

2014-02

Intercolony movement of pre-breeding seabirds over oceanic scales: implications of cryptic age-classes for conservation and metapopulation dynamics

Bicknell, AWJ

<http://hdl.handle.net/10026.1/12069>

10.1111/ddi.12137

DIVERSITY AND DISTRIBUTIONS

Wiley

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

Inter-colony movement of pre-breeding seabirds over oceanic scales: implications of cryptic age-classes for conservation and metapopulation dynamics

Anthony W. J. Bicknell^{1*}, Mairi E. Knight², David T. Bilton², Maria Campbell³, James B. Reid⁴, Jason Newton⁵ and Stephen C. Votier¹

¹Environment and Sustainability Institute, University of Exeter, Penryn, Cornwall, UK

²Marine Biology and Ecology Research Centre, Plymouth University, Plymouth PL4 8AA, UK

³Sir Alister Hardy Foundation for Ocean Sciences, Plymouth PL1 2PB, UK

⁴Joint Nature Conservation Committee, Aberdeen AB11 9QA, UK

⁵NERC Life Sciences Mass Spectrometry Facility, Scottish Universities Environmental Research Centre, East Kilbride G75 0QF, UK

*Corresponding author: a.bicknell@exeter.ac.uk

Article Type = Biodiversity Research

(A) RUNNING TITLE

Inter-colony movement of pre-breeding seabirds

(A) ABSTRACT

(B) Aim

Demographic linkage between subpopulations plays a critical role in population processes. Metapopulation dynamics, however, remains one of the most poorly understood aspects of population biology. This is especially true for small, pelagic seabirds because their discrete subpopulations are located on offshore islands, separated by vast areas of open-ocean making monitoring logistically challenging. Seabird populations often contain large numbers of immature pre-breeders that may be important for subpopulation connectivity and demography, but are poorly studied. Here we provide evidence for inter-colony movement of pre-breeding Leach's storm-petrels *Oceanodroma leucorhoa* among three colonies spanning the North Atlantic Ocean. We discuss their influence on metapopulation dynamics and the extinction risk of a subpopulation under threat from extreme predation.

(B) Location

North Atlantic Ocean Islands (Scotland, Canada & Iceland)

(B) Methods

We use a novel application of Bayesian stable isotope mixing models to infer recent movement of pre-breeding birds between three major breeding populations in the North Atlantic. Carbon and nitrogen stable isotope values from breeding birds (central place foragers) sampled at each colony were used as model sources and pre-breeding birds as model mixtures.

(B) Results

Of 134 pre-breeding Leach's storm-petrels sampled at three colonies across the North Atlantic, 5 had isotope mixing model estimates dissimilar (<25%) to their colony of capture and were instead isotopically similar to another breeding region. Nineteen further pre-breeders had highly mixed signatures (<50% for the colony of capture) indicating possible recent movement among colonies.

(B) Main Conclusions

Our findings provide evidence for inter-population connectivity of pre-breeding Leach's storm-petrels among colonies spanning the North Atlantic. These results highlight the significance of cryptic young age-classes in metapopulation dynamics and the demographic processes. Moreover, they provide us with a better understanding of how one subpopulation remains extant, despite experiencing extreme predation rates.

(B) Keywords

Extinction risk, dispersal, Leach's storm petrel, metapopulation, predation, stable isotopes.

(A) INTRODUCTION

Highly fragmented populations are reliant upon dispersal to maintain demographic and genetic connectivity (Bowler & Benton, 2005; Lowe & Allendorf, 2010), yet isolation of these subpopulations (demes) can make them vulnerable to extinction (Matthiopoulos *et al.*, 2005). When sufficient dispersal occurs between subpopulations to influence local demographics, but subpopulation independence is maintained, this can be considered a metapopulation (Hanski, 1998). Estimating inter-population connectivity is essential for predicting population and metapopulation dynamics, as well as the potential for subpopulations to buffer the effect of environmental change (Kokko & López-Sepulcre, 2006), but remains one of the most poorly understood processes in population biology. For species with delayed maturation, there is a paucity of empirical data on the movement of pre-breeding individuals, although prospecting behaviour is known to play an important role in breeding location decision making (Dittmann *et al.*, 2005; Caut *et al.*, 2008; Robinson & Beckerman, 2013). This knowledge gap is problematic because for long-lived iteroparous species immatures may represent a significant proportion of the fully grown population (Lebreton *et al.*, 2003), play an important role in the demographic process (Votier *et al.*, 2008) and also have a higher dispersal propensity than breeders (Lebreton *et al.*, 2003; Votier *et al.*, 2008).

Many colonial nesting seabirds breed under conditions conducive to the formation of metapopulations. Breeding colonies are discrete subpopulations, separated by a matrix of unsuitable habitat (i.e. the open ocean), and seabirds have excellent dispersal capabilities to aid connectivity (Inchausti & Weimerskirch, 2002; Breton *et al.*, 2006). However, the extent to which seabird colonies function as metapopulations is poorly understood (Oro, 2003). This arises in part because of the logistic constraints of studying (often) remote colonies, comprising large numbers of individuals, separated by vast distances at sea. Moreover, because fidelity to breeding locations is high among most seabirds (Schreiber & Burger, 2002), pre-breeding rather than breeding birds are likely to contribute most to inter-colony connectivity. Seabird populations can consist of large numbers of young pre-breeders (>50% of the population (Klomp & Furness, 1992)), but due to the fact that they rarely come to land (where the majority of seabird research occurs) they lead cryptic lives (Votier *et al.*, 2011). Previous research using capture-mark-recapture techniques suggests pre-breeding seabirds play an important role in metapopulation dynamics (Inchausti & Weimerskirch, 2002;

Lebreton *et al.*, 2003; DeMots *et al.*, 2010; Turner *et al.*, 2010), but this process is virtually unknown for species where marking at birth and subsequent re-sighting is logistically unviable. Stable isotopes signatures of avian tissues are frequently used to investigate migratory connectivity and origins of terrestrial birds (Wunder *et al.*, 2005), and have also been combined with other biochemical markers to assign seabirds to colony of origin (Gómez-Díaz & González-Solís, 2007). However, these rely upon (and are limited by) a precise knowledge of the timing and pattern of moult in each species, and if the main moult occurs outside the breeding season (which is the case for many taxa) then analysis of feather isotopes is not appropriate for investigating the movements of pre-breeders. Here we propose an application of analysing stable isotope signatures in blood to test for inter-colony movement of pre-breeding seabirds at an oceanic scale.

Our study focusses on a species of conservation concern in the EU, the Leach's storm-petrel *Oceanodroma leucorhoa* (Vieillot). This is a small (<45g), burrow-nesting Procellariiforme that breeds at a small number of widely distributed colonies, separated by large tracts of open ocean, across the North Atlantic and Pacific. At the second largest colony in Europe on St Kilda, Scotland, a ~54% decline in breeding Leach's storm-petrels from 90,000 individuals in 1999 to 41,000 individuals in 2006 (Newson *et al.*, 2008), raised concerns for the viability of this regionally important population. This reduction is partly attributable to predation by great skuas *Stercorarius skua* (Brunnich), yet the estimated consumption of ~21,000 Leach's storm-petrels year⁻¹ by skuas exceeds the observed decline (Phillips *et al.*, 1999; Miles, 2010). One explanation for this disparity is that prospecting pre-breeders or breeding immigrants from other very large Leach's storm-petrel colonies in the North Atlantic may be buffering the impacts of skua predation (Votier *et al.*, 2006; Bicknell *et al.*, 2012). Over 5 million pairs of Leach's storm petrel breed in Iceland and eastern Canada (Bicknell *et al.*, 2012), indicating huge numbers of potential prospectors in the North Atlantic. Fidelity to breeding locations is high (Blackmer *et al.*, 2004), but recent work has revealed genetic homogeneity among North Atlantic colonies suggesting the occurrence of effective natal dispersal (Bicknell *et al.*, 2012).

We used stable isotopes in blood to test for inter-population connectivity of pre-breeding Leach's storm-petrels spanning >3000km in the north Atlantic. This approach provides answers to questions on an immediate ecological time scale inaccessible using other techniques (e.g. genetic markers, but see; McCoy *et al.*, 2005), but is critical to assess current metapopulation dynamics and conservation threats. First we measured stable isotopes in red blood cells (RBC) of breeders from three colonies representing the main North Atlantic population centres, to check for isotopic differences among regions, in tandem with confirmatory data on zooplankton from the same regions. Second, we used a stable isotope mixing model (SIAR) to estimate the probability of pre-breeders moving among colonies and therefore allowing an assessment of the importance of this age-class in maintaining colony connectivity at ocean-basin scales.

(A) METHODS

Leach's storm-petrel samples

Leach's storm-petrels were sampled from Gull Island, Canada (47°15'N, 52°46'W) and St Kilda, Scotland (57°49'N, 08°35'W) in August 2008, and Vestmannaeyjar, Iceland (63°25'N, 20°17'W) in August 2009 (Fig. 1a). Between 10-20µl of blood was collected from the brachial vein of breeders in burrows (incubated an egg or brooding a chick), as well as pre-breeders caught in mist-nets at night under appropriate regional licences. To ensure the status of pre-breeders only birds that met all of the following criteria were included: (1) caught

away from the main breeding areas; (2) attracted by a chatter call lure played on speakers close to the mist-net; (3) no regurgitation of prey items when caught or handled; and (4) had no obvious brood patch. Blood was separated into plasma and RBC using a centrifuge within 2-3 hours of sampling, and then freeze-stored until analysis.

(B) Stable isotope analysis

Carbon and nitrogen stable isotopes show naturally occurring gradients that can be used to infer movement at the individual-level (Hobson, 2007). Carbon ($\delta^{13}\text{C}$) values are representative of the primary carbon source and show a number of spatial gradients in marine ecosystems (such as inshore vs. offshore, pelagic vs. benthic, and latitude (Hobson, 2007)). Nitrogen ($\delta^{15}\text{N}$) values show a consistent step-wise enrichment by trophic level and also reflect the nitrogen pool supporting primary producers at the base of different food webs (Owens, 1987; Jennings & Warr, 2003). We used $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of RBC because this tissue typically reflects diet ~3-4 weeks prior to sampling (Bearhop *et al.*, 2002) and because there is little confounding influence of lipids (Cherel *et al.*, 2005). Breeding adult Leach's storm-petrels are constrained to tend their eggs or chicks (return to the nest every 1-4 days; Ricklefs *et al.*, 1985) with an estimated foraging range over 200km (Hedd *et al.*, 2009), such that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values represent the region close to the colony of capture. Pre-breeders are not constrained in the same way and therefore, if they move between different colonies, may have mixed isotope signatures. We used the Bayesian stable isotope mixing model SIAR (Parnell *et al.*, 2010) to calculate the median probability of pre-breeder isotope signatures attributable to the three colonies of capture, where breeder isotopes are the sources and pre-breeders the mixtures. The sources and mixtures were therefore derived from the same trophic level obviating the need for trophic enrichment factors in the model. We assume that any potential differences in assimilation efficiency or physiology between breeders and immature birds did not influence the relationship between isotope values in prey and blood.

(B) SIAR mixing model parameters and performance

To provide an independent test of regional isotopic distinction (not used in any model), we analysed zooplankton samples collected by the Continuous Plankton Recorder Survey (CPR - managed by the Sir Alister Hardy Foundation for Ocean Science) in oceanic waters representative of the three regions. This was not to directly reflect the diet of Leach's storm-petrels (although they do consume some zooplankton (Hedd & Montevecchi, 2006)) but instead to determine whether regional differences in the stable isotope values of breeder RBC are consistent at lower trophic levels within the same year. Adult life stages (CV and CVI) of *Calanus helgolandicus* and *C. finmarchicus* were removed from 27 formalin preserved "silks" (collection mesh representing 10km towed transects) sampled on 5 survey routes (2 in Canadian region, 2 in Icelandic region and 1 in Scottish region), which crossed oceanic regions representative of each colony during July 2008 (Fig. 1a; Table S1). Isotopic values from multiple CPR routes sampled within the Canadian and Icelandic regions were similar and therefore combined into a value for each region (Fig. S1).

Key to mixing model efficacy is accurate characterisation of potential sources (prey samples in diet reconstruction, but colony-specific regions in this instance). Independent data from CPR samples and the literature were used to check our source coverage assumptions. It is also desirable for the mixture values (in this case pre-breeders) in mixing models to lie within the fuzzy convex hull of the source isotope values (breeders), and this was checked using an iso-space plot (Parnell *et al.*, 2012).

To assess SIAR model performance and sensitivity to a small sample size of breeders at one colony (Gull Island, Canada), we re-ran the model using estimates for Gull Island based on subsampled data. We replicated the small sample size for each of the other two sources by randomly sampling 4 $\delta^{13}\text{C}$ breeder values from their ranges, repeated 10 times to produce a range of possible means for each source (colony). The difference between the lowest mean of the range and the original source mean (all the samples) was averaged from the two sources and then subtracted from the original Gull Island mean. This produced an estimated mean to be used in a sensitivity analysis (see Supplementary data, Dryad repository; DOI: doi:10.5061/dryad.q2610). The average of the St Kilda and Vestmannaeyjar $\delta^{13}\text{C}$ standard deviations was used as the estimated standard deviation. This process was repeated for the $\delta^{15}\text{N}$ data. These estimates represent a conservative scenario in terms of source differentiation and variance (i.e. by bringing the sources closer together and increasing the variance; see Fig. S1).

(B) Stable isotope sample preparation

All samples were freeze-dried, homogenised and ~0.7 mg weighed into a tin cup for analysis. Each zooplankton sample (tin cup) consisted of approximately 10-20 individual animals. Metabolic synthesis of lipid discriminates against ^{13}C (DeNiro & Epstein, 1977) and generally yields low $\delta^{13}\text{C}$ values in tissues with high lipid content when compared with an organisms' dietary input (Tieszen *et al.*, 1983). Therefore, because of highly variable lipid content between *C. helgolandicus* and *C. finmarchicus* (Ventura, 2006), lipids were extracted prior to analysis. Inorganic carbonates were also removed from these samples, as these tend to increase $\delta^{13}\text{C}$ and do not reflect the organisms dietary intake (DeNiro & Epstein, 1978). Extraction and removal methods, as well as correction for formalin preservation, are described in detail elsewhere (Bicknell *et al.*, 2011).

Analyses were conducted at the East Kilbride Node of the Natural Environment Research Council Life Sciences Mass Spectrometry Facility via continuous flow isotope ratio mass spectrometry using a Costech (Milan, Italy) ECS 4010 elemental analyser interfaced with a Thermo Electron (Bremen, Germany) Delta XP mass spectrometer. Isotope ratios are reported as δ -values and expressed as ‰ according to the equation:

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

where; X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ and R_{standard} is the ratio of the international references PDB for carbon and AIR for nitrogen. The standard deviation of multiple analyses of an internal gelatine standard in each experiment was better than 0.2‰ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. All statistics and models were run in R version 2.15.1 (R Development Core Team, 2011).

(A) RESULTS

(B) Isotopic differences among regions (sources)

Breeding Leach's storm-petrels were isotopically segregated among colonies (MANOVA, Pillai, $F_{2,31} = 50.86$, $P < 0.0001$). Univariate analysis revealed $\delta^{15}\text{N}$ was significantly different between all colonies (ANOVA, $F_{2,31} = 55.18$, $P < 0.0001$) and $\delta^{13}\text{C}$ was significantly different between Vestmannaeyjar, Iceland and the other colonies (ANOVA, $F_{2,31} = 46.05$, $P < 0.0001$; St Kilda, Scotland, $t = 9.26$, $P < 0.0001$; Gull Island, Canada, $t = 5.91$, $P < 0.0001$), while Gull Island and St Kilda were similar (Fig. 1b).

Calanus copepods were also isotopically segregated among the geographic regions found for the breeder samples (MANOVA, Pillai, $F_{2,80} = 93.17$, $P < 0.0001$, Fig. S2). Univariate analysis showed significant $\delta^{15}\text{N}$ differences between Iceland and the other regions (ANOVA, $F_{2,80} = 212.84$, $P < 0.0001$; Scotland, $t = 20.39$, $P < 0.0001$; Canada, $t = 10.44$, P

<0.0001), while Scotland and Canada were similar. $\delta^{13}\text{C}$ differences were found among all regions (ANOVA, $F_{2,80} = 208.55$, $P < 0.0001$).

(B) Isotopic evidence for inter-colony movement using SIAR

Isotope values of pre-breeders were more variable than breeders, but (with the exception of a single outlier) pre-breeder values nested within breeder variation (Fig. 1b), suggesting good characterization of sources.

SIAR outputs revealed that of 134 pre-breeding Leach's storm-petrels caught at three colonies, many had isotopes dissimilar to their colony of capture (Fig. 2). For instance, 5 St Kilda pre-breeders had median probability estimates <25% for their colony of capture and were instead isotopically similar to Iceland (Fig. 2). Nineteen other pre-breeders (9 caught on St Kilda, 7 on Gull Island and 3 on Vestmannaeyjar) had mixed signatures (<50% for the colony of capture) indicating possible recent movement into their region of capture (Fig. 2). A comparison of model outputs (original vs "sensitivity") revealed changes to the input values for Gull Island had very little effect on the results (Table S2, Figs. S3 & S4).

(A) DISCUSSION

Using a novel application of stable isotope mixing models, we found evidence that pre-breeding Leach's storm-petrels moved long-distances across the North Atlantic (spanning >3000km), among breeding colonies in Scotland, Iceland and Canada. These findings are significant for a number of reasons. First, they reveal the potential for long-distance dispersal at the ocean basin scale and lend credibility to the idea that Leach's storm-petrel colonies may act as a metapopulation. This provides important insight into population dynamics and also suggests this inter-colony exchange may have implications for buffering localised mortality (Bicknell *et al.*, 2012). Second, this work also provides evidence that the large pool of pre-breeders play a critical role in population and metapopulation dynamics of seabirds. We discuss the implications of these findings for population biology in general, and seabird conservation in particular, as well as the use of stable isotope mixing models to study movement of cryptic pre-breeders below.

(B) Stable isotopes and dispersal

The stable isotope mixing model used here obviates many of the constraints of studying inter-colony connectivity of Leach's storm-petrels (e.g. small size, large population, exhaustive re-sighting effort). However the same technique could also be applied to many other taxa, as long as there is clear isotopic differentiation among subpopulations (regions). We found isotopic differences among breeders from the three colonies sampled across two years, and this difference was confirmed through analysis of zooplankton sampled in the same three regions in a single year (Fig. S1).

One assumption of mixing models is that consumer tissues are in equilibrium with their diet (Martínez del Río & Wolf, 2005). Movements between isotopically distinct regions will not immediately be reflected in consumer tissues, for instance avian blood has a half-life of approximately 14 days (Bearhop *et al.*, 2002; Podlesak *et al.*, 2005). Therefore, the more time an individual spends in a new area the greater the isotopic similarity to that region as equilibrium approaches. Therefore the extent of movement among colonies assessed here is most likely to be an underestimate because only individuals moving relatively quickly between isotopically distinct regions will have values dissimilar to their colony of capture. Only 5 St Kilda pre-breeders can confidently be assessed as recent arrivals from the Icelandic region, but this still provides strong evidence for their movement between colonies and is

consistent with previous studies using other approaches (such as genetic markers) (Bicknell *et al.*, 2012).

Important to mixing model efficacy is good characterisation of potential sources - here the sources are the large foraging regions close to Leach's storm-petrel colonies, but may also include other at-sea areas such as over-winter locations and migratory pathways. Visual inspection of iso-space plots of sources and mixtures suggest we have achieved this (Fig. 1). However we did not sample all Leach's storm-petrel colonies in the North Atlantic but instead sampled the major oceanic water masses close to these colonies. For instance the vast majority of the North American breeding population are found in Canada (>95% (Huntingdon *et al.*, 1996; Mitchell *et al.*, 2004)), with the largest colonies on the north and south of Newfoundland. While we only sampled the north, given the large foraging range of this species (Hedd *et al.*, 2009) they most likely integrate a signature derived from water masses around much of Newfoundland. Moreover, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of copepods from a CPR route south of Newfoundland (Fig. S1), and data from the literature (Gulf of Maine (Estrada *et al.*, 2005)), are similar to copepods from north Newfoundland suggesting our assumption is robust. A further possibility is that some Leach's storm-petrels sampled had recently returned from their wintering quarters or migratory staging grounds. While we cannot completely exclude this possibility, it seems unlikely given the close match of our source and mixture isotope values (Fig. 1). However, a single pre-breeder caught on St Kilda had an extremely high RBC $\delta^{13}\text{C}$ value (Fig. 1), which, because of large scale $\delta^{13}\text{C}$ gradients in the Atlantic (associated partly with temperature (Graham *et al.*, 2010) and an inverse relationship with latitude (Paiva *et al.*, 2010)) suggests this bird was probably a late arrival from lower latitude waters. We did not include this bird in further analyses, but it gives us some confidence that we can identify recently returning migrants in our analysis.

The CPR copepod samples confirmed regional isotopic differences but also revealed a different pattern of nitrogen and carbon isotope values at a lower trophic level (Fig. S2), compared to the breeding Leach's storm-petrel samples (Fig. 1b). The feeding ecology of Leach's storm-petrels is not known, or believed, to differ between regions (or between pre-breeders and breeders), suggesting the change in isotopic pattern found at a higher trophic level may be attributed to food web structure/length in the regions. Further research and analyses (e.g. compound specific isotope analysis) is required to elucidate the potential cause of these differences, but highlights that variation among regions and across different trophic levels may be pronounced, which should be considered in future spatial or comparison studies.

Stable isotope mixing models provide an additional tool to infer movement of individuals between isotopically distinct regions or ecosystems. The use of additional elements in the analysis (e.g. oxygen or sulphur or highly-branched isoprenoids (Brown *et al.*, 2013)) may help provide more accuracy of the models through further differentiation of regions, but relies upon regionally distinct signatures. Combining stable isotope analyses with other indirect techniques, such as genetics, and/or direct methods, such as tracking, can build evidence for movement and dispersal of individuals. However for small and cryptic age-classes or species, such as Leach's storm-petrels, indirect methods and innovative analysis are currently the only realistic way to provide evidence for movement of individuals over large spatial scales.

(B) Predation on St Kilda

Our SIAR analysis suggests ~1 in 10 pre-breeders at St Kilda had recently arrived from another region, which could explain the continued persistence of this colony. The extremely

high, long-term predation by great skuas (~21,000 birds a year since 1996; Phillips *et al.*, 1999; Miles, 2010) would be unsustainable for this relatively small colony (~20,000 breeding pairs in 2006; Newson *et al.*, 2008). A rescue effect could manifest via compensatory recruitment (Votier *et al.*, 2008) or because skuas eat large numbers of prospecting pre-breeders (Mougeot & Bretagnolle, 2000), or a combination of both. The lack of potential recent arrivals caught on Gull Island and Vestmannaeyjar compared with St Kilda, suggests pre-breeder movement among colonies may not be random, which would be indicative of a sink population sustained by larger source populations across the North Atlantic. Further work is required to determine whether this is the case or not.

Natal dispersal is thought to be important for inter-population exchange and metapopulation dynamics in a wide range of taxa (Paradis *et al.*, 1998; Clobert *et al.*, 2001; Inchausti & Weimerskirch, 2002; Telfer *et al.*, 2003; Berry *et al.*, 2004; Dittmann *et al.*, 2005; Caut *et al.*, 2008; Robinson & Beckerman, 2013), but can be very difficult to study. Here, we were able to provide indirect evidence of connectivity among populations through prospecting pre-breeding individuals during the breeding period, and identify potential source/sink metapopulation dynamics over large spatial scales. Moreover this behaviour is likely helping the persistence of a local sub-population under extreme predation pressure. This further highlights the need to understand connectivity of disjunct populations of highly vagile species to be able to implement effective conservation measures at relevant spatial scales.

(A) ACKNOWLEDGEMENTS

Thanks to all that helped with fieldwork and logistics in Scotland, Iceland and Canada, the SAHFOS workers and the international funding consortium that supports the CPR survey. The National Trust for Scotland and Scottish Natural Heritage (SNH) allowed access to St Kilda. Sampling was under license from Canada Wildlife Services, the Government of Newfoundland and Labrador, the Icelandic Ministry of the Environment, SNH and the UK Home Office. The work was funded by the NERC (NE/F007213/1) and JNCC. The JNCC works with and on behalf of the four UK statutory nature conservation organizations: Council for Nature Conservation and the Countryside, the Countryside Council of Wales, Natural England and SNH.

(A) REFERENCES

- Bearhop, S., Waldron, S., Votier, S.C. & Furness, R.W. (2002) Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiological and Biochemical Zoology*, **75**, 451-458.
- Berry, O., Tocher, M.D. & Sarre, S.D. (2004) Can assignment tests measure dispersal? *Molecular Ecology*, **13**, 551-561.
- Bicknell, A.W.J., Campbell, M., Knight, M.E., Bilton, D.T., Newton, J. & Votier, S.C. (2011) Effects of formalin preservation on stable carbon and nitrogen isotope signatures in Calanoid copepods: implications for the use of Continuous Plankton Recorder Survey samples in stable isotope analyses. *Rapid Communications in Mass Spectrometry*, **25**, 1794-1800.
- Bicknell, A.W.J., Knight, M.E., Bilton, D., Reid, J.B., Burke, T. & Votier, S.C. (2012) Population genetic structure and long-distance dispersal among seabird populations: Implications for colony persistence. *Molecular Ecology*, **21**, 2863-2876.

- Blackmer, A.L., Ackerman, J.T. & Nevitt, G.A. (2004) Effects of investigator disturbance on hatching success and nest-site fidelity in a long-lived seabird, Leach's storm-petrel. *Biological Conservation*, **116**, 141-148.
- Bowler, D.E. & Benton, T.G. (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews*, **80**, 205-225.
- Breton, A.R., Diamond, A.W. & Kress, S.W. (2006) Encounter, survival and movement probabilities from an Atlantic puffin (*Fratercula arctica*) metapopulation. *Ecological Monographs*, **76**, 133-149.
- Brown, T.A., Bicknell, A.W.J., Votier, S.C. & Belt, S.T. (2013) Novel molecular fingerprinting of marine avian diet provides a tool for gaining insights into feeding ecology. *Environmental Chemistry Letters*, 1-6.
- Caut, S., Angulo, E. & Courchamp, F. (2008) Caution on isotopic model use for analyses of consumer diet. *Canadian Journal of Zoology*, **86**, 438-445.
- Cherel, Y., Hobson, K.A. & Hassani, S. (2005) Isotopic discrimination between food and blood and feathers of captive penguins: Implications for dietary studies in the wild. *Physiological and Biochemical Zoology*, **78**, 106-115.
- Clobert, J., Danchin, E., Dhondt, A.A. & Nicholls, J.D. (2001) *Dispersal*. Oxford University Press, Oxford.
- DeMots, R.L., Novak, J.M., Gaines, K.F., Gregor, A.J., Romanek, C.S. & Soluk, D.A. (2010) Tissue–diet discrimination factors and turnover of stable carbon and nitrogen isotopes in white-footed mice (*Peromyscus leucopus*). *Canadian Journal of Zoology*, **88**, 961-967.
- DeNiro, M.J. & Epstein, S. (1977) Mechanism of carbon isotope fractionation associated with lipid synthesis. *Science*, **197**, 261-263.
- DeNiro, M.J. & Epstein, S. (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta*, **42**, 495-506.
- Dittmann, T., Zinsmeister, D. & Becker, P.H. (2005) Dispersal decisions: common terns, *Sterna hirundo*, choose between colonies during prospecting. *Animal Behaviour*, **70**, 13-20.
- Estrada, J.A., Lutcavage, M. & Thorrold, S.R. (2005) Diet and trophic position of Atlantic bluefin tuna (*Thunnus thynnus*) inferred from stable carbon and nitrogen isotope analysis. *Marine Biology*, **147**, 37-45.
- Gómez-Díaz, E. & González-Solís, J. (2007) Geographic assignment of seabirds to their origin: Combining morphologic, genetic, and biogeochemical analyses. *Ecological Applications*, **17**, 1484-1498.
- Graham, B., Koch, P.L., Newsome, S.D., McMahon, K. & Aurioles, D. (2010) Using Isoscapes to Trace the Movements of Foraging Behaviour of Top Predators in Oceanic Ecosystems. *Understanding movement, pattern, and process on Earth through isotope mapping* (ed. by J.B. West, G.J. Bowen, T.E. Dawson and K.P. Tu). Springer, Netherlands.
- Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41-49.
- Hedd, A. & Montevecchi, W.A. (2006) Diet and trophic position of Leach's storm-petrel *Oceanodroma leucorhoa* during breeding and moult, inferred from stable isotope analysis of feathers. *Marine Ecology Progress Series*, **322**, 291-301.
- Hedd, A., Montevecchi, W.A., Davoren, G.K. & Fifield, D.A. (2009) Diets and distributions of Leach's storm-petrels (*Oceanodroma leucorhoa*) before and after an ecosystem shift in the Northwest Atlantic. *Canadian Journal of Zoology*, **87**, 787-801.
- Hobson, K. (2007) Isotope tracking of migrant wildlife. *Stable Isotopes in Ecology and Environmental Science* (ed. by R. Michener and K. Lajtha), pp. 155-175. Blackwell Publishing Ltd, Oxford, UK.
- Huntingdon, C.E., Butler, R.G. & Mauk, R.A. (1996) Leach's storm-petrel. *The Birds of North America* (ed. by A. Poole and F. Gill). The Academy of Natural Sciences, Philadelphia, PA and the American Ornithologist Union, Washington, DC.

- Inchausti, P. & Weimerskirch, H. (2002) Dispersal and metapopulation dynamics of an oceanic seabird, the wandering albatross, and its consequences for its response to long-line fisheries. *Journal of Animal Ecology*, **71**, 765-770.
- Jennings, S. & Warr, K.J. (2003) Environmental correlates of large-scale spatial variation in the $\delta^{15}\text{N}$ of marine animals. *Marine Biology*, **142**, 1131-1140.
- Klomp, N.I. & Furness, R.W. (1992) Non-breeders as a buffer against environmental stress: declines in numbers of great skuas on Foula, Shetland, and prediction of future recruitment. *Journal of Applied Ecology*, **29**, 341-348.
- Kokko, H. & López-Sepulcre, A. (2006) From Individual Dispersal to Species Ranges: Perspectives for a Changing World. *Science*, **313**, 789-791.
- Lebreton, J.D., Hines, J.E., Pradel, R., Nichols, J.D. & Spendelov, J.A. (2003) Estimation by capture-recapture of recruitment and dispersal over several sites. *Oikos*, **101**, 253-264.
- Lowe, W.H. & Allendorf, F.W. (2010) What can genetics tell us about population connectivity? *Molecular Ecology*, **19**, 3038-3051.
- Martínez del Rio, C. & Wolf, B.O. (2005) Mass-balance models for animal isotopic ecology. *Physiological and Ecological Adaptations to Feeding in Vertebrates* (ed. by J.M. Starck and T. Wang), pp. 141-174. Science Publishers, Enfield, New Hampshire.
- Matthiopoulos, J., Harwood, J. & Thomas, L. (2005) Metapopulation consequences of site fidelity for colonially breeding mammals and birds. *Journal of Animal Ecology*, **74**, 716-727.
- McCoy, K.D., Boulinier, T. & Tirard, C. (2005) Comparative host-parasite population structures: disentangling prospecting and dispersal in the black-legged kittiwake *Rissa tridactyla*. *Molecular Ecology*, **14**, 2825-2838.
- Miles, W.T.S. (2010) *Ecology, behaviour and predator-prey interactions of great skuas and Leach's storm-petrels at St Kilda*. PhD, University of Glasgow, Glasgow.
- Mitchell, I.P., Newton, S.F., Ratcliffe, N. & Dunn, T.E. (2004) *Seabird Populations of Britain and Ireland*. T & A D Poyser, London.
- Mougeot, F. & Bretagnolle, V. (2000) Predation as a cost of sexual communication in nocturnal seabirds: an experimental approach using acoustic signals. *Animal Behaviour*, **60**, 647-656.
- Newson, S.E., Mitchell, I.P., Parsons, M., O'Brien, S.H., Austin, G.E., Benn, S., Black, J., Blackburn, J., Brodie, B., Humphreys, E., Leech, D.I., Prior, M. & Webster, M. (2008) Population decline of Leach's storm-petrel *Oceanodroma leucorhoa* within the largest colony in Britain and Ireland. *Seabird*, **21**, 77-84.
- Oro, D. (2003) Managing seabird metapopulations in the Mediterranean: constraints and challenges. *Scientia Marina*, **67**, 13-22.
- Owens, N.J.P. (1987) Natural Variations in ^{15}N in the Marine Environment. *Advances in Marine Biology* (ed. by J.H.S. Blaxter and A.J. Southward), pp. 389-451. Academic Press Inc., Oxford, UK.
- Paiva, V.H., Xavier, J., Geraldès, P., Ramirez, I., Garthe, S. & Ramos, J.A. (2010) Foraging ecology of Cory's shearwaters in different oceanic environments of the North Atlantic. *Marine Ecology Progress Series*, **410**, 257-268.
- Paradis, E., Baillie, S.R., Sutherland, W.J. & Gregory, R.D. (1998) Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology*, **67**, 518-536.
- Parnell, A.C., Inger, R., Bearhop, S. & Jackson, A.L. (2010) Source Partitioning Using Stable Isotopes: Coping with Too Much Variation. *PLoS ONE*, **5**, e9672.
- Parnell, A.C., Phillips, D.L., Bearhop, S., Semmens, B.X., Ward, E.J., Moore, J.W., Jackson, A.L. & Inger, R. (2012) Bayesian Stable Isotope Mixing Models. In: Cornell University Library

- Phillips, R.A., Thompson, D.R. & Hamer, K.C. (1999) The impact of great skua predation on seabird populations at St Kilda: a bioenergetics model. *Journal of Applied Ecology*, **36**, 218-232.
- Podlesak, D.W., McWilliams, S.R. & Hatch, K.A. (2005) Stable isotopes in breath, blood, feces and feathers can indicate intra-individual changes in the diet of migratory songbirds. *Oecologia*, **142**, 501-510.
- R Development Core Team (2011) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.
- Ricklefs, R.E., Day, C.H., Huntingdon, C.E. & Williams, J.B. (1985) Variability in feeding rate and meal size of Leach's storm-petrel at Kent Island, New Brunswick. *Journal of Animal Ecology*, **54**, 883-898.
- Robinson, M.R. & Beckerman, A.P. (2013) Quantifying multivariate plasticity: genetic variation in resource acquisition drives plasticity in resource allocation to components of life history. *Ecology Letters*, n/a-n/a.
- Schreiber, E.A. & Burger, J. (2002) *Biology of Marine Birds*. CRC Press, Boca Raton, Florida.
- Telfer, S., Piertney, S.B., Dallas, J.F., Stewart, W.A., Marshall, F., Gow, J.L. & Lambin, X. (2003) Parentage assignment detects frequent and large-scale dispersal in water voles. *Molecular Ecology*, **12**, 1939-1949.
- Tieszen, L.L., Boutton, T.W., Tesdahl, K.G. & Slade, N.A. (1983) Fractionation and turnover of stable carbon isotopes in animal tissues: Implications for $\delta^{13}\text{C}$ analysis of diet. *Oecologia*, **57**, 32-37.
- Turner, T.F., Collyer, M.L. & Krabbenhoft, T.J. (2010) A general hypothesis-testing framework for stable isotope ratios in ecological studies. *Ecology*, **91**, 2227-2233.
- Ventura, M. (2006) Linking biochemical and elemental composition in freshwater and marine crustacean zooplankton. *Marine Ecology Progress Series*, **327**, 233-246.
- Votier, S., Grecian, W., Patrick, S. & Newton, J. (2011) Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. *Marine Biology*, **158**, 1-8.
- Votier, S.C., Birkhead, T.R., Oro, D., Trinder, M., Grantham, M.J., Clark, J.A., McCleery, R.H. & Hatchwell, B.J. (2008) Recruitment and survival of immature seabirds in relation to oil spills and climate variability. *Journal of Animal Ecology*, **77**, 974-983.
- Votier, S.C., Crane, J.E., Bearhop, S., de Leon, A., McSorley, C.A., Minguéz, E., Mitchell, I.P., Parsons, M., Phillips, R.A. & Furness, R.W. (2006) Nocturnal foraging by great skuas *Stercorarius skua*: implications for conservation of storm-petrel populations. *Journal of Ornithology*, **147**, 405-413.
- Wunder, M.B., Kester, C.L., Knopf, F.L. & Rye, R.O. (2005) A test of geographic assignment using isotope tracers in feathers of known origin. *Oecologia*, **144**, 607-617.

(A) DATA ACCESSIBILITY

All the raw and corrected stable isotope data, model parameter files and model comparison results have been deposited in the Dryad repository; DOI: doi:10.5061/dryad.q2610

(A) BIOSKETCH

The authors have diverse research interests (e.g. dispersal, phylogeography, speciation, individual specialisation, foraging & spatial ecology, conservation genetics, conservation management and policy), which include the use of molecular techniques to address ecological

and evolutionary questions, and how the results may be applied to species and biodiversity conservation.

(A) AUTHOR CONTRIBUTIONS

AWJB, SCV, MEK, DTB and JBR conceived the ideas; AWJB, SCV, MC and JN collected and/or processed samples; AWJB and SCV analysed the data; AWJB and SCV led the writing.

Figure 1 a. Leach's storm-petrel colonies and CPR sampling locations in the North Atlantic. Black = Canadian region, Green = Icelandic region and Red = Scottish region. Stars = colony locations, Triangles = CPR sample locations. Arrows indicate direction and relative amount of pre-breeder movement inferred from SIAR results. **b.** $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope values for breeders (bars; mean ± 2 sd) and individual pre-breeder (filled circles) by colony. Black = Gull Island, green = Vestmannaeyjar and red = St Kilda. (Photo taken by Richard Steel)

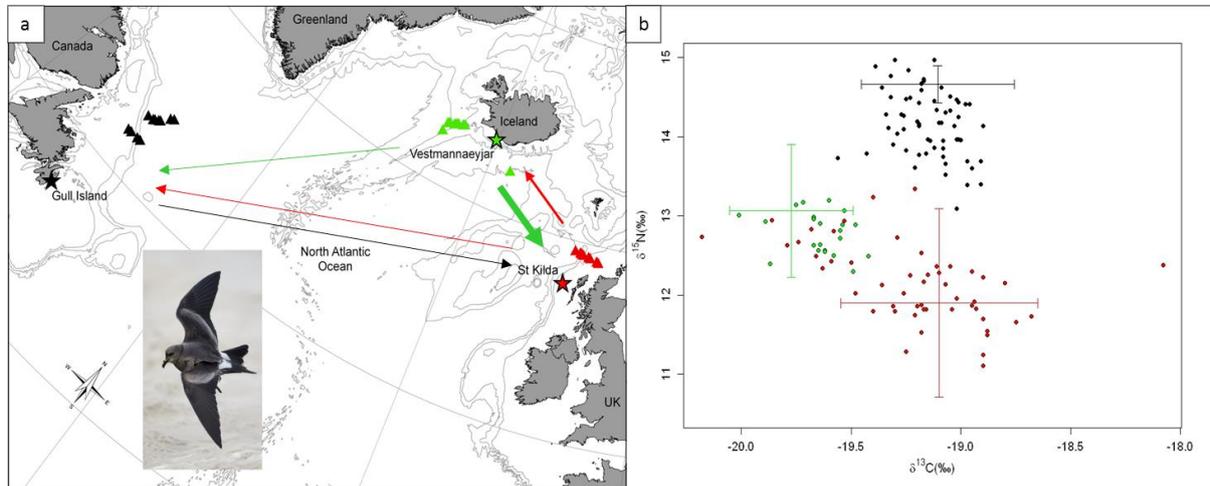
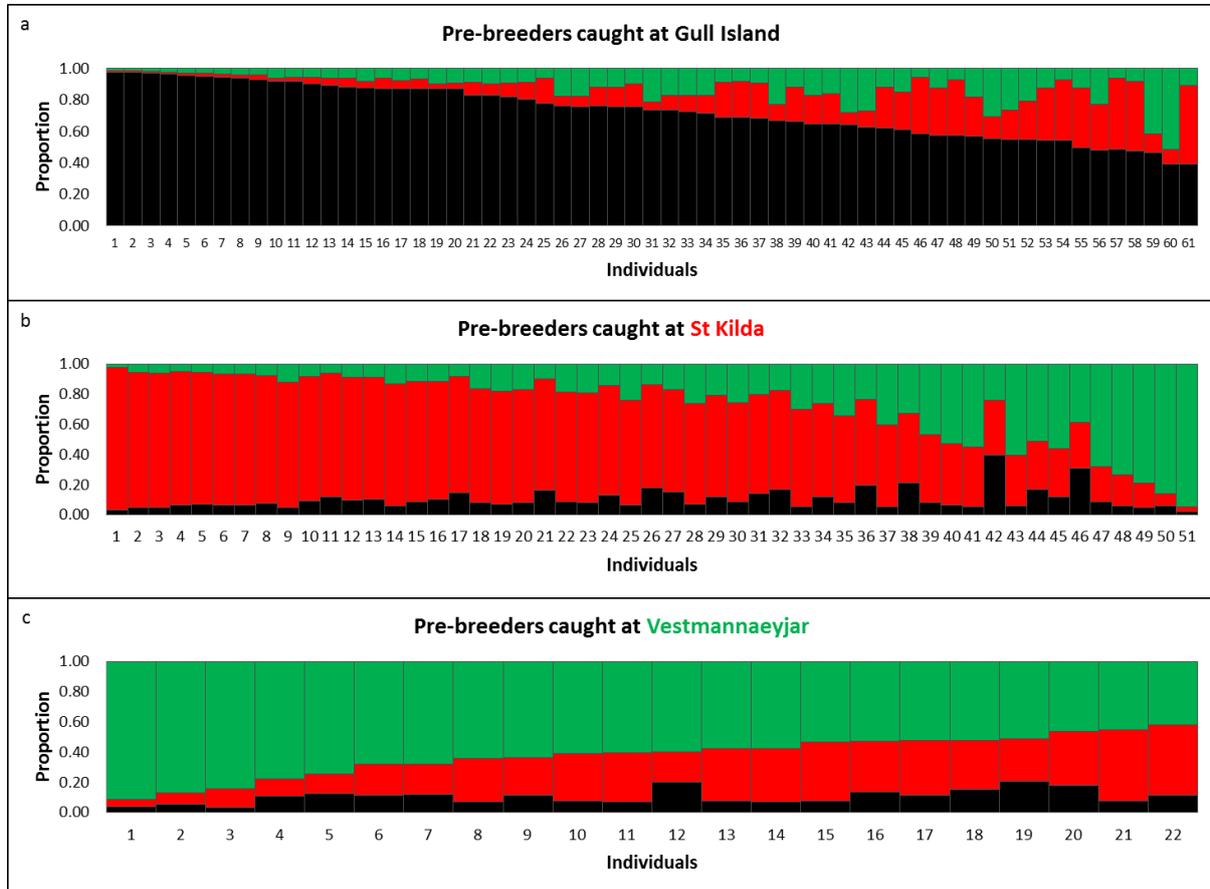


Figure 2 SIAR proportion estimates for individual pre-breeding Leach’s storm-petrels caught at three colonies in the North Atlantic. **a)** Birds caught at Gull Island, Canada, **b)** Birds caught at St Kilda, Scotland, **c)** Birds caught at Vestmannaeyjar, Iceland. Black bar = Gull Island proportion estimate, red bar = St Kilda proportion estimate, green bar = Vestmannaeyjar proportion estimate.



SUPPORTING INFORMATION

Supporting Data file (

Table S1 {Leach's storm-petrel and *calanus* copepod sample sizes and tissue type. b = breeding adult Leach's storm-petrel, nb = non-breeding Leach's storm-petrel, * = each sample represents 10-20 individual copepods.}

Location	Species	Type	N
<u>Colony</u>			
Gull Island, Canada	<i>Oceanodroma leucorhoa</i>	Red Blood Cells	04 (b), 61 (nb)
Vestmannaeyjar, Iceland	<i>Oceanodroma leucorhoa</i>	Red Blood Cells	12 (b), 22 (nb)
St Kilda, Scotland	<i>Oceanodroma leucorhoa</i>	Red Blood Cells	18 (b), 51 (nb)
<u>Atlantic Region</u>			
Newfoundland Shelf	<i>Calanus finmarchicus</i>	Whole organism	36* (2 CPR routes)
Reykjanes Ridge/Iceland Basin	<i>Calanus finmarchicus</i>	Whole organism	29* (2 CPR routes)
Shetland basin	<i>Calanus helgolandicus</i>	Whole organism	18* (1 CPR route)

Table S2 {Mean change in individual SIAR proportion estimates for sampled pre-breeding Leach's storm-petrels when comparing results between the original and sensitivity model (estimated Gull Island source $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and standard deviations).}

Pre-breeder colony of capture	Model source	Change in individuals proportion estimates (range)	Change in individuals proportion estimate (mean \pm 1sd)
Gull Island, Canada	<i>Gull Island</i>	-0.06 – 0.12	+0.01 \pm 0.06
	<i>St Kilda</i>	-0.04 – 0.05	-0.01 \pm 0.03
	<i>Vestmannaeyjar</i>	-0.07 – 0.07	+0.01 \pm 0.04
St Kilda, Scotland	<i>Gull Island</i>	-0.08 – 0.00	-0.05 \pm 0.03
	<i>St Kilda</i>	0.00 – 0.05	+0.03 \pm 0.01
	<i>Vestmannaeyjar</i>	0.00 – 0.05	+0.03 \pm 0.02
Vestmannaeyjar , Iceland	<i>Gull Island</i>	-0.08 – -0.01	-0.05 \pm 0.02
	<i>St Kilda</i>	0.00 – 0.04	+0.02 \pm 0.01
	<i>Vestmannaeyjar</i>	0.01 – 0.07	+0.04 \pm 0.01

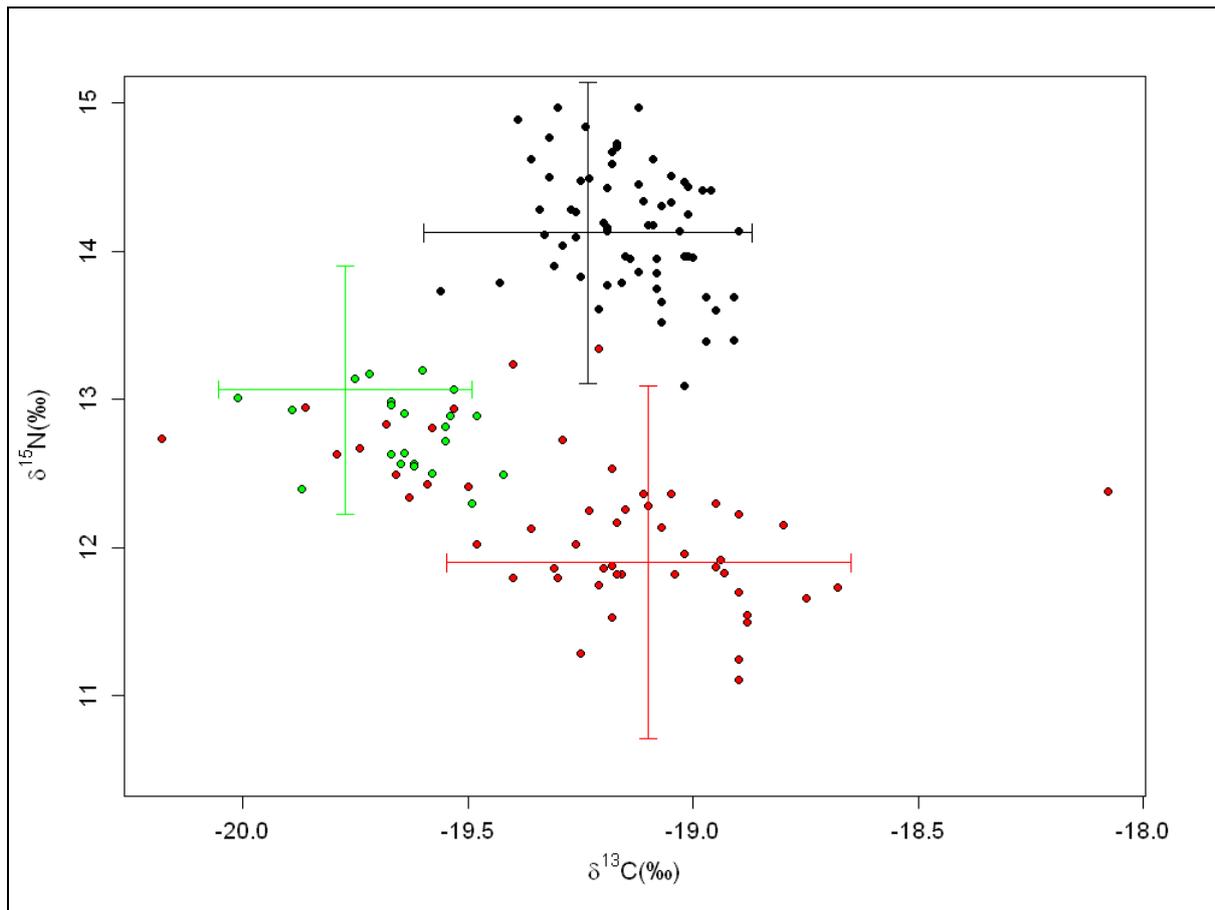


Figure S1 { $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope values for breeders (bars; mean \pm 2sd) and individual pre-breeders (filled circles) used in the “sensitivity” model. Black = Gull Island (estimated values), green = Vestmannaeyjar and red = St Kilda. }

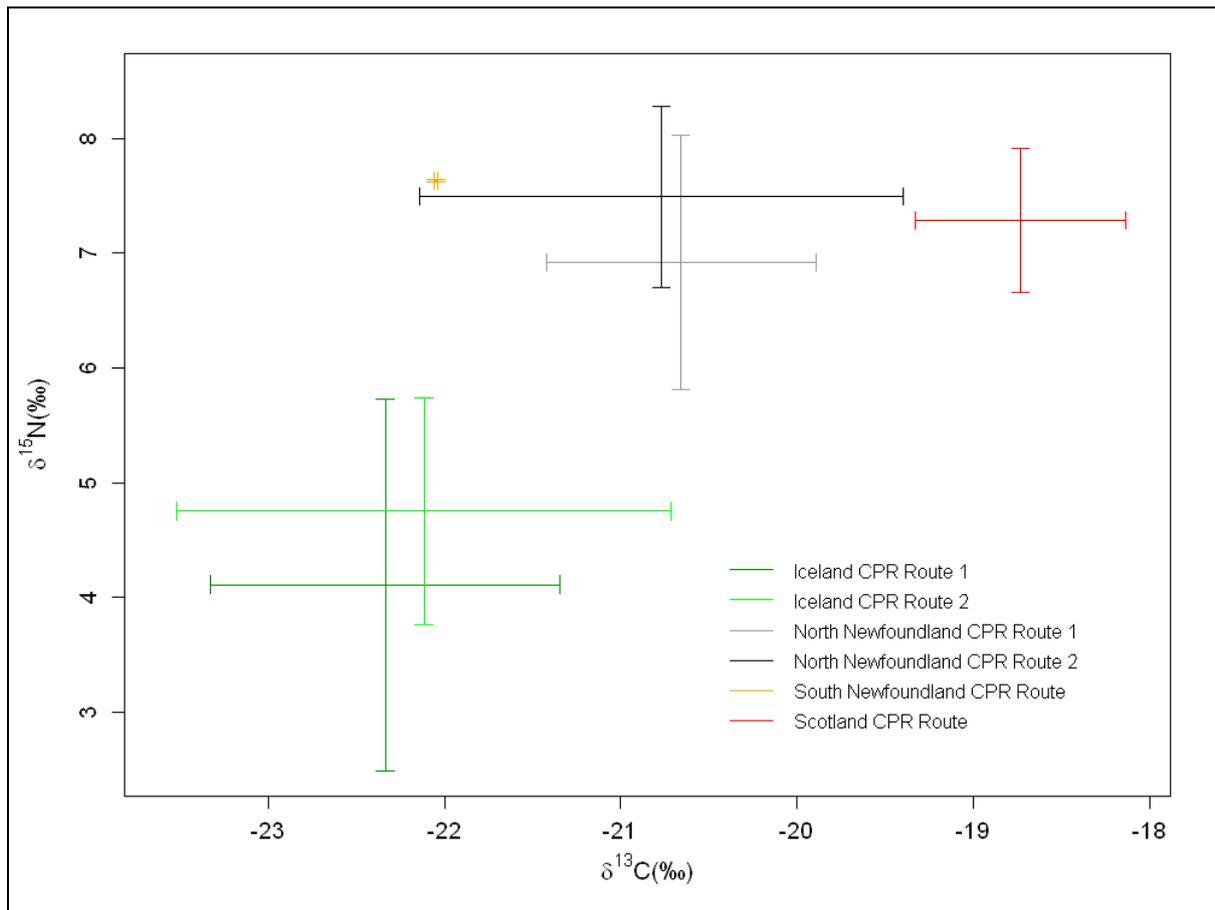


Figure S2 {*Calanus* copepod $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope bivariate plot confirming the regional isotopic differences at this lower trophic level. Corrected means and 2 standard deviation bars for samples collected from the SAHFOS Continuous Plankton Recorder in oceanic regions off the coast of Newfoundland, Canada (both north and south), Iceland and Scotland (shown in Figure 1).}

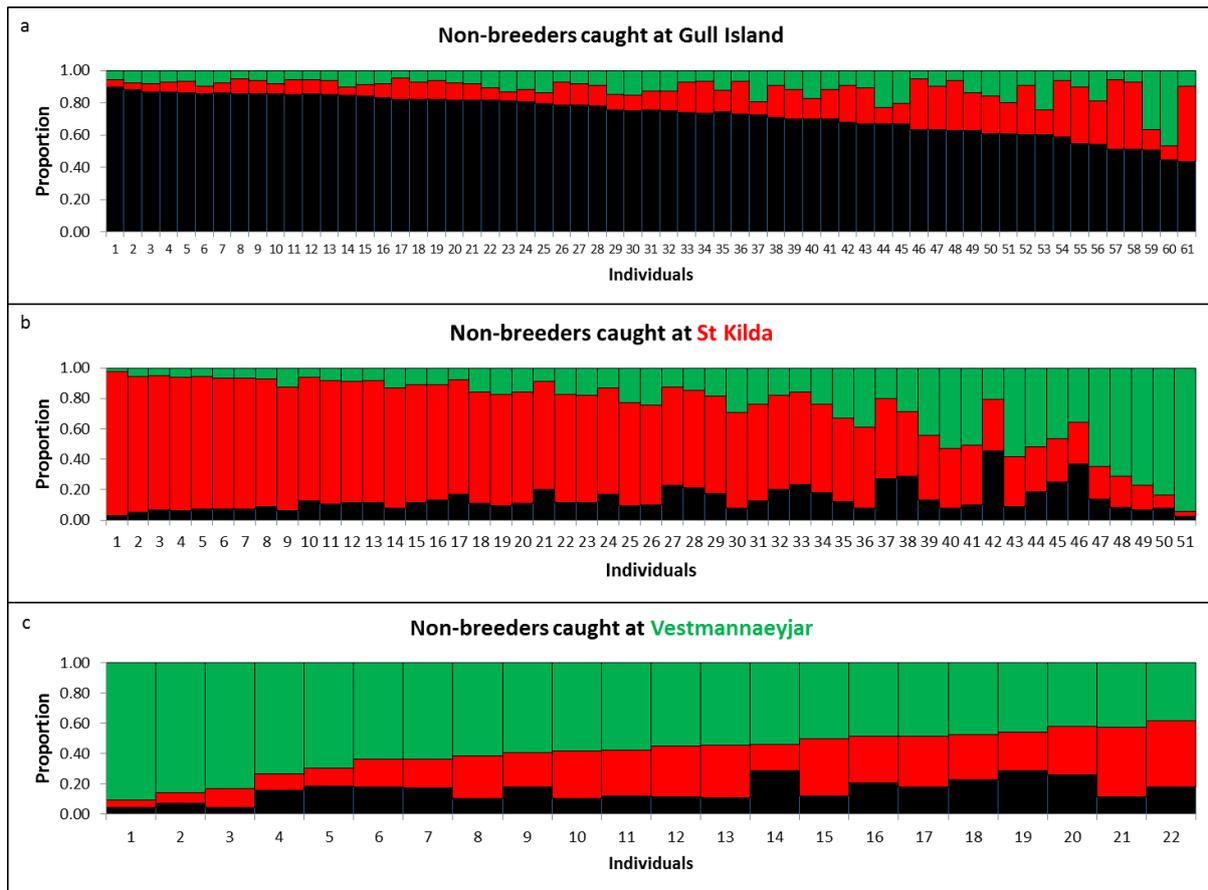


Figure S3 {Sensitivity model results. SIAR median proportion estimates for individual pre-breeding Leach's storm-petrels caught at three colonies in the North Atlantic based on estimated Gull Island source $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and standard deviations. a) Birds caught at Gull Island, Canada, b) Birds caught at St Kilda, Scotland, c) Birds caught at Vestmannaeyjar, Iceland. Black bar = Gull Island proportion estimate, red bar = St Kilda proportion estimate, green bar = Vestmannaeyjar proportion estimate. }

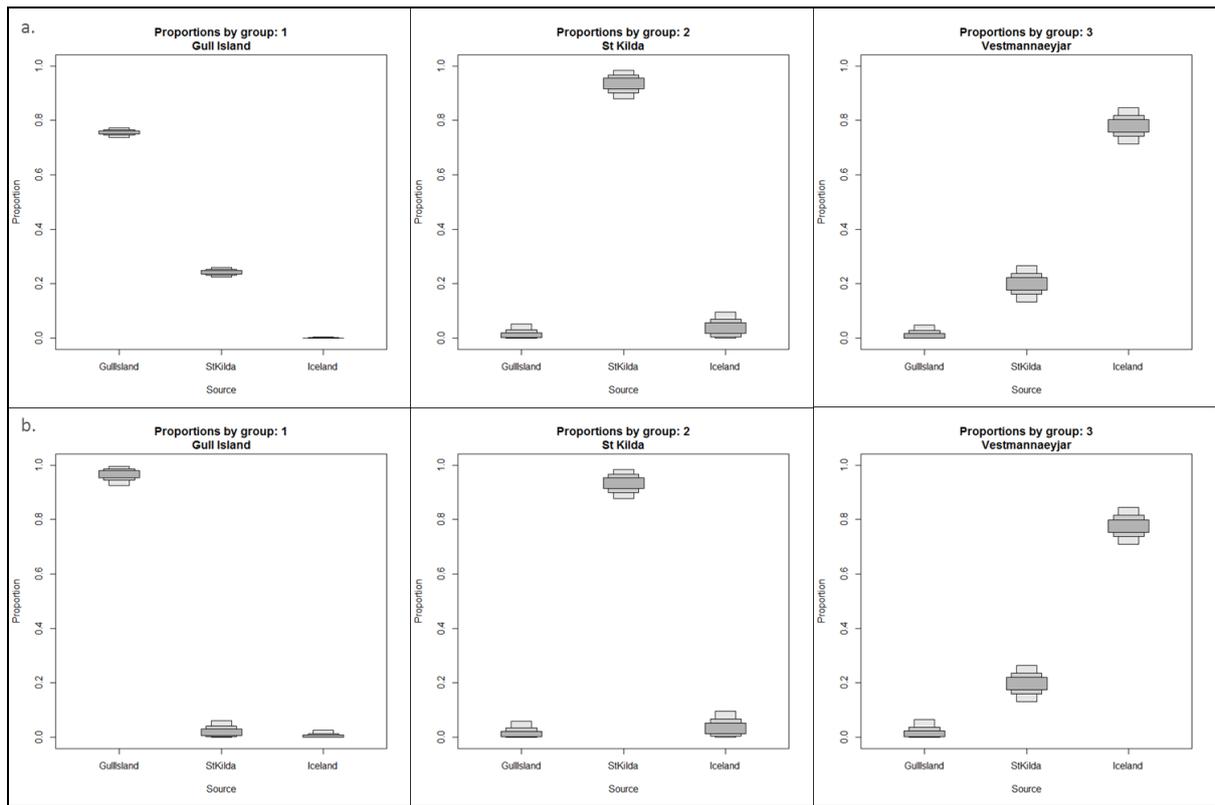


Figure S4 {Mixing model proportion estimates and credibility intervals (25, 75 & 95%) for pre-breeding Leach's storm-petrels caught at three colonies (Gull Island – Canada, St Kilda – Scotland and Vestmannaeyjar – Iceland). a. Model results by colony of capture (group) using original source $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and standard deviations, b. Sensitivity model results by colony of capture (group) using estimated Gull Island source $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and standard deviations. }