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# Moult chronology and strategies of sympatric Great (Ardenna gravis) and Sooty (A. grisea) Shearwaters based on stable isotope analysis

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Moult is an energetically demanding period, during which flight may be impaired and foraging ranges may become constrained. During the non-breeding period, Great Ardenna gravis and Sooty Ardenna grisea Shearwaters migrate from South Atlantic breeding colonies to aggregate at North Atlantic feeding grounds. We investigated whether both shearwater species used coastal Newfoundland, Canada, as a moulting area and used stable isotope ratios ( $\delta^{15}$ N,  $\delta^{13}$ C) of recently moulted primary feathers (P1, P5, P10) to infer moult location/diet for both species. Moult scores indicated that both species finished their moult (i.e. P6-10) in coastal Newfoundland, which was further corroborated with similar stable isotope ratios for Great ( $\delta^{15}N = 15.17 \pm 1.13\%$ )  $\delta^{13}C = -18.66 \pm 0.54\%$  and Sooty Shearwaters  $(15.54 \pm 0.74\%) - 18.43 \pm 0.78\%$ ; however, Sooty Shearwater moult was more advanced relative to that of Great Shearwater. In contrast, isotopic ratios of P1 and P5, which were grown before arriving in coastal Newfoundland, differed between and within species, suggesting divergent locations/diet during early moult. For Great Shearwaters, P1/P5 isotopic ratios were more variable (broader niche breadth) than P10, suggesting that some individuals started moulting in the South Atlantic prior to trans-equatorial migration, whereas others start moulting in the North Atlantic Ocean. Sooty Shearwaters had two distinct groupings of either higher or lower  $\delta^{15}N$  in P1/P5, suggesting that individuals began moulting either on the Newfoundland Shelf or further offshore based on comparisons to reference shearwater feathers grown in known locations. These findings illustrate distinct locations and/or diets at the start of primary feather moult, both within and between species, but diets converged when aggregated together at the end of moult in coastal North America, where growing feathers of both species were sampled. More importantly, we identified an important area for both Sooty and Great Shearwaters to complete their moult in coastal Newfoundland. Protecting this moulting area would minimize disturbance and the impacts of threats (e.g. by-catch) to both species during this energetically demanding period. The area has been suggested previously to be an important candidate area for protection due to annually persistent prey aggregations that can be spatiotemporally delimited based on specific prey habitat requirements.

Keywords: Ardenna, feathers, moulting, primaries, shearwaters, stable isotope, Staffelmauser.

Moult is an important part of the annual cycle of bird species and does not usually overlap with

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breeding periods because both are energetically demanding activities (Lindstrom *et al.* 1993, Howell 2010, but see van Bemmelen *et al.* 2018). In addition, simultaneous moult of several flight feathers could impair flight, which precludes efficient flight and thus long-distance migration. As such, an important factor in the evolution of moult strategies for a migratory bird species is thought to be food availability (Barta et al. 2008) in conjunction with the timing of breeding and migration (Langston & Rohwer 1996, Rohwer 1999, Bridge 2006). Indeed, the 'winter moult' (i.e. moult on the non-breeding grounds) for transequatorial migrants, such as shearwaters, tends to occur in highly productive areas in the opposite hemisphere, where food availability is high (Brown 1988, Bridge 2006, Barta et al. 2008, Howell 2010). As wing moult affects a bird's ability to fly (Tucker 1991, Swaddle & Witter 1997), moult tends to occur after trans-equatorial migration. when long-distance movements are no longer necessary (Brown 1988, Bridge 2006). As such, foraging ranges can become constrained during moult and sympatric species occupying a similar trophic niche might evolve different moult strategies, including moulting at different times of the year or in different locations (i.e. temporal or spatial niche partitioning), thereby reducing interspecific competition where food availability is limited (Barta et al. 2008).

Great Shearwaters (Ardenna gravis) breed in the South Atlantic Ocean (Tristan da Cunha and Falkland Islands) whereas Sooty Shearwaters (Ardenna grisea) breed in the South Atlantic Ocean (Falkland Islands) and in higher numbers in the Pacific Ocean (Howell 2012). Both species migrate to the North Atlantic during their non-breeding season (May to October: Howell 2012) where they have a sympatric distribution. On the northeast coast of Newfoundland, Great and Sooty Shearwaters aggregate in high abundance near Capelin Mallotus villosus spawning sites (Davoren 2013, Carvalho & Davoren 2019), which is the main prey species in the area during the summer for most predators (Gulka et al. 2017), including shearwaters (Carvalho & Davoren 2020). Although both shearwater species share a similar annual cycle, they appear to differ in the timing of migration and the timing and regions of moult. Indeed, although the timing of breeding does not appear to differ (Carboneras et al. 2020a, 2020b), tagged Sooty Shearwaters started their migration to the Northern Hemisphere after the breeding season in March (Hedd et al. 2012), whereas tagged Great Shearwaters used the Patagonia shelf (Southern Hemisphere) after the breeding season in April-May (Ronconi et al. 2018) prior to migration. Great Shearwaters are known to undergo flight feather moult in coastal areas of eastern Canada (Brown 1988, Powers *et al.* 2017, 2020; cf. Bugoni *et al.* 2015), whereas Sooty Shearwaters appear to moult offshore in the North Atlantic, based on observations of newly moulted feathers upon arrival in inshore areas (Brown 1988). Given that both species also forage together in the North Atlantic at naturally occurring prey sources associated with physical oceanographic features, such as upwellings (Brown *et al.* 1981, Ronconi *et al.* 2010a) and prey fish spawning sites (Davoren 2013, Carvalho & Davoren 2019), it is possible that moulting regions overlap.

As feathers are inert once fully grown, stable isotope analysis of this tissue type has been used to estimate dietary composition and/or location during the period of moult when feathers are grown (e.g. Cherel et al. 2000, Ramos et al. 2009a, Dehnhard et al. 2011). In the marine environment, carbon stable isotope ratios ( $\delta^{13}C$ ) mav be used to indicate the general location of foraging areas, and nitrogen stable isotope ratios ( $\delta^{15}N$ ) are typically used to indicate trophic levels of consumers (Hobson et al. 1994). In addition, divergent stable isotope ratios in different primary feathers of the same individual have revealed either distinct moulting locations or dietary changes during moult (Ramos et al. 2009b, Meier et al. 2017). There are issues with this, however, as inferring different moult locations from stable isotope ratios relies on divergent baseline stable isotopic ratios and, when comparing between different times of year or among years, assumes that region-specific baselines do not shift across time. When stable isotope analysis is paired with tracking devices, divergent stable isotope ratios have been identified from different moulting locations of seabirds (Thompson et al. 2015, Cherel et al. 2016, Carpenter-Kling et al. 2020), including Cory's Shearwaters Calonectris borealis (Ramos et al. 2009a) and Sooty Shearwaters (Hedd et al. 2012). In the Southern Hemisphere, Great and Sooty Shearwaters are known to feed on fisheries discards, including squid bait and offal from sharks and tunas (Petry et al. 2008, Bugoni et al. 2010), which occupy higher trophic levels relative to lower trophic level fish and invertebrate prey that are captured in the Northern Hemisphere (Ronconi et al. 2010a). In addition, Hong et al. (2019) found that  $\delta^{13}C$  of Great Shearwaters increased with latitude among sampling sites in the Northern Hemisphere. This suggests the potential to identify distinct moulting areas by sampling a number of feathers, because the moult of primary feathers for these species is sequential and ascending, starting at the inner primary feather (P1) and moving to the outer feather (P10; Thompson *et al.* 2000, Bugoni *et al.* 2015).

The objective of this study was to describe the moult patterns and chronology of flight feathers (i.e. primaries, secondaries) of Great and Sooty Shearwaters during the non-breeding season on the northeast Newfoundland coast. We predicted that Sooty Shearwaters would exhibit more advanced moult than Great Shearwaters, given their earlier timing of migration. We also use feather stable isotope ratios of carbon ( $\delta^{13}$ C) and nitrogen ( $\delta^{15}$ N) to examine whether isotopic niches overlapped between species during early. mid- and late moult as well as among these moult periods within species. To interpret potential moult locations based on stable isotope ratios of feathers, we compared our  $\delta^{13}C$  and  $\delta^{15}N$  values with reference feathers of both species grown in known locations, acknowledging the potential for region-specific baseline shifts in isotopic ratios across time. We predicted that species-specific isotopic niches would show minimal overlap within early-late moult, given divergent moulting locations previously reported. As moult represents an energetically demanding part of the annual cycle of avian species (Lindstrom et al. 1993), it is critical to determine important regions used for moulting along with the timing of their use for protection. In addition, a better understanding of moult patterns and stable isotope ratios from multiple feathers will provide insight into migratory patterns and niche partitioning of these similar species during their non-breeding season.

# METHODS

## **Data collection**

Starting in early July, we monitored the presence of both species using shore- and boat-based observations while conducting other research in the study area to allow the identification of timing of arrival and, thus, the initiation of sampling. Great and Sooty Shearwaters were captured at sea at night on the northeast coast of Newfoundland from an ~13-m-long commercial fishing boat using a spotlight and a long-handled, large dip-net (Ronconi *et al.* 2010b) during July and August in 2014 and 2015 (Supporting Information Fig. S2 and Table S1). In 2014 only, a few drops of blood

were collected from individuals (n = 110) using a 21-25 gauge needle and syringe from the tarsal vein (see details in Carvalho & Davoren 2020) and placed on sample preservation FTA® cards for genetic sexing (Fridolfsson & Ellegren 1999). Flight feathers (i.e. primaries, secondaries) were scored following Ginn and Melville (1983). The moult score is based on the age (old or new) and development (length) of the feather, with scores ranging from 0 to 5: 0 - old feather; 1 - absence of featheror new feather complete inside of the pin; 2 new feather emerging from the sheath up to onethird grown: 3 - new feather between one- and two-thirds grown: 4 - new feather bigger than two-thirds with remains of waxy sheath at its base; 5 - new feather fully developed with no trace of waxy sheath at its base. As moult in Procellariiformes, including shearwater species, is typically symmetrical (Bridge 2006, Ramos et al. 2009b), we scored only the right wing. Finally, a small area  $(\sim 1 \text{ cm}^2)$  of feather was sampled from the tip of growing or newly grown inner (P1), mid- (P5) and outer (P10) primary feathers for stable isotope analysis. When P10 was not available (non-existent or too short for sample collection, i.e. score 1 or 2), P8 or P9 were sampled instead. The moult score dataset was supplemented with Great and Sooty Shearwaters captured in the Bay of Fundy, Nova Scotia (July-September, 2005-2014; Ronconi et al. 2010a), Gulf of Maine (July 2014; Power et al. 2017), Sable Island, Nova Scotia (dead birds, June 2011, 2012), and Brazilian coast in the South Atlantic (February and April, 2006; Bugoni et al. 2015; Table 1).

## Stable isotope analysis

Carbon and nitrogen stable isotope ratios of primary feathers (P1, P5 and P10) were determined for a subset of individuals sampled within the study area on the northeast Newfoundland coast during July–August 2014 and 2015 (Table 2). Feathers were subsetted for stable isotope analysis by chronologically choosing every second bird throughout the sampling period. Samples of primary feathers were washed in 0.25 M NaOH to eliminate surface contamination (Bearhop *et al.* 2002). Samples were then cut into small pieces using stainless steel scissors, homogenized, weighed (0.7–1 mg) and placed in a tin capsule. All samples were shipped to the Chemical Tracers Lab (University of Windsor) where stable carbon and **Table 1.** Number of Great and Sooty Shearwaters (range per year shown in parentheses) with primary and secondary moult scores recorded within each non-breeding location, along with the years sampled and number of individuals sampled for stable isotope analysis of feathers.

Species	Location	Years	Moult score primary	Moult score secondary	Feather samples	
Great Shearwater	Newfoundland	2014–2015	126 (51–75)	123 (51–72)	48 (10–38)	
	Bay of Fundy	2005–2012, 2014	381 (16–90)	344 (16–90)		
	Gulf of Maine	2014	13			
	Sable Island	2011–2012	7 (2–5)	7 (2–5)		
	South Atlantic (Brazilian coast) <sup>a</sup>	2006	67			
	Total		594	408		
Sooty Shearwater	Newfoundland	2014–2015	76 (35–41)	76 (35–41)	29 (10–19)	
	Bay of Fundy	2005-2009	23 (1–10)	23 (1–10)		
	South Atlantic (Brazilian coast) <sup>a</sup>	2006	2			
	Total		101	99		

<sup>a</sup>Data derived from Bugoni et al. (2015).

**Table 2.** Mean ( $\pm$ se) stable isotope ratios ( $\delta^{13}$ C and  $\delta^{15}$ N) and isotopic niche breadth (SEA<sub>c</sub>) of the primary feathers (P1, P5 and P10) from Great (GRSH) and Sooty (SOSH) Shearwaters captured in July–August during 2014 and 2015 on the northeast coast of Newfoundland.

Species	Feather	n (2014/2015)	δ <sup>13</sup> C (‰)	δ <sup>15</sup> N (‰)	Niche breadth SEA <sub>c</sub> ( $\%^2$ )
GRSH	P1	38/10	$-17.29 \pm 0.12^{a}$	$16.02 \pm 0.20^{a}$	3.61
	P5	38/10	$-17.03 \pm 0.13^{a}$	$16.19 \pm 0.23^{a}$	3.36
	P10	38/10	$-18.66 \pm 0.08^{\circ}$	$15.17 \pm 0.16^{\circ}$	1.87
SOSH	P1	19/10	$-18.12 \pm 0.10^{ m bc}$	$14.80 \pm 0.35^{\circ}$	2.48
	P5	19/10	$-17.77 \pm 0.05^{b}$	$14.82 \pm 0.34^{\circ}$	1.55
	P10	19/10	$-18.43 \pm 0.15^{\circ}$	$15.54 \pm 0.14^{c}$	1.85

Significantly different  $\delta^{13}$ C and  $\delta^{15}$ N values (P < 0.05) among primaries are indicated by different letters (e.g. a, b), while values that are not significantly different (P > 0.05) are indicated by the same letters.

nitrogen isotope ratios ( $\delta^{13}$ C,  $\delta^{15}$ N) were quantified using an Elemental Analyzer – Isotope Ratio Mass Spectrometer (Thermo Delta V). Stable isotope ratios are expressed in  $\delta$  notation as parts per thousand (%) deviation from the international standards Vienna Pee Dee Belemnite (PDB) for carbon ( $\delta^{13}$ C) and atmospheric air for nitrogen ( $\delta^{15}$ N), according to the following equation:  $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$ , where X is  $^{15}$ N or  $^{13}$ C and R is the ratio of heavy to light isotopes (i.e.  $^{15}$ N/<sup>14</sup>N or  $^{13}$ C/<sup>12</sup>C). Precision was assessed as the standard deviation of replicate analyses of three standards (NIST1577c, tilapia muscle and USGS 41) and was  $\leq 0.21\%$  for  $\delta^{15}$ N values and  $\leq 0.14\%$  for  $\delta^{13}$ C values.

#### **Data analysis**

The sums of the moult score on primaries (0 to 50, 'Primary Moult Score', PMS) and secondaries (0 to 105, 'Secondary Moult Score', SMS) were

used as response variables in analyses and graphs investigating moult chronology, or the timing of moult. Within the 2014 dataset, a general linear model determined no differences between males and females in PMS (Great Shearwater:  $F_{1.70} = 1.93$ , P = 0.17; and Sooty Shearwater:  $F_{1,36} = 0.26, P = 0.61$ ) or SMS (Great Shearwater:  $F_{1.67} = 0.93$ , P = 0.34; and Sooty Shearwater:  $F_{1,36} = 0.002, P = 0.97$ ) and, thus, sexes were not determined for the birds sampled during 2015 and sexes were pooled in analyses. We used a general linear model to compare PMS and SMS separately (response variables) between three fixed factors: species (Great Shearwater, Sooty Shearwater), year (2014, 2015) and capture dates. Additionally, we used a general linear mixed-effect model to compare  $\delta^{15}$ N and  $\delta^{13}$ C (response variables) between species and between feathers within species, using species (Great Shearwater, Sooty Shearwater) and feathers (P1, P5, P10) as fixed factors and individual as a random effect in the model for

each response variable. Post-hoc Tukey honest significant difference (HSD) tests were conducted using only the fixed effects from the model and  $\alpha$ values were adjusted for multiple comparisons (Bonferroni). Sex was not included in the models because no differences in  $\delta^{13}C$  were found between sexes for Great ( $F_{1,110} = 0.47$ , P = 0.50) or Sooty Shearwaters ( $F_{1, 55} = 0.82$ , P = 0.37) sampled during 2014 (all feathers combined). Similarly, no differences in  $\delta^{15}N$  were found between sexes for Sooty Shearwaters ( $F_{1, 55} = 0.80$ , P = 0.38), but female Great Shearwaters had lower  $\delta^{15}$ N values (15.5  $\pm$  0.2‰) compared with males  $(16.1 \pm 0.2\%)$ ;  $F_{1,110} = 4.22$ , P = 0.04). Additionally, no differences were found between years within each species for  $\delta^{13}C$  (Great Shearwater:  $F_{1,139} = 2.45$ , P = 0.12; Sooty Shearwater:  $F_{1,85} = 0.27$ , P = 0.61) or for  $\delta^{15}$ N for Great Shearwaters ( $F_{1,139} = 3.76$ , P = 0.06), but  $\delta^{15}$ N values were higher during 2014 (15.5  $\pm$  0.2%) than during 2015 (14.1  $\pm$  0.3%) for Sooty Shearwaters ( $F_{1.85} = 17.57$ , P < 0.0001). Analyses were performed in JMP Pro 14.1.0.

To aid in interpreting potential moult locations of birds captured in coastal Newfoundland from  $\delta^{15}$ N and  $\delta^{13}$ C values of our feather samples, we compared our  $\delta^{15}N$  and  $\delta^{13}C$  values with values from shearwater feathers sampled in known moulting locations from previous studies (Fig. 1). These reference samples included feathers collected from Great Shearwaters sampled at sea in the Bay of Fundy (growing secondary feathers; R. A. Ronconi unpubl. data), along the Brazilian Coast in the South Atlantic (growing body feathers: Bugoni et al. 2010) and Flemish Cap (growing primary feathers, P1 and P5; P. C. Carvalho unpubl. data), as well as grown primaries (P5) from Sooty Shearwaters that were assumed to have moulted on the Grand Banks and Mid-Atlantic Ridge (Hedd et al. 2012). Although we acknowledge the potential for region-specific baseline shifts in isotopic ratios across time, we did not have reference prey samples or baseline stable isotope samples from all potential moulting areas (given the large geographical range of potential areas where they might be moulting). To estimate the percentage overlap of our  $\delta^{15}N$  and  $\delta^{13}C$  values with each reference location, a convex hull of the  $\delta^{15}N$  and  $\delta^{13}C$  values of each reference location was overlaid on a  $\delta^{15}N\!-\!\delta^{13}C$  biplot, and the number of our data points falling within the convex hull of each reference location was determined (see Fig. S1). When the convex hulls of multiple reference locations overlapped, we determined the number of our points simultaneously falling within multiple reference regions.

To examine the species-specific variability in our  $\delta^{15}N$  and  $\delta^{13}C$  values within early, mid- and late primary moult, the isotopic niche breadth for each feather (P1, P5, P10) for both species was calculated as the Standard Ellipse Area, corrected for small sample size (SEA<sub>c</sub>) using Stable Isotope Bayesian Ellipses in R (SIBER: Jackson et al. 2011). The Standard Ellipse Area represents the standard deviation around the bivariate mean and encompasses  $\sim 40\%$  of the data and, thus, is used to represent the 'core' population niche breadth (Jackson et al. 2011). Based on the isotopic niche, we estimated niche overlap among primary feathers within and between species by the area of SEA<sub>c</sub> overlap divided by the sum of the SEA<sub>c</sub> for the primaries, minus the area of overlap, all multiplied by 100.

# RESULTS

In total, 202 birds (126 Great and 76 Sooty Shearwaters) were captured and moult scores were collected on the northeastern coast of Newfoundland during July–August in 2014 and 2015. When supplemented with datasets from other non-breeding areas (Nova Scotia, Gulf of Maine, South Atlantic), primary moult scores from 594 Great and 101 Sooty Shearwaters were available (Table 1).

#### Moult pattern and chronology

The moult patterns of flight feathers were similar for Great and Sooty Shearwaters on the northeast Newfoundland coast. Primary feather moult was sequential, starting with the inner primaries and ending with the outer primary (P10) for both species (Fig. 2). The majority (86%) of Great Shearwaters in active moult were moulting one to three primaries simultaneously, whereas ~14% were moulting four primaries, a few individuals were moulting up to five primaries (<1%) and one individual was moulting seven primaries at once. The majority (90%) of Sooty Shearwaters in active moult were moulting up to three primaries simultaneously, with few individuals moulting up to four primaries (10%). The number of primary feathers growing simultaneously was higher when PMS was lower in both species (linear regression:



Figure 1. Map showing locations used for moulting references based on stable isotope data ( $\delta^{15}$ N and  $\delta^{13}$ C) from feathers.

Great Shearwater:  $R^2 = 0.19$ ,  $F_{1,124} = 30.85$ , P < 0.001; Sooty Shearwater:  $R^2 = 0.55$ ,  $F_{1,74} = 91.02$ , P < 0.001). The moult pattern of the secondary feathers was more complex and started at three points: S21 outward, S5 and S1 inward, with S4 usually being the last to moult (Fig. 2). Although both species had similar moult patterns, Sooty Shearwaters on the northeast Newfoundland coast had a more advanced moult than Great Shearwaters, indicated by a significantly higher PMS (Great Shearwater:  $39.6 \pm 0.8$  and Sooty Shearwater:  $42.9 \pm 0.5$ ;  $F_{1,198} = 24.5$ , P < 0.0001) and SMS (Great Shearwater:  $61.3 \pm 3.2$  and Sooty Shearwater:  $78.0 \pm 3.0$ ;  $F_{1,195} = 29.5$ , P < 0.0001). Moult score also differed significantly among capture dates (PMS:  $F_{1,198} = 45.5$ , P < 0.0001; SMS:  $F_{1,195} = 52.7$ , P < 0.0001) but not between years (PMS:  $F_{1,198} = 0.3$ , P = 0.62; SMS:  $F_{1,195} = 1.3$ , P = 0.26). Furthermore, Sooty Shearwaters had completed moult on the first six primaries (P1–P6) while Great Shearwaters had only the first four primaries completed (P1–P4) when sampled during the first 2 weeks after arrival in our study area (15–31 July in 2014 and 2015; Fig. 2). Individuals sampled in August on the northeast Newfoundland coast were excluded from this moult pattern analysis (Fig. 2) because the majority of birds



**Figure 2.** Mean ( $\pm$ se) moult score of primary (grey bars) and secondary (white bars) feathers of Great Shearwaters (GRSH, n = 118) and Sooty Shearwaters (SOSH, n = 60) captured during their non-breeding season (15–31 July in 2014 and 2015) in the North Atlantic. The starting point and direction of the moult wave pattern are indicated by the arrows.

caught were Great Shearwaters (most Sooty Shearwaters had departed the study area), thereby precluding interspecific comparisons during the same period. When combining all birds caught across study locations and years (Table 1), moult chronology for both primary and secondary feathers indeed was more advanced in Sooty Shearwaters relative to Great Shearwaters (Fig. 3).

#### **Stable isotopes**

Carbon stable isotope ratios of primary feathers differed between species ( $F_{1,72.6} = 15.04$ , P < 0.001) and within species ( $F_{2,145.1} = 69.48$ , P < 0.001) but the interaction between species and feather was also significant ( $F_{2,145.1} = 17.22$ , P < 0.001). Post-hoc tests revealed that for the inner primary (P1), which was moulted by both species prior to arriving in the Newfoundland study area, Great Shearwaters had a significantly higher mean  $\delta^{13}$ C compared with Sooty Shearwaters (P < 0.001; Table 2; Fig. 4). For P5,  $\delta^{13}$ C was also higher for Great relative to Sooty Shearwaters (P < 0.001; Table 2; Fig. 4). For the outer primary (P10), which was moulted by both species in the study area, no differences in  $\delta^{13}C$  were observed between species (P = 0.75; Table 2; Fig. 4). For Great Shearwaters,  $\delta^{13}C$  did not differ between P1 and P5 (P = 0.36), but P10 was significantly lower than P1 (P < 0.001) and P5 (P < 0.001; Table 2; Fig. 4). In contrast,  $\delta^{13}C$  for Sooty Shearwaters did not differ significantly among primary feathers  $(P1 \times P5: P = 0.23; P1 \times P10: P = 0.37)$ , with the exception of P5 being higher than P10 (P < 0.001; Table 2; Fig. 4). For Great Shearwaters,  $\delta^{13}C$  appeared to be more variable during early moult (i.e. P1 and P5) relative to later (i.e. P10; Fig. 4a).



**Figure 3.** Mean  $\pm$  se moult score of primary feathers (PMS, top) and secondary feathers (SMS, bottom) for Great (black) and Sooty (grey) Shearwaters during February–September (2005–2015) from all study locations combined (see Table 1). Sample sizes of Great Shearwaters (GRSH) and Sooty Shearwaters (SOSH) caught and moult scored in each period are provided at the top of the graph (GRSH/SOSH). Moult scores from dead birds are indicated with an asterisk. Dashed lines represent the maximum total moult score. Individuals from February and April were captured in the South Atlantic, only for primary feather moult scores (Bugoni *et al.* 2015).

Nitrogen stable isotope ratios of primary feathdiffered significantly between species  $(F_{1.76.3} = 7.73, P = 0.007)$  but not within species  $(F_{2,148,1} = 0.34, P = 0.71)$  and the interaction between species and feather was significant  $(F_{2,148.1} = 14.18, P < 0.001).$ Post-hoc tests revealed that  $\delta^{15}$ N was higher for Great relative to Sooty Shearwaters for P1 (P < 0.006; Table 2; Fig. 4) and P5 (P = 0.001; Table 2; Fig. 4) but not for P10 (P = 0.89; Table 2; Fig. 4). For Great Shearwaters,  $\delta^{15}N$  for P1 and P5 were similar (P = 0.98), but P10 was lower relative to P1 (P = 0.003) and P5 (P < 0.002; Table 2; Fig. 4). For Sooty Shearwaters,  $\delta^{15}N$  did not differ significantly among primaries (P1  $\times$  P5: P = 1.00; P1 × P10: P = 0.11; P5 × P10: P = 0.12; Table 2; Fig. 4). The  $\delta^{15}N$  for P1, however, appeared to separate into two distinct groups, with most individuals (n = 21) having higher  $\delta^{15}N$  values  $(15.81 \pm 0.20\%)$ , while others (n = 8) were lower  $(12.15 \pm 0.25\%)$ ; Fig. 4b). The same pattern was observed for P5 (n = 21,  $12.88 \pm 0.15\%$  and n = 8,  $12.03 \pm 0.19\%$ ; Fig. 4b). Individuals with lower  $\delta^{15}$ N on P1 and P5, however, converged to similar  $\delta^{15}$ N values later during moult (i.e. P10) with the other group (higher  $\delta^{15}$ N). In summary,  $\delta^{15}$ N for Great Shearwaters seemed to be more variable over all primaries relative to Sooty Shearwaters.

For Great Shearwaters, SEA<sub>c</sub> was broader before arrival in the study area than while moulting in the study area (Table 2). The isotopic niche overlap between both species was highest while residing together in coastal Newfoundland (P10: 44.4%) and lower in feathers moulted earlier (P1: 5.8%, P5: 9.3%). Within species, Great Shearwaters had a higher overlap between P1 and P5 (64.8%), no overlap between P1 and P10 (0%), and negligible overlap between P5 and P10 (0.1%). For Sooty Shearwaters, the overlap between P1 and P5 was lower (23.6%) relative to Great Shearwaters, but it was higher between P1



**Figure 4.** Primary feather stable isotope ratios ( $\delta^{15}$ N and  $\delta^{13}$ C) and standard ellipse area (SEA) of P1 (open circle; dotted line ellipse), P5 (grey circle; grey ellipse) and P10 (black circle; black ellipse) for Great (a) and Sooty Shearwaters (b) captured during July–August on the northeast coast of Newfoundland. Mean  $\pm$  sd stable isotope ratios of feathers from Great Shearwaters (GRSH) sampled in the Bay of Fundy (growing secondary feathers; R. A. Ronconi unpubl. data), South Atlantic (growing body feathers; Bugoni *et al.* 2010) and Flemish Cap (growing primary feathers, P1 and P5; P. C. Carvalho unpubl. data) as well as grown primary feathers (P5) from Sooty Shearwaters (SOSH) that were assumed to have moulted on the Grand Banks and Mid-Atlantic Ridge (Hedd *et al.* 2012) are also indicated.

and P10 (12.3%) and between P5 and P10 (30.8%).

The  $\delta^{15}N$  and  $\delta^{13}C$  values during early moult (P1, P5) for Great Shearwaters showed considerable overlap with the reference feather convex hulls grown in the South Atlantic and Bay of Fundy (P1: 64%, P5: 54%), with some of these

points overlapping with the South Atlantic reference exclusively (P1: 20%; P5: 12%; Figs 4a and S1). Similarly, the early moult of Sooty Shearwaters showed considerable overlap with the South Atlantic and Bay of Fundy reference locations (P1: 67%; P5: 66%), with some points overlapping with the South Atlantic reference exclusively (P1: 11%; P5: 7%) and others also overlapping with the Mid-Atlantic Ridge (P1: 19%) and Flemish Cap (P5: 10%) convex hulls (Figs 4b and S1). At least onethird of the early moulting points fell outside the reference convex hulls for both Great Shearwaters (P1: 37%; P5: 44%) and Sooty Shearwaters (P1: 33%; P5: 34%; Fig. S1). In contrast, at least twothirds of the late moult points (i.e. P10) fell outside the reference convex hulls for both Great Shearwaters (63%) and Sooty Shearwaters (70%; Fig. S1). The remaining late moult points primarily overlapped with areas in the northern hemisphere for Great Shearwaters (Mid-Atlantic Ridge: 15%; Grand Banks: 8%; Bay of Fundy: 15%) and Sooty Shearwaters (Mid-Atlantic Ridge: 3%; Grand Banks: 7%; Bay of Fundy: 17%; South Atlantic: 3%).

### DISCUSSION

Our findings indicate that at least some Sooty Shearwaters finished their moult in coastal waters. contrary to previous reports suggesting this species finished moulting offshore before moving to coastal areas (Brown 1988, Keijl 2011). Additionally, we identified an overlapping area where both Sooty and Great Shearwaters complete their moult in coastal Newfoundland (Carvalho & Davoren 2019, 2020, present study). Stable isotope ratios in feathers grown in coastal Newfoundland (i.e. P10) were similar between shearwater species and showed high isotopic niche overlap, suggesting a similar dietary niche when found together in coastal Newfoundland. Higher dietary niche overlap may be possible due to the high abundance of prey during the summer in the study area, resulting from the inshore migration of high abundances of spawning Capelin (Davoren 2013). Given that P10 were observed growing for both species in the study area on the northeast Newfoundland coast, the high proportion of P10 stable isotope ratios falling outside our reference collections probably indicates a coastal stable isotopic signature for these species. The  $\delta^{15}N$  and  $\delta^{13}C$  values of P10 from a small portion of individuals also overlapped with the reference collections from the Grand Banks, suggesting that these individuals may move between these areas during late moult, which is corroborated by limited tracking data on Great Shearwaters (n = 2; P. C. Carvalho unpubl. data).

In contrast, stable isotope ratios for the inner and mid-primaries (i.e. P1 and P5) differed between Great and Sooty Shearwaters, suggesting that these species moult in different locations or consume different prey types during early moult. Although we acknowledge the potential for region-specific baseline shifts in isotopic ratios across time and we cannot preclude that both species feed on different prey in the same region, tracking studies have identified divergent stable isotope ratios from different moulting locations of seabirds (Ramos et al. 2009a, Hedd et al. 2012, Thompson et al. 2015, Cherel et al. 2016). In support of this, migration chronology appears to differ between these two species, where tagged Great Shearwaters used the Patagonia shelf (Southern Hemisphere) in April-May after the breeding season (Ronconi et al. 2018), whereas tagged Sooty Shearwaters started their migration to the Northern Hemisphere after the breeding season in March (Hedd et al. 2012). Therefore, our data suggest that the majority of Great Shearwaters undergo early moult (P1, P5) in the Southern Hemisphere or areas south of our study area (Bay of Fundy; see also Hong et al. 2019), and some Sooty Shearwaters may complete early moult offshore (Mid-Atlantic Ridge, Flemish Cap), which aligns with rapid post-breeding dispersal found previously (Hedd et al. 2012). However, we acknowledge that the age and breeding status of the individuals captured at our study area are not known and could potentially be biased towards one age group or breeding status.

The moult pattern for both species is similar to the *Staffelmauser* patterns reported for other shearwaters and Procellariiformes (Thompson *et al.* 2000, Arroyo *et al.* 2004, Allard *et al.* 2008, Ramos *et al.* 2009b, Meier *et al.* 2017), with an ascending pattern (starting at inner primaries and finishing with outer primaries). We were not able to determine whether P2 was moulted before P1, as most individuals were captured in later moult (P1–P4 completed), but this pattern has been reported for Sooty Shearwaters and other Procellariiformes (Thompson *et al.* 2000, Arroyo *et al.* 2004, Allard *et al.* 2008). The simultaneous growth of inner primaries is supported by the higher number of feathers growing when the primary moult score is low and also by the similar stable isotope ratios ( $\delta^{13}$ C and  $\delta^{15}$ N) for P1 and P5 for both species. As moulting should be suspended during northward migration, our findings suggest a possible time constraint to complete annual primary moult in the North Atlantic. Information on secondary feather moult is rare for most seabird species (Bridge 2006). In our study, the secondary moult pattern for both species followed patterns described previously for other shearwater species (e.g. Cory's Shearwaters; Ramos et al. 2009b) and Procellariiformes (e.g. Northern Fulmars Fulmarus glacialis; Thompson et al. 2000), where secondary feathers moult in waves. This moult pattern may have evolved to minimize gaps in flight feathers and, thus, energetic costs of flight during moult (Lindstrom et al. 1993, Hedenström & Sunada 1999), as secondaries (S1-S4) adjacent to primaries (P1-P5) moult at different times.

Although similar patterns of flight feather moult (i.e. primaries, secondaries) were observed for Great and Sooty Shearwaters, Sooty Shearwaters showed more advanced moult relative to Great Shearwaters. Indeed, the higher moult score for both primary and secondary feathers in Sooty relative to Great Shearwaters (Fig. 3) suggests differences in the timing of moult, given that feather growth rates are similar for species of similar body size (~6 mm/day for larger seabirds; Langston & Rohwer 1996). Timing of moult can be influenced by several ecological factors, including breeding status and time of migration (i.e. breeders, nonbreeders, failed breeders; Alonso et al. 2009). breeding location (Alonso et al. 2009, Catry et al. 2013), body condition (parasites; Langston & Hillgarth 1995), age class (immature and juveniles; Howell 2010, van Bemmelen et al. 2018) and food availability (Barta et al. 2008). If one species completes moult in advance of another similar, sympatric species, this species may depart moulting/ non-breeding grounds if food availability decreases, which would allow niche partitioning. Interestingly, prey availability decreases in the study area once Capelin spawning is complete (Carvalho & Davoren 2019), and Sooty Shearwaters, the slightly smaller (40–51 cm; Carboneras et al. 2020a) and less competitive species compared with Great Shearwaters (43-51 cm; Carboneras et al. 2020b, Carvalho et al. 2020), have more advanced moult and, thus, tend to leave the area in early August (P. C. Carvalho pers. obs.). In contrast, Great Shearwaters remain until late in the summer (mid- to late August), when they have completed moult (i.e. P8-P10: P. C. Carvalho pers. obs.). Alternatively, if Sooty Shearwaters arrive in the Northern Hemisphere earlier and begin their moult earlier than Great Shearwaters, their advanced moult might allow them to be more mobile and avoid interactions with the more competitive Great Shearwater. In support of this, Sooty Shearwaters migrate earlier in the spring from their South Atlantic breeding colony to the North Atlantic (March: Hedd et al. 2012) relative to Great Shearwaters (April-May; Ronconi et al. 2018). In contrast, as the timing of southward migration for both species in autumn is similar, peaking in early September (Hedd et al. 2012, Powers et al. 2017), advanced moult in Sooty Shearwaters does not appear to be linked to earlier migration southward.

The high overlap of isotopic niches for Great and Sooty Shearwater feathers grown in the study area (i.e. P10) suggests that they feed on similar prey while in the study area, probably highly abundant spawning Capelin. This is corroborated by a narrower niche breadth while in the study area, probably reflecting a primarily Capelin-based diet. Additionally, Capelin collected in the study area in both years had similar  $\delta^{13}C$  (-20.2 to -20.4%) and  $\delta^{15}N$  (12.0–12.2%; Carvalho & Davoren 2020) to our shearwater feathers although these have not been corrected with a discrimination factor. The isotopic niche breadth of both shearwater species in the study area has been shown to narrow throughout the summer season also suggesting convergence on a similar prey type/ diet (Gulka et al. 2017, Carvalho & Davoren 2020), which has been found for other marine predator species in coastal Newfoundland (Gulka et al. 2017, Jenkins & Davoren 2021). Additionally, these two species also show high spatial overlap at sea (Carvalho & Davoren 2019, Carvalho et al. 2020).

A previous study suggested that Great Shearwaters delay wing-moult until arriving in waters off Canada (Brown 1988), which was supported by reports of individuals observed moulting in the Bay of Fundy and Gulf of Maine (Ronconi *et al.* 2010a, Powers *et al.* 2020) and on the coast of Newfoundland (Brown 1988). In support of this, stable isotope ratios of some P1 and P5 feathers overlapped with reference feathers moulted in the North Atlantic (Bay of Fundy), indicated by lower

 $\delta^{13}$ C (R. A. Ronconi unpubl. data; Fig. 4). Stable isotope ratios of some P1 and P5 feathers, however, also overlapped with the South Atlantic feather reference (especially higher  $\delta^{13}$ C), suggesting that some other individuals may have begun moulting in the South Atlantic (Brazilian coast; Quillfeldt et al. 2008, Bugoni et al. 2010), which is also supported by the lower primary moult scores from that region (Fig. 3; Bugoni et al. 2015). The overlap in stable isotope ratios between the Bay of Fundy and Brazilian coast, however, make it difficult to conclude where Great Shearwaters began moulting. Some individuals have been observed moulting primary feathers during the breeding season in the South Atlantic, but it was hypothesized that those individuals were non-breeding birds, either failed breeders or immature birds (Watson 1971, Bugoni et al. 2015). Great and Sooty Shearwaters captured and sampled in the South Atlantic (Bugoni et al. 2010) have higher blood  $\delta^{13}C$  values compared with individuals caught in the North Atlantic (Ronconi et al. 2010a, Carvalho & Davoren 2020), possibly reflecting their reliance on fishery discards in South Atlantic waters and/or divergent stable isotopic baselines between these regions. Similarly, Hong et al. (2019) revealed a significant decrease in  $\delta^{13}$ C in blood (red blood cells) with increases in latitude for Great Shearwaters sampled in the North Atlantic. Our findings together with these previous studies suggest that Great Shearwaters begin their flight feather moult in the South Atlantic, but further research is required to confirm this.

Sooty Shearwaters in the Atlantic were hypothesized to complete flight feather moult between late April and early June in an offshore area west of the Mid-Atlantic Ridge, and to a lesser extent on the southern Grand Bank off Newfoundland (Hedd et al. 2012). In support of this, Sooty Shearwaters have been observed with a complete set of new flight feathers in coastal areas of eastern Canada (Brown 1988) and moulting flight feathers offshore (Keijl 2011), suggesting that they may moult prior to arriving in coastal Newfoundland. Our findings, however, indicate that some Sooty Shearwaters complete their moult in coastal areas. In support of this, dead individuals in coastal Africa were found moulting their flight feathers in the South Atlantic between December and June, possibly immatures and failed breeders (Cooper et al. 1991). We also found distinct groupings of  $\delta^{15}$ N values within Sooty Shearwaters during early moult (i.e. P1, P5), suggesting that individuals of the same species also may moult in different areas. Sooty Shearwaters were previously found to use two distinct feeding areas during moult, resulting in different stable isotope ratios within primary feathers (P5; Hedd et al. 2012). Interestingly, one group of individuals in our study had similar. lower  $\delta^{15}$ N values to those found by Hedd *et al.* (2012) on the Mid-Atlantic Ridge (i.e. lower  $\delta^{15}$ N), suggesting that they started their moult (P1-P5) in this offshore area. In contrast, the other group of individuals had similar, higher  $\delta^{15}$ N values than those found on the Grand Banks (Hedd et al. 2012), suggesting that they started their moult (P1-P5) in more inshore areas. In addition, the stable isotope ratios of early moult feathers (P1-P5) of a few individuals also overlapped within the South Atlantic and Bay of Fundy reference values, suggesting that individuals of Sooty Shearwaters may also start their moult prior to northward migration, but much less so than Great Shearwaters. Segregation in non-breeding areas has also been reported for Sooty Shearwaters in the Pacific Ocean, where three distinct areas could be defined using stable isotope values and geolocators (Shaffer et al. 2006, Thompson et al. 2015). By the end of the moult (P10), however, stable isotope ratios of most individuals converged towards a higher  $\delta^{15}$ N, which may indicate a Capelin signature based on our Capelin (prey) data for the area.

In conclusion, primary and secondary feather growth patterns showed a similar moult sequence but different moult timing, and stable isotope ratios identified distinct moult locations or diet of similar shearwater species on the non-breeding grounds. Sympatric species might evolve temporal and/or spatial segregation to avoid interspecific competition while moulting, which is an energetically demanding period of the annual cycle when flight might be impaired while simultaneously growing multiple flight feathers. Indeed, stable isotope ratios are useful tracers of areas where moult occurs in migratory seabirds (Cherel et al. 2006, Phillips et al. 2009) as well as a good indicator of the schedule of moult (Ramos et al. 2009a). Tracking devices combined with stable isotope ratios of feathers would be useful to evaluate the importance of the potential moulting areas identified in this study. Identifying key moulting locations will be important for marine spatial planning for effective conservation of these species in the future. We identified an overlapping area where both Sooty and Great Shearwaters complete their moult in coastal Newfoundland (Carvalho & Davoren 2019, 2020, present study), which has been previously described as a 'biological hotspot' where many other seabird, whale and predatory fish species aggregate over persistent Capelin spawning aggregations (Davoren 2013). Protecting this moulting area would minimize disturbance and the impacts of threats (e.g. by-catch) to both species during this energetically demanding moult period, due to reduced flight efficiency. This area was suggested previously to be an important candidate area for protection due to annually persistent prey aggregations that can be spatiotemporally delimited based on specific prey habitat requirements.

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# **AUTHOR CONTRIBUTIONS**

P.C.C. contributed to study design, sample/data collection, analysis and writing the manuscript. R.A.R. and L.B. contributed to data and critical review. G.K.D. contributed to study design, study supervision, critical review and writing of the manuscript.

## ETHICAL NOTE

None.

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## **Data Availability Statement**

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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# SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Figure S1**. Primary feather stable isotope ratios  $(\delta^{15}N \text{ and } \delta^{13}C)$  of P1 (open circle; dotted line ellipse), P5 (grey circle; grey ellipse) and P10 (black circle; black ellipse) for Great (top) and Sooty (bottom) Shearwaters captured during July–August on the northeast coast of Newfoundland. Convex hulls (used as references) were based on the stable isotope ratios of feathers from Great Shearwaters sampled in the Bay of Fundy (BF, growing secondary feathers; R. A. Ronconi unpubl, data), South Atlantic (SA; growing body feathers; Bugoni *et al.* 2010) and Flemish Cap (FC; growing primary feathers, P1 and P5; P. C. Carvalho

unpubl. data) as well as grown primary feathers (P5) from Sooty Shearwaters that were assumed to have moulted on the Grand Banks (GB) and Mid-Atlantic Ridge (MAR; Hedd *et al.* 2012).

**Figure S2**. The number of Great (black) and Sooty (grey) Shearwaters captured during 5-day periods of July-August 2014 and 2015 on the northeast coast of Newfoundland. Note that '206' is July 25.

Table S1. Summary of the number of individuals captured each year per species on the northeast Newfoundland coast. Note that the first capture date in 2014 was July 13 for Great Shearwaters (GRSH) and July 15 for Sooty Shearwaters (SOSH) and in 2015 was July 16 for Sooty Shearwaters and July 19 for Great Shearwaters.