii* skins in this study share the same diagnostic SNP as modern CDF birds, including the three novel haplotypes (Fig. 1, Supplementary Figure S2, Supplementary Tables S1, S2 and S3). These results support the previous predictions of contemporary and historical transequatorial separation of the extant *P. cookii* populations, revealed by our tracking and isotopic analyses, and suggests that these two populations have been genetically structured for a minimum of 100 years.

Discussion

Intrinsic factors argued to restrict gene flow between seabird populations include natal philopatry [19], divergent breeding timetables [39,40] and differences in breeding and non-breeding distributions [8,12,17], though how these interact is poorly understood. Our combined results suggest that the use of population specific non-breeding habitats plays an interactive role in the restriction of gene flow, as both a pre-mating and post-mating barrier. In regards to the former, migration routes of differing lengths or directions, are widely recognised pre-mating barriers in migrant terrestrial bird species [5,41,42]. In *P. cookii* differences in the duration of migratory movement or non-breeding distribution

seem to underlie the pronounced breeding asynchrony between the populations. Moreover, regional differences in the timing of peak primary productivity, or the onset of gonad development based upon differences in day length and temperature shifts [43], could amplify asynchronies in breeding timetables beyond those mediated by differences in route or non-breeding residency times alone. Thus, it is not segregation during the non-breeding season *per se.* that represents a pre-mating barrier to gene flow. Rather, it is the interaction between differing non-breeding distributions and divergent breeding timetables, combined with high natal philopatry, which restricts gene flow.

In regards to the latter, adult Cook's petrel desert their chicks up to two weeks prior to fledging and, as seen in many migratory species [5,41], chicks presumably follow an inherited migratory direction and timing [5,42]. Studies of migrant terrestrial bird species indicate that the inheritance of suboptimal migration routes during secondary contact represents a post-mating barrier to gene flow [10, 40]. Although secondary contact is presumably rare in *P. cookii*, the inheritance of an alternative or intermediate migratory strategy would place individuals at a selective disadvantage if it led to the occupancy of suboptimal non-breeding grounds or breeding timetables that were out of synchrony with the rest of the population [10, 40].

Habitat specialisation during both the breeding and non-breeding season is also likely to promote divergence among the two extant *P. cookii* populations via local adaptation. For example, when breeding, *P. cookii* exhibit divergent, although overlapping distributions and diets in response to regional differences in oceanography [25 (current study)]. Moreover, the populations differ in body mass [22] with smaller LBI birds foraging in warmer low-latitude waters compared to larger CDF conspecifics [25]. That individuals

from these two populations also occupy oceanic waters with similarly divergent characteristics during the non-breeding period (i.e., LBI birds occupy warmer less productive waters than CDF birds; Fig. 1) suggests population-specific adaptation to differing marine habitats, possibly linked to body size. Indeed, differences in seabird habitat use related to body size have been observed in other studies, particularly in species with pronounced sexual size dimorphism [44-46]. It remains uncertain whether body size differences between populations of *P. cookii* are a cause or consequence of divergent habitat use. Regardless, our data support and extend local adaptation hypotheses by suggesting that conspecific seabird populations can become tied to particular marine habitats during the breeding [18,39,47] and non-breeding periods [(current study)], presenting opportunities for population divergence.

Overall, this study demonstrates the use of integrative techniques to track space use, behaviour, foraging, and breeding to demonstrate clear spatial segregation of non-breeding distribution between two populations which, mediated by its influence on breeding phenology, appears to represent an intrinsic barrier to gene flow, and has lead to local adaptation in a highly mobile seabird.

Methods

Tracking and environmental data

P. cookii breeding on LBI and CDF were equipped with light-based geolocation loggers (British Antarctic Survey, Mk14) in November-December 2007 (LBI, 36° 11'S, 175° 04'E, n = 13; CDF, 46° 11'S, 167° 38'E, n = 14) during early incubation. Loggers were deployed on birds of known breeding history using published [25] with the total package weighing < 1% of body mass. The sex of all birds were previously determined using

molecular methods [25,48]. The following breeding season, 24 (89%) birds (LBI n = 12 and CDF n = 12) returned to breed and were recaptured in January - March 2009 at their same breeding burrows, and loggers were removed. Two loggers (LBI n =1 and CDF n = 1) failed to download resulting in 11 datasets from each population for processing and analyses.

Light data from the loggers were processed using Multitrace software (Jensen Software Systems) and locations (2 d^{-1}) were estimated with an expected mean accuracy ± SD of 186 ± 114 km [49]. Sunrise and sunset times were identified based on light curve thresholds, with latitude calculated from day/night length and longitude calculated from the time of local midday/midnight relative to Greenwich Mean Time. As a result of day length uniformity around the equinoxes, clearly erroneous locations occurring 3-4 weeks either side of the equinox were excluded. Furthermore, points that involved movements of > 1600 km in one day [50], those with interruptions to light curves around sunset and sunrise, or that were clearly outside of the known or possible range for *P. cookii*, were removed from the data set.

Totals of 7,886 and 9,082 locations were obtained for LBI and CDF *P. cookii* respectively, of which 9.7% and 10.6% were excluded after filtering. Filtered locations were then used to estimate year-round utilisation distribution (UD) kernels for each population following methods detailed in ref [51]. In brief, 2-D Gaussian kernel densities were estimated using custom routines created in MatLab [51] (The Mathworks, Natick, MA, USA). Kernels were calculated using a Lambert Cylindrical Equal Area projection on an 80 km grid with grid cells normalized for bird effort by dividing each cell by the number of birds contributing the locations within a cell. The kernel smoothing

parameter (h) was estimated using an adaptive method [52] to estimate an optimal local value, following ref. [53]. Based published methods [25], a 1,000 km buffer was used around each colony to define breeding habitat, and the 80% contour of UD kernels, calculated individually, were used to define the core non-breeding distributions for each bird [50]. Dates of the first and last locations to enter and exit the core non-breeding habitats were used to define migration timing for each individual. Individuals'migration distances were calculated by summing the point to point distances travelled during post-breeding and pre-breeding movements between these core areas.

Satellite-derived remotely-sensed environmental data were used to contrast the core habitats of *P. cookii* from LBI and CDF during the non-breeding period (presence dataset) as well as those available, but not used, within each population-specific region (absence dataset). For the presence dataset, environmental data were extracted for logger locations falling within the 20% UD for each tracked bird using a 1° longitude by 2° latitude grid centred (the approximate error of geolocation estimates) on the date and coordinates of the location [51]. For the absence dataset, environmental data were extracted from ten randomly selected locations, derived within a 1,000 km radius buffer of each logger location and centred on the corresponding logger location date. Environmental data extracted for the random locations were averaged to give a mean absence estimate to contrast presence values. Remotely-sensed environmental data were obtained from NOAA's Environmental Research Division (http://coastwatch.pfel.noaa.gov/thredds/catalog.html) including 5-day composites of chlorophyll *a* (Chl *a*) concentration (mg Chl m^{-3}) at a spatial resolution of 0.1° resolution [54] and 8-day composites sea surface temperature (SST) in °C with a spatial resolution of 0.1° [55]. Bathymetric data were obtained from the ETOPO2 dataset [56].

355

356 **Stable isotopes**

357 To contrast population-specific dietary signals during the non-breeding period, we
358 conducted stable isotope analyses of C ($\delta^{13}C$) and N ($\delta^{15}N$) ratios in body feathers
359 collected from modern LBI and CDF *P. cookii* and museum specimens held at the
360 Californian Academy of Sciences (n = 9) and American Museum of Natural History (n
361 = 10). Single body feathers were collected from breeding *P. cookii* in 2006 and from
362 tracked birds upon their recapture in 2009, with no resampling of birds between years.
363 Modern and historical feathers were cleaned with 70% ethanol, then washed in distilled
364 water to remove contaminants, dried in at 50°C and cut into fine fragments using
365 scissors. Stable isotope analyses of $\delta^{15}N$ and $\delta^{13}C$, using a subsample (approximately
366 0.7 mg) of each homogenised feather, were carried out on a DeltaPlus (Thermo-
367 Finnigan) continuous flow isotope ratio mass spectrometer using protocols outlined by
368 ref [25]. Measurement precision of the isotope analysis was 0.29‰ for $\delta^{15}N$ and 0.24‰
369 for $\delta^{13}C$. To account for the Seuss effect, the temporal biasing of the atmospheric CO_2
370 pool to more negative $\delta^{13}C$ values as a result of the burning of fossil CO_2, $\delta^{13}C$ data
371 from historical feathers where normalised by subtracting a year-specific factor $\delta^{13}C = -1$
372 $+ 1.1^{(2009\text{-year (1905 or 1913))}*0.027}$ following ref [57].

373

374 **Genetic analyses**

375 Toe pad skin samples were collected from the same historical Cook's petrel specimens
376 from which feathers were sampled for stable isotope analyses (Supplementary Table S1
377 and S2). DNA extraction and polymerase chain reaction (PCR) set up was performed in
378 a physically isolated dedicated ancient DNA laboratory. Contamination was monitored
379 using extraction and PCR negative controls and genomic DNA was isolated as per ref

[58]. A 375 base pair (bp) region of the mitochondrial *cytochrome c oxidase subunit 1* gene (COI) was amplified using two sets of primers that amplified two overlapping fragments: AWCF1 and AWCintR2 [58]; LCRintF2 5'-TCATAATTGGGGGATTTGGA-3' (designed using Primer3 software [59]) and AWCintR3 [58]. This region corresponds to the first 375 bp of the 677 bp fragment sequenced by ref [38]. PCR products were purified using a QIAquick PCR Purification kit (Qiagen) then sequenced bidirectionally from independent PCRs [58]. Sequences were concatenated and aligned using Sequencher version 4.8 (Gene Codes), deposited in NCBI GenBank (accession numbers HQ263645 to HQ263663) and compared with those in ref [38].

Statistical analyses

Habitat data extractions, processing and analyses, were conducted using Matlab. Non-parametric Mann-Whitney U tests were used to test for differences between presence and absence habitat data for the extracted environmental parameters at an intra-population level, and for the presence data at an inter-population level. Mean environmental parameter values for individual birds were used as the sampling unit. Mann-Whitney U tests were initially used to compare stable isotope values between years (2006 and 2009) for LBI and CDF. Isotope data ($\delta^{15}N$ and $\delta^{13}C$) were subsequently pooled for each population and permutation-based non-parametric ANOVA, with pair-wise comparisons using the Bonferroni correction method, conducted to compare isotope values between individuals from the breeding populations (LBI and CDF) and museum skin specimens (CAS 1905 and AMNH 1913) using the programme PERMANOVA. Sex was initially included as a factor in all analyses, but excluded as a result of non-significant differences.

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Author Contributions

M.J.R, D.R.T, P.M.S, M.E.H, S.A.S, and T.E.S designed the research. M.J.R, T.J.L, R.A.P., L.R and S.A.S processed and analysed spatial data. M.J.R., H.A.L, and T. E. S conducted genetic analyses, and S.J.B, M.E.H and M.J.R processed and analysed isotope data. M.J.R wrote paper and all authors discussed the results and contributed to the manuscript.

Competing financial interests: The authors declare no competing financial interests.

Figure legends

Fig. 1. Pacific migrations of tracked *P. cookii*

Movements of *P. cookii* breeding on Little Barrier Island (red circle, North Island) and Codfish Island (purple circle, South Island), New Zealand. Approximate post-breeding and pre-breeding migration routes of tracked LBI (red dashed lines) and CDF (purple dashed lines) birds begin and end with mean migration departure and arrival dates (white text). Red and purple tones, and associated contour lines, represent the 95%, 75%, 50%, and 25% kernel estimates for LBI and CDF birds respectively. Pie charts show the geographic distribution of cytochrome *c* oxidase subunit 1 mtDNA haplotypes sequenced from modern *P. cookii* populations (charts attached to LBI and CDF colony locations) and historical *P. cookii* skins collected in the North (BC) and South Pacific (HC) Ocean in 1905 and 1913 respectively (charts attached to white circles showing approximate collection location). Pie chart size reflects genetic analysis sample size: modern *P. cookii* LBI n = 26 and CDF n = 19; historical *P. cookii BC* n = 9 and HC n = 10.

Fig. 2 Isotope ratios of contemporary and historic *P. cookii* feathers

Feather isotope signatures of *P. cookii* (±SD) from LBI (red circle, 2006 (untracked) and 2008 (tracked) combined, n = 31) and CDF (purple circle, 2006 (untracked) and

2008 (tracked) combined, n = 29) and from historical skins collected in the North Pacific (BC) (black circle, 1905, n = 9) and South Pacific Ocean (HC) (clear circle, 1913, n = 10).

Fig. 3 Characteristics of selected oceanic habitats

Box plots of median values for remotely sensed environmental data (a. water depth, b. sea surface temperature, c. chlorophyll *a* concentration) from logger locations of *P. cookii* tracked from Little Barrier Island (LBI, n = 11) and Codfish Island (CDF, n = 11) during occupancy of core non-breeding habitats (LBI Pres. and CDF Pres., 20% UD) and in randomly selected proximate locations (LBI Abs. and CDF Abs.) see Methods. Asterisks represent significance of difference for group comparisons: * p = 0.05, ** p = 0.01, *** p = 0.001, - = not significant. Box plots illustrate 25^{th}, 50^{th} (median), and 75th percentiles, error bars represent minimum and maximum values falling within 1.5 Inter Quartile Range, and crosses plot the outliers.

References

1 Dor, R., Safran, R. J., Sheldon, F. H., Winkler, D. W. & Lovette, I. J. Phylogeny of the genus Hirundo and the barn swallow subspecies complex. *Molecular Phylogenetics and Evolution* **56**, 409-418, doi:DOI: 10.1016/j.ympev.2010.02.008 (2010).

2 Irwin, D. E. & Irwin, J. H. in *Birds of Two Worlds: The Ecology and Evolution of Migration* (eds R Greenberg & P P Marra) 27-40 (Johns Hopkins University Press, Baltimore, 2005).

3 Mayr, E. *Systematics and the Origin of Species*. (Columbia University Press, 1942).

4 Irwin, D. E., Bensch, S., Irwin, J. H. & Price, T. D. Speciation by distance in a ring species. *Science* **307**, 414-416, doi:10.1126/science.1105201 (2005).

5 Bearhop, S. *et al.* Assortative mating as a mechanism for rapid evolution of a migratory divide. *Science* **310**, 502-504 (2005).

6 Sorenson, M. D., Sefc, K. M. & Payne, R. B. Speciation by host switch in brood parasitic indigobirds. *Nature* **424**, 928-931, doi:http://www.nature.com/nature/journal/v424/n6951/suppinfo/nature01863_S1.html (2003).

7 Galarza, J. A. *et al.* The influence of oceanographic fronts and early-life-history traits on connectivity among littoral fish species. *Proceedings of the National Academy of Sciences* **106**, 1473-1478, doi:10.1073/pnas.0806804106 (2009).

8 Friesen, V. L., Burg, T. M. & McCoy, K. D. Mechanisms of population differentiation in seabirds. *Molecular Ecology* **16**, 1765-1785, doi:10.1111/j.1365-294X.2006.03197.x (2007).

9 Natoli, A., Birkun, A., Aguilar, A., Lopez, A. & Hoelzel, A. R. Habitat structure and the dispersal of male and female bottlenose dolphins (*Tursiops truncatus*). *Proceedings of the Royal Society of London B: Biological Sciences* **272**, 1217-1226, doi:10.1098/rspb.2005.3076 (2005).

10 Egevang, C. *et al.* Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proceedings of the National Academy of Sciences of the United States of America* **107**, 2078-2081, doi:10.1073/pnas.0909493107 (2010).

11 Shaffer, S. A. *et al.* Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 12799-12802, doi:10.1073/pnas.0603715103 (2006).

12 Burg, T. M. & Croxall, J. P. Global relationships amoungst black-browed and grey-headed albatrosses: analysis of population structure using mitochondrial DNA and microsatellites. *Molecular Ecology* **10**, 2647-2660 (2001).

13 Austin, J., White, R. & Ovenden, J. Population-genetic structure of a philopatric, colonial nesting seabird, the short-tailed shearwater (*Puffinus tenuirostris*) *Auk* **111**, 70-79 (1994).

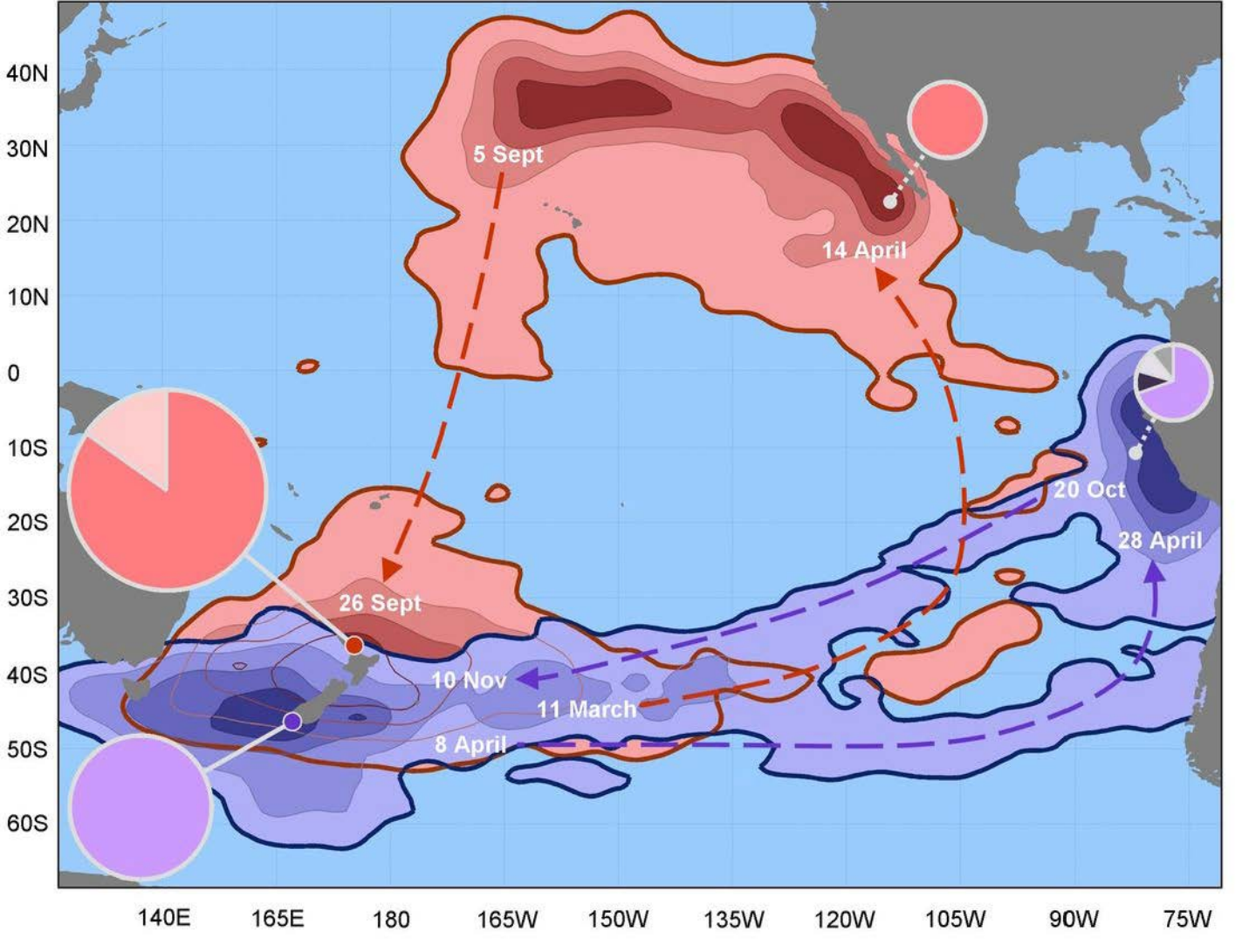
14 Avise, J. C., Nelson, W. S., Bowen, B. W. & Walker, D. Phylogeography of colonially nesting seabirds, with special reference to global matrilineal patterns in the sooty tern (*Sterna fuscata*) *Molecular Ecology* **9** (2000).

15 Techow, N. M. S. M. *et al.* Speciation and phylogeography of giant petrels Macronectes. *Molecular Phylogenetics and Evolution* **54**, 472-487, doi:DOI: 10.1016/j.ympev.2009.09.005 (2010).

16 Morris-Pocock, J. A., Steeves, T. E., Estela, F. A., Anderson, D. J. & Friesen, V. L. Comparative phylogeography of brown (*Sula leucogaster*) and red-footed boobies (*S. sula*): The influence of physical barriers and habitat preference on gene flow in pelagic seabirds. *Molecular Phylogenetics and Evolution* **54**, 883-896, doi:DOI: 10.1016/j.ympev.2009.11.013 (2010).
17 Gómez-Díaz, E., González-Solís, J. & Peinado, M. A. Population structure in a highly pelagic seabird, the Cory's shearwater *Calonectris diomedea*: an examination of genetics, morphology and ecology *Marine Ecology Progress Series* **382**, 197-209 (2009).
18 Dearborn, D. C., Anders, A. D., Schreiber, E. A., Adams, R. M. M. & Mueller, U. G. Inter-island movements and population differentiation in a pelagic seabird. *Molecular Ecology* **12**, 2835-2843 (2003).
19 Steeves, T. E., Anderson, D. J. & Friesen, V. L. A role for nonphysical barriers to gene flow in the diversification of a highly vagile seabird, the masked booby (*Sula dactylatra*). *Molecular Ecology* **14**, 3877-3887 (2005).
20 Burger, E. A. & Shaffer, S. A. Applications of tracking and data-logging technology in research and conservation of seabirds. *The Auk* **125**, 253-264 (2008).
21 Phillips, R. A., Croxall, J. P., Silk, J. R. D. & Briggs, D. R. Foraging ecology of albatrosses and petrels from South Georgia: two decades of insights from tracking technologies. *Aquatic Conservation: Marine and Freshwater Ecosystems* **17**, 6-21 (2008).
22 Imber, M. J., West, J., A. & Cooper, W. J. Cook's petrel (*Pterodroma cookii*): historic distribution, breeding biology, and effects of predators. *Notornis* **50**, 221-230 (2003).
23 Rayner, M. J. *et al.* Predictive habitat modelling improves the population census accuracy of a burrowing seabird: a study of the endangered Cook's petrel. *Biological Conservation* **138**, 235-247 (2007).
24 Rayner, M. J., Parker, K. A. & Imber, M. J. Population census of Cook's petrel *Pterodroma cookii* breeding on Codfish Island (New Zealand) and the global conservation status of the species. *Bird Conservation International* **18**, 211-218 (2008).
25 Rayner, M. J. *et al.* Foraging ecology of the Cook's petrel *Pterodroma cookii* during the austral breeding season: a comparison of its two populations. *Marine Ecology Progress Series* **370**, 271-284 (2008).
26 Marchant, S. & Higgins, P. J. *Handbook of Australasian, Antarctic and New Zealand Birds. Volume 1 Ratites to Ducks*. (Oxford University Press, 1990).
27 Murphy, R. C. On *Pterodroma cookii* and its allies. *American Museum Novitates* **370** (1929).
28 Falla, R. A. Review of the smaller Pacific forms of *Pterodroma* and *Cookilaria*. *Emu* **42**, 111-118 (1942).
29 Gonzalez-Solis, J., Croxall, J. P., Oro, D. & Ruiz, X. Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. *Frontiers in Ecology and the Environment* **5**, 297-301, doi:doi:10.1890/1540-9295(2007)5[297:TMAMIT]2.0.CO;2 (2007).
30 Landers, T. J., Rayner, M. J., Phillips, R. A. & Hauber, M. E. Dynamics of seasonal movements by a trans-pacific migrant, the westland petrel. *Condor* **113**, 71-79 (2011).
31 Ismar, S. M. H., Phillips, R. A., Rayner, M. J. & Hauber, M. E. Geolocation tracking of the annual migration of adult australasian gannets (*Morus serrator*)

breeding in New Zealand. *The Wilson Journal of Ornithology* **123**, 121-125 (2011).
32 Rayner, M. J., Taylor, G. A., Thompson, D. R., Torres, L. G., Sagar, P. M., Shaffer, S. A. Migration and diving activity in three post-breeding flesh-footed shearwaters (*Puffinus carneipes*). *Journal of Avian Biology* (in press).
33 Gill, R. E. *et al.* Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? *Proceedings of the Royal Society B: Biological Sciences* **276**, 447-457, doi:10.1098/rspb.2008.1142 (2009).
34 Spear, L. B., Howell, S. N. G. & Ainley, D. G. Notes on the at-sea identification of some Pacific gadfly petrels (Genus: *Pterodroma*). *Colonial Waterbirds* **15**, 202-218 (1992).
35 Hobson, K. A. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* **120**, 314-326 (1999).
36 Phillips, R., Bearhop, S., McGill, R. & Dawson, D. Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabirds during the nonbreeding period. *Oecologia* **160**, 795-806, doi:10.1007/s00442-009-1342-9 (2009).
37 Cherel, Y., Phillips, R. A., Hobson, K. A. & McGill, R. Stable isotope evidence of diverse species-specific and individual wintering strategies in seabirds. *Biology Letters* **2**, 301-303, doi:10.1098/rsbl.2006.0445 (2006).
38 Rayner, M. J., Carragher, C. J. F. & Hauber, M. E. Mitochondrial DNA analysis reveals genetic structure in two New Zealand Cook's petrel (*Pterodroma cookii*) populations. *Conservation genetics* **11**, 2073-2077 (2010).
39 Monteiro, L. R. & Furness, R. W. Speciation through temporal segregation of Madeiran storm petrel (*Oceanodroma castro*) populations in the Azores? *Proceedings of the Royal Society of London B: Biological Sciences* **353**, 945-953, doi:10.1098/rstb.1998.0259 (1998).
40 Friesen, V. L. *et al.* Sympatric speciation by allochrony in a seabird. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 18589-18594, doi:10.1073/pnas.0700446104 (2007).
41 Marra, P. P., Hobson, K. A. & Holmes, R. T. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* **282**, 1884-1886, doi:10.1126/science.282.5395.1884 (1998).
42 Irwin, D. E. Speciation: new migratory direction provides route toward divergence. *Current Biology* **19**, 1111-1113, doi:DOI: 10.1016/j.cub.2009.11.011 (2009).
43 Berthold, P., Helbig, A. J., Mohr, G. & Querner, U. Rapid microevolution of migratory behaviour in a wild bird species. *Nature* **360**, 668-670 (1992).
44 Phillips, R. A., Silk, J. R. D., Phalan, B., Catry, P. & Croxall, J. P. Seasonal sexual segregation in two *Thalassarche* albatrosses: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proceedings of the Royal Society B: Biological Sciences* **271**, 1283-1292 (2004).
45 Shaffer, S. A., Weimerskirch, H. & Costa, D. P. Functional significance of sexual dimorphism in wandering albatrosses, *Diomedea exulans*. *Functional Ecology* **15**, 203-210 (2001).
46 Weimerskirch, H., Cherel, Y., Cuenot-Chaillet, F. & Ridoux, V. Alternative foraging strategies and resource allocation by male and female wandering albatrosses. *Ecology* **78**, 2051-2063 (1997).

47 Gómez-Díaz, E., González-Solís, J., Peinado, M. A. & Page, R. D. M. Phylogeography of the Calonectris shearwaters using molecular and morphometric data. *Molecular Phylogenetics and Evolution* **41**, 322-332 (2006).
48 Fridolfsson, A. K. & Ellegren, H. A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology* **30**, 116-221 (1999).
49 Phillips, R. A., Silk, J. R. D., Croxall, J. P., Afanasyev, V. & Briggs, D. R. Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series* **266**, 265-272 (2004).
50 Guilford, T. *et al.* Migration and stopover in a small pelagic seabird, the Manx shearwater *Puffinus puffinus*: insights from machine learning. *Proceedings of the Royal Society B: Biological Sciences* **276**, 1215-1223, doi:10.1098/rspb.2008.1577 (2009).
51 Shaffer, S. A. *et al.* Spatio-temporal habitat use by breeding sooty shearwaters *Puffinus griseus*. *Marine Ecology Progress Series* **391**, 209-220 (2009).
52 Worton, B. J. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**, 164-168 (1989).
53 Sheather, S. J. & Jones, M. C. A reliable data-based bandwidth selection method for kernel density estimation. *Journal of the Royal Statistical Society B* **53**, 683-690 (1991).
54 O'Reilly, J. E. *et al.* Ocean color chlorophyll algorithms for SeaWiFS. *Journal of Geophysical Research* **103**, 24937-24953, doi:10.1029/98jc02160 (1998).
55 Powell, B. S. *et al.* 4DVAR data assimilation in the intra-americas sea with the Regional Ocean Modeling System (ROMS). *Ocean Modelling* **23**, 130-145 (2008).
56 Smith, W. H. F. & Sandwell, D. T. Global sea floor topography from satellite altimetry and ship depth soundings. *Science* **277**, 1956-1962, doi:10.1126/science.277.5334.1956 (1997).
57 Quillfeldt, P., Masello, J., McGill, R., Adams, M. & Furness, R. Moving polewards in winter: a recent change in the migratory strategy of a pelagic seabird? *Frontiers in Zoology* **7**, 15 (2010).
58 Patel, S., Waugh, J., Millar, C. D. & Lambert, D. M. Conserved primers for DNA barcoding historical and modern avian samples from New Zealand and Antarctic birds. *Molecular Ecology Resources* **10**, 431-438 (2009).
59 Rozen, S. & Skaletsky, H. Primer3 on the WWW for general users and for biologist programmers. *Methods in Molecular Biology* **132**, 365-386 (2000).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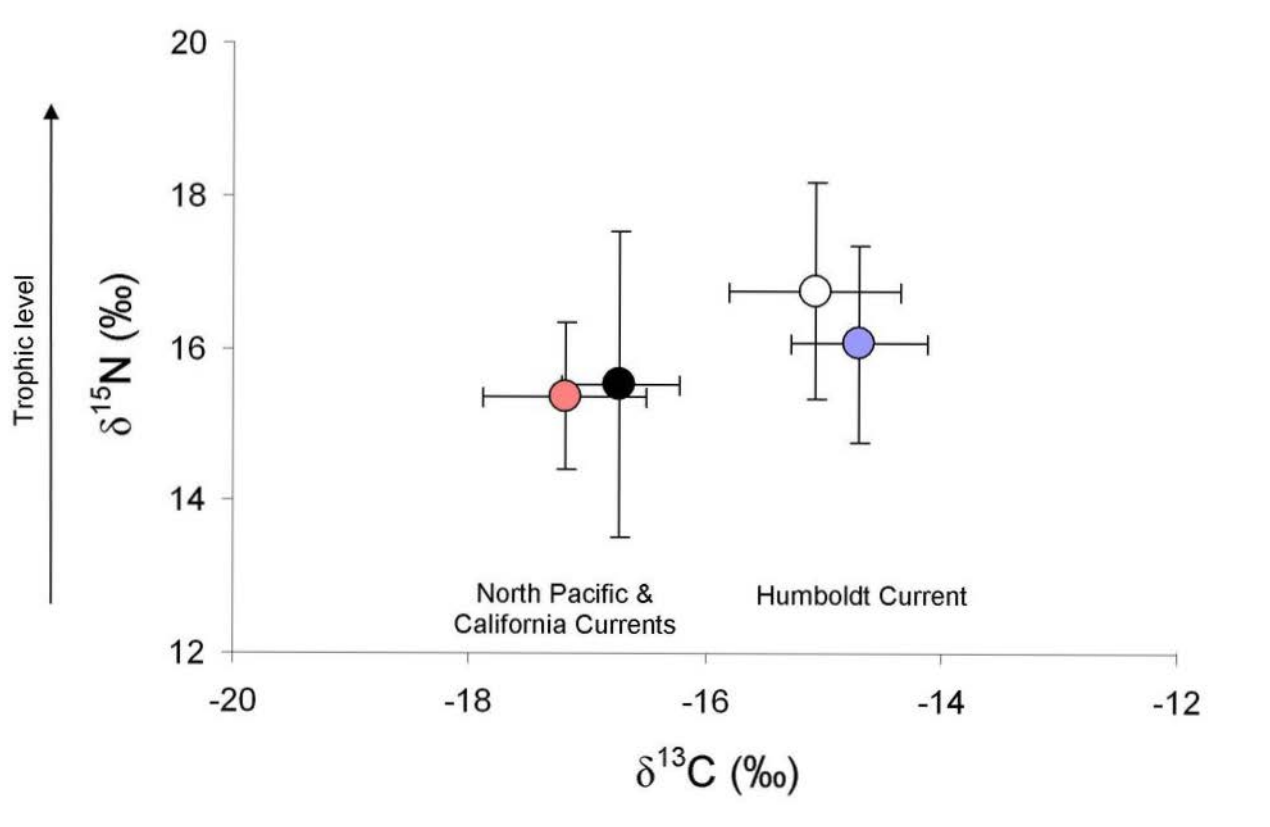
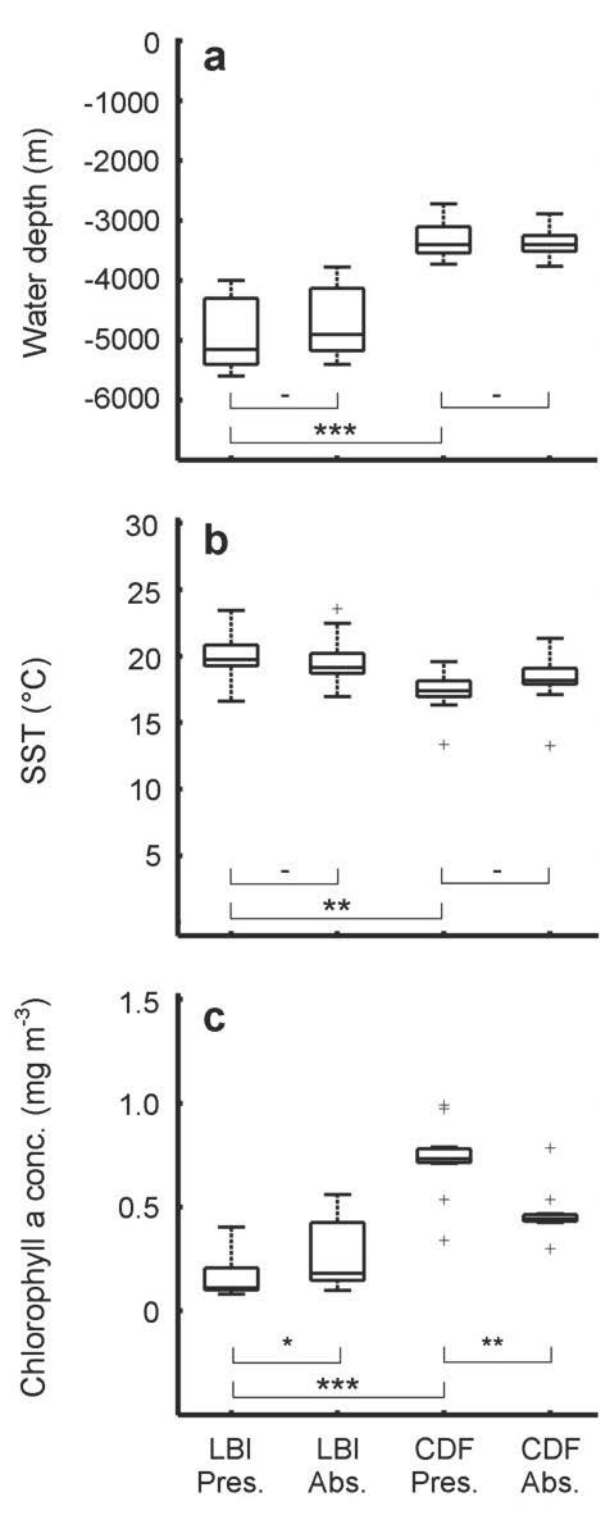

Trophic level
20
18
16
14
12
δ^{15}N (‰)
-20
-18
-16
-14
-12
δ^{13}C (‰)
North Pacific &
California Currents
Humboldt Current


a
Water depth (m)
0
-1000
-2000
-3000
-4000
-5000
-6000
-
-
***
b
SST (°C)
30
25
20
15
10
5
-
-
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c
Chlorophyll a conc. (mg m-3)
1.5
1.0
0.5
0
*
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LBI Pres.
LBI Abs.
CDF Pres.
CDF Abs.