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Summary for

Reconstructing important phases of the annual cycle of four species of storm-petrels using stable isotope analyses and ptilochronology

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Introduction

Seabirds being a part of the marine food chains[1] and transporting nutrients and contaminants between habitats[2], link marine, coastal and terrestrial ecosystems[3]. Currently, seabirds are under threat from several processes (e.g. invasive species, overfishing, climate change[4]). Environmental changes affect the productivity of all trophic levels of the food chain, including seabirds[5], through changing the composition and phenology of small phytoplankton[6]. Changes in seabird population dynamics directly influence nutrient flows[7,8] and may thus have unexpected ramifications for coastal ecosystems. Therefore, seabirds can be used as sentinels for marine ecosystem health and productivity[9,10]. To be able to translate fluctuations in seabird abundance and breeding success to a proxy for marine ecosystem health, we need to understand the challenges they face throughout all stages of their life.

The annual cycle of seabirds can be divided into several important phases, which may partially overlap. In pelagic seabirds, which spend the majority of the year at open sea, the annual cycle can be separated into the breeding period, the only time they return to land, and the non-breeding period, often spanning most of the year. Aside from the energetically demanding breeding period (especially through incubation and chick provisioning[11,12]), other important and energetically costly phases of the avian annual cycle are the moulting period (due to plumage gaps decreasing flight efficiency[13,14]), and in several pelagic seabirds, migration away from the breeding grounds. Knowledge about the ecology of the different stages of the avian annual cycle is crucial to understand the challenges species face throughout the year, especially given the fact that the events during one stage may cause carry-over effects into subsequent stages[15–18].

For this dissertation four species of storm-petrels breeding sympatrically were studied; two species from the family *Hydrobatidae* on the Northern hemisphere (European storm-petrel, *Hydrobates pelagicus*, ESP; Leach's storm-petrel, *Oceanodroma leucorhoa*, LSP) and two species from the family *Oceanobatidae* on the Southern hemisphere (black-bellied storm-petrel, *Fregetta tropica*, BBSP; Wilson's storm-petrel, *Oceanites oceanicus*, WSP). The studied storm-petrels are typical pelagic seabirds and thus should be highly mobile throughout the year[19]. Therefore, they shed a limited number of feathers at once during moult and feather growth takes them up to several weeks[20,21]. Due to their abundance[22], they serve as integral parts of marine ecosystems both as predator and prey[23]. However, studying their foraging, breeding and movement ecology throughout the year remains challenging, as they mostly to breed in hard-to-reach burrows or crevices and after the hatching of the egg adults only visit the colonies at night[24,25]. Storm-petrels, similarly to other petrel species, may convert part of their stomach contents into nutrient rich oil[26,27], complicating diet composition studies further. Due to the small size of storm-petrels, tracking devices have only very recently become miniaturised enough to use for fine-scale movement studies[19,28–31]. As such, alternate methods are necessary to study the ecology of the storm-petrels.

Stable isotope analyses have been used extensively to study seabird ecology[32–34]. Stable carbon isotope ratios ($\delta^{13}C$) vary little between trophic levels and can thus be used to determine foraging habitats[35]. The trophic component of stable oxygen isotope ratios ($\delta^{18}O$) is less well known and varies depending on diet and location[36], but the trophic enrichment factor between seawater and feathers can be calculated from recent water samples and feather material (e.g. from regrowing feathers). In contrast, stable nitrogen isotope ratios ($\delta^{15}N$) do differ strongly and predictably between predator and prey in food webs (3 – 4 ‰)[37], and can thus be used to provide information on consumer trophic level[38]. The stable isotope compositions of different tissues reflect the foraging ecology at different stages and time scales; blood stable isotopes reflect the trophic position and foraging area during the last weeks[39], while feathers remain inert after formation and thus reflect the foraging ecology at the time of feather synthesis[40].

Ptilochronology can be used to reconstruct energy availability during moult. This method uses feather growth bar width as a proxy for feather growth rate[41,42]. During the formation of feathers alternating light and dark bands are formed, which correlate with periods of activity and rest (e.g. day – night rhythms[43]; activity linked to twilight periods[44]). Individuals with relatively larger growth bars are assumed to have more energy available for feather synthesis than individuals with relatively smaller growth bars[41,45].

Aims and hypotheses

The aim of this doctoral project was to reconstruct the foraging and movement ecology of storm-petrels at different annual phases, using stable isotope and ptilochronology methods.

Firstly, energy availability during moult between the four species of storm-petrels was compared. It has been hypothesised that, as ESP and LSP are known to partially overlap the end of the breeding period with the start of tail feather (i.e. right outer rectrix) moult[46–49] while BBSP and WSP fully moult during the non-breeding period[25], the Northern species would have a lower energy availability during moult (i.e. smaller growth bars) than the Southern species.

Secondly, stable isotopic niche partitioning during breeding in the Southern species was studied, and the effect of parents foraging at different trophic levels on chick growth was examined. The expectation was to find that BBSP foraged at a higher trophic level than WSP, as BBSP diets are known to contain a larger proportion of fish than WSP diets, which consist mostly of crustaceans[24,50–52]. Additionally, chicks were expected to be fed at a higher trophic level than adults ingested themselves[53–55, but see 56].

Lastly, differences in moult distribution between all four species (i.e. ESP, LSP, BBSP, WSP) were studied and correlated to variation in body morphology, feather growth rate and δ^{15}N. Differences in moult distribution between the species within each hemisphere were expected (as the timing of the breeding and non-breeding periods is mirrored between the hemispheres and the non-breeding periods thus only partially overlap, species were not compared between hemispheres). Additionally, intra-specific variation in moult distribution linked to body morphology with larger individuals migrating to farther moulting grounds than smaller individuals[34] was expected. Moreover, differences in moult distribution were expected to affect feather growth rate and δ^{15}N as moulting areas may differ in food availability.

Methods

The field work for this project was carried out in two locations, during two consecutive breeding seasons. During the austral summer of 2017 and 2018 (January – April) BBSP and WSP adults were captured using mist-nets set up at night, and by taking incubating adults from nests in breeding colonies around the Henryk Arctowski Polish Polar Station on King George Island, South Shetland Islands, Antarctica (62°09′S, 58°27′W). Each captured individual was weighed to the nearest 0.1 g, its tarsus length was measured to the nearest 0.1 mm and its wing length to the nearest 1 mm. Tissue samples (feather and blood) were taken for stable isotope and ptilochronological analyses from each individual. Additionally, chick growth rate (i.e. body weight, tarsus length and wing length) of both species was measured every three days, weather permitting, and feather samples for stable isotope analyses were collected. In August of 2018 and 2019 adult ESP and LSP were captured at night using mist-nets set up in a mixed breeding colony on Mykines, Faroe Islands (62°05′N, 07°39′W). Each individual was weighed, and measured (tarsus length and wing length), and tissue samples for stable isotope and ptilochronological analyses were collected.

Stable isotopes ($\delta^{15}N$, $\delta^{13}C$ and $\delta^{18}O$) compositions of the feather and blood samples were analysed using a mass spectrometer. Feather length was measured from the tip to the base of the calamus with callipers to the nearest 0.1 mm. Growth bar width was measured to the nearest 0.1 mm, following Grubb 1989[41]. Mean growth bar width per feather was treated as a proxy for feather growth rate.

All statistical analyses were performed in R[57]. Statistical methods differed per tested hypothesis and are fully detailed in particular papers.

Results and discussion

Paper no. 1 – Feather growth rate differences: Distinct differences in feather growth rate between species in both hemispheres were found. Part of these differences could be related to size differences, as larger species generally have higher feather growth rates. The expected feather growth rate for each storm-petrel species was estimated based on the feather growth rates of a large set of species from different avian families, reported in literature. Feather growth rate does not linearly increase with body feather length, such that larger species have relatively lower feather growth rates compared to feather length. The expected feather growth rates differed significantly from the observed feather growth rates in both hemispheres, but in opposite directions. Both Northern species had significantly lower observed feather growth rates than expected, while both Southern species had significantly higher feather growth rates than expected. This implies that the Northern species had less energy available for feather synthesis than the Southern species. It suggests that these differences are caused by the partial overlap of breeding and moult in the Northern species, forcing them to allocate their energy between both processes, while moulting Southern species are free from the costs of breeding and can allocate more energy to moulting.

Paper no. 2 – Niche partitioning during the breeding period: Analyses showed that chicks of both WSP and BBSP were fed at a higher trophic level than the adults ingested themselves, likely to compensate for the higher nutritional demands of the growing chick. However, while BBSP chicks were provisioned at a higher trophic level than the other studied groups, the isotopic niches of the adults of both species and the WSP chicks showed considerable overlap. Additionally, pre-laying females (as indicated by chick down isotope compositions) had wider stable isotope niches than chick and adults during the chick-rearing period. Pre-laying females are free roaming while chick-rearing adults are central-place foragers forced to return to the nest for chick-provisioning. In both species, chick growth rate was negatively correlated with $\delta^{15}N$ values, indicating nutritional stress. Nutritional stress may cause the use of endogenous instead of dietary amino acids in protein synthesis, thus inflating $\delta^{15}N$ values. The higher trophic level of the larger BBSP chicks may be due to a higher nutritional demand caused by a longer stay in the nest and relatively larger body mass gain, despite chick growth rates being similar to the smaller WSP chicks. The sympatric breeding of BBSP and WSP should lead to niche partitioning to avoid competition over resources. The apparent overlap in foraging niches as implied by the overlapping isotopic niches, may be caused by sharing main prey species and the relative simplicity of the Antarctic food chain. Only few species (e.g. krill and myctophid fish)[58–60] take key positions in the diet compositions of many predators, thus reducing the detectability of foraging niche partitioning through stable isotope analyses.

Paper no. 3 – Moulting distribution: Moulting distribution as implied by different $\delta^{13}C$ and $\delta^{18}O$ compositions differed between species in both the Northern and Southern hemisphere. In three out of the four studied species (i.e. ESP, LSP and WSP), individuals could be separated into groups with different moulting distributions based on several variables. In all three mentioned species $\delta^{13}C$ and $\delta^{18}O$ compositions differed between years, implying either inter-annual differences in moulting grounds locations or inter-annual differences in the $\delta^{13}C$ and $\delta^{18}O$ compositions at the moulting grounds. Additionally, ESP and WSP could be further separated based on morphological variation, implying either an effect of morphology on migration strategy (e.g. distance to the breeding ground) or foraging behaviour (e.g. foraging in different oceanic zones). Furthermore, WSP showed $\delta^{15}N$ differences between moulting groups, caused either by differences in moulting area affecting $\delta^{15}N$ composition at the base of the food chain, or by differences in diet and thus trophic level. By implementing a geographical distribution prediction model based on oceanic $\delta^{13}C$ and $\delta^{18}O$ isoscapes, combined with chlorophyll-*a* concentrations (a proxy for primary production) and observations of birds at sea, potential moulting areas of the studied species were predicted. The Northern species were predicted to moult in temperate and tropical Atlantic zones, while BBSP was predicted to moult on the Southern hemisphere north of the Subtropical Front, and WSP showed more variation in moulting distribution including groups predicted to moult south of the Subtropical front and as far north as the Arctic and northern Pacific.

Conclusions

The results of my PhD dissertation show that (1) indirect techniques such as stable isotope analyses and ptilochronology may provide valuable insights into the different stages of the avian annual cycle of elusive seabirds that are otherwise hard to study; (2) that distinct differences in moulting strategies and distribution exist between storm-petrels breeding on both hemispheres; and (3) that distinct differences exist between sympatrically breeding species in foraging, chick provisioning and moulting strategies. Different moult-breeding schedules may affect energy allocation into feather synthesis, and variation in moulting distribution may be affected by different aspects within each species. Additionally, the amount of variation in moulting distribution may differ between species. Lastly, the results of this dissertation show that, in contrast to expectations that sympatrically breeding species should show niche partitioning to avoid interspecific competition, the high productivity of the Antarctic marine ecosystem may facilitate foraging niche overlap of sympatrically living species. This study forms the basis for further research into the foraging and movement ecology of storm-petrels at more fine-scale analyses, made possible by ongoing technical advances in animal tracking and stable isotope methods. Furthermore, the results can be used to properly delineate key conservation areas, to decide where to direct protection efforts, and to form conservation planning in the vast ocean.

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