

**COEXISTENCE OF TWO SYMPATRIC MIGRATORY SHEARWATER SPECIES  
DURING THEIR NON-BREEDING SEASON ON THE EAST COAST OF  
NEWFOUNDLAND**

By

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## Thesis Abstract

In the marine environment, prey aggregations are not uniformly distributed, which drives predator species to aggregate in specific areas of high food availability. When multiple species aggregate to forage, interspecific competition can occur if prey are limited. On the east coast of Newfoundland, a small forage fish, capelin (*Mallotus villosus*), move inshore to spawn during the summer, and become the main prey for most marine predators in the study area. During the same period, non-breeding seabirds, great and sooty shearwaters (*Ardenna gravis* and *A. grisea*), migrate and aggregate in coastal Newfoundland. I investigated how these two similar shearwaters species coexist during the summer (July and August) under varying capelin availability. Based on at-sea surveys, great and sooty shearwaters were highly associated with each other and typically distributed along the coast in shallow waters (< 50 m) at or nearby capelin spawning sites. Stable isotope ratios ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) from the blood and primary feathers moulted in the study area showed that both species were also feeding on similar prey types, with high isotopic niche overlap. Behavioural experiments examining species interactions during prey capture, however, revealed that great shearwaters displayed more bold and aggressive behaviour compared to sooty shearwaters. Additionally, stable isotope ratios of both primary feathers (P1 and P5) moulted prior to arrival in coastal Newfoundland differed between species and sooty shearwaters had an advanced stage of moult compared to great shearwaters upon arrival, both suggesting temporal and spatial segregation during early moult. In conclusion, both species share a similar annual cycle and feed on similar prey while using coastal Newfoundland to complete their moult and replenish body storages before southward migration to the breeding grounds. However, subtle differences in foraging behaviour to capture prey were observed, revealing how these species can coexist while using the same resources at the same location and time.

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*“In a world full of people, only some want to fly... isn't that crazy?” - Crazy, Seal*

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## General Introduction

In the marine environment, food resources (prey) are distributed in an unpredictable and patchy manner. Consequently, multiple predator species tend to concentrate in specific areas where prey aggregates (e.g., Ainley et al. 2009, Davoren 2013) and, thus, interspecific competition may occur if resources are limited (Begon et al. 2006). Interspecific competition is when one species affects the ability of another to grow, survive and reproduce (Begon et al. 2006). Competition is traditionally classified as either exploitative, when one species reduces the availability of a resource through exploitation without direct interaction, or interference competition, when individuals directly interact during competition for the resource (Schoener 1983). Each species has a set of resources and environmental conditions (niche) that it requires to grow, survive and reproduce (n-dimensional hypervolume; Hutchinson 1957), which can be constrained by interactions with other species. In this context, the competitive exclusion principle states that similar species, sharing the same resource or set of resources (niche) in limited supply, would not be able to coexist (Hardin 1960). However, it is possible to observe in nature, several cases of similar species coexisting (Tokeshi 1999), which may be due to partitioning of limited resources, or niche partitioning (Tokeshi 1999, Begon et al 2006).

Most seabirds breed in multispecies colonies, resulting in high numbers of different species overlapping in space and time. During breeding, seabirds act as central-place foragers (Orians and Pearson 1979), whereby they forage at sea within a limited range of the colony and then must return to the colony to incubate or provision offspring. As a result, multiple species forage within a small area around colonies and, thus, breeding seabirds have been used to understand how animals may compete and partition limited resources (Forero et al. 2004, Bond et al. 2010, Navarro et al. 2013, Mancini et al. 2014). In seabird communities, trophic niche partitioning occurs through prey specialization (e.g., different prey types or sizes; Mancini et al. 2014),

differences in foraging depths (e.g., surface feeding, pursuit diving; Balance et al. 1997;) and locations (i.e. spatial partitioning: e.g., offshore, inshore; Quillfeldt et al. 2013) and also timing (e.g., nocturnal, diurnal; Navarro et al. 2013). For species within the same foraging guild (e.g., pursuit-divers, surface-feeders), the niche overlap, a proxy of the potential for interspecific competition, is expected to be more pronounced. Previous studies, however, have shown that similar species have slight morphological and/or behavioural differences, which result in subtle partitioning of resources (Paredes et al. 2008, Suryan and Fischer 2010, Linnenbjerg et al. 2013; Navarro et al. 2013). Additionally, sympatric species of auks, albatrosses, petrels and shearwaters are known to forage at different locations (Phalan et al. 2007, Navarro et al. 2009, 2013, Linnenbjerg et al. 2013, Quillfeldt et al. 2013), possibly allowing the coexistence of these similar species. Little is known, however, about seabird competition and resource partitioning during the non-breeding season. Many animal species, including birds, have evolved the strategy of long-distance migration during the non-breeding season, likely in response to seasonality of resources (e.g., low prey availability) on the breeding grounds and outside of the breeding season (Alerstam et al. 2003, Salewski and Bruderer 2007). During non-breeding, migratory seabirds no longer act as central-place foragers, but high abundances of multiple species still often aggregate within regions of high prey density (Hunt et al. 1999), to replenish energy stores for reproduction and return migration. In this context, competition among seabird species may occur, if prey availability fluctuates in these local areas during non-breeding.

Stable isotopes have been used to describe the trophic niche breadth, a proxy of the variety of prey in the diet, of a species (Bearhop et al. 2004). By combining carbon and nitrogen stable isotope ratios, researchers can quantify the isotopic niche breadth of a species, which is defined as an area (in  $\delta$ -space) with isotopic values ( $\delta$ -values, usually  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) as coordinates

(Newsome et al. 2007). Using a multi-species approach, niche breadth can be used to determine the degree of dietary niche overlap, which may represent resource partitioning between sympatric species (Suryan and Fischer 2010, Young et al 2010, Linnebjerg et al 2013, Cherel et al. 2014) and seabird assemblages (Forero et al. 2004, Mancini et al. 2014). Nitrogen isotope ratios ( $^{15}\text{N}/^{14}\text{N}$ , or  $\delta^{15}\text{N}$ ) are thought to indicate the trophic position of a species, while carbon isotope ratios ( $^{13}\text{C}/^{12}\text{C}$ , or  $\delta^{13}\text{C}$ ) reflect basal food sources. In the marine environment, the latter can be used to discriminate food obtained from coastal and oceanic areas, high and low latitude regions, and pelagic and benthic areas (Quillfeldt et al. 2005, Cherel and Hobson 2007). Moreover, stable isotopes of different tissues can be used to evaluate niche breadth and niche overlap on multiple temporal scales, as each tissue has a characteristic isotopic turnover rate (Hobson and Clark 1993; Evans Ogden et al. 2004). For instance, different blood components can give dietary information from two distinct periods, with red blood cells (RBCs) representing diet over the past few weeks, while the plasma represents diet over the past few hours or days. In addition, once fully grown, feathers are inert and, thus, have been used to estimate dietary composition during the period of its synthesis. Indeed, stable isotope signatures in feathers have been used to determine the moulting location of other long-distance migrating seabirds, including albatross (Cherel et al. 2000) and shearwater species (Ramos et al. 2009) during the breeding and non-breeding season, as the long distances traveled can result in distinctly different isotopic signatures if the prey base differs between regions (Hobson 1999, Dehnhard et al. 2011). In addition, divergent stable isotope ratios in different primary feathers of the same individual have revealed either distinct moulting locations or changes in prey types during moult (Ramos et al. 2009).

On the northeast coast of Newfoundland, a small forage fish, capelin (*Mallotus villosus*), is the main natural prey source of most marine predators (Carscadden et al. 2002, Burke and Montevecchi 2008, Davoren 2013). Capelin migrates inshore during the summer to spawn on beaches and also at deep-water sites (15-40 m; Davoren et al. 2012, Penton and Davoren 2012). Associated with the deep-water spawning sites, breeding and non-breeding seabirds and whales aggregate in high abundances to feed on spawning capelin (Davoren 2013). After spawning, capelin either die (mostly males) or migrate back to offshore areas near the shelf break (Davoren et al. 2006). As such, capelin availability varies substantially throughout the summer, transforming the foraging habitat for seabird predators in coastal regions from an high abundance food supply (i.e. during capelin spawning) into low abundance food supply (i.e. pre- and post-spawning). Additionally, the timing of capelin arrival inshore, as well as the inshore spawning biomass shows high inter-annual variation (Davoren et al. 2012, Crook et al. 2017). Therefore, among and within year variation in capelin availability likely influences interactions and competition among closely related predator species.

Great shearwater (*Ardenna gravis*) and sooty shearwaters (*Ardenna grisea*) are trans-equatorial migrants that share a similar annual cycle. They both breed in the southern hemisphere (October-April) and migrate to the northern hemisphere during their non-breeding season (May-September; Brooke 2004, Howell 2012), where they perform a complete moult (Howell 2010). On the northeast coast of Newfoundland, great and sooty shearwaters coexist during the summer and share their non-breeding grounds with other breeding species (murre, gannets, razorbills, puffins, gulls). They have been observed in mixed-species feeding assemblages associated with spawning aggregations of capelin (Davoren 2013). In the North Atlantic, non-breeding great and sooty shearwaters are among the main consumers of forage fish during the summer (Barrett et al.

2006). Both species appear to occupy a similar trophic niche when they have a sympatric distribution during the non-breeding season, as evidenced by similar diets (e.g., euphausiids, capelin, squid, herring) from stomach content analysis (Brown et al. 1981) as well as stable isotope and fatty acid signatures (Ronconi et al. 2010c). Despite considerable overlap in diet, there is some indication of subtle resource partitioning between species in the Bay of Fundy (Ronconi et al. 2010c). In general, the two species appear to similarly concentrate their foraging activity during dawn and dusk (Raymond et al. 2010, Ronconi et al. 2010a). The feeding behaviour of both shearwaters species is similar, whereby they typically feed by surface-seizing, pursuit-plunging and pursuit-diving (Ashmole 1971). Maximum dive depths, however, differ between species, with sooty shearwaters having deeper maximum dive depths (up to 69 m, Shaffer et al. 2009) than great shearwaters (up to 19 m, Ronconi et al. 2010a). Despite differences in maximum dive depth, both species most often perform shallow dives (<10 m; Raymond et al. 2010, Ronconi et al. 2010a). In the southern hemisphere, great shearwaters are known to follow boats and feed on discards and offal from fisheries (Olmos 1997, Bugoni et al. 2010), as do sooty shearwaters, but to a lesser extent (Wood 1993, Jackson 1988). When feeding on discards and offal during chumming, the larger great shearwater has been reported to displace the slightly smaller sooty shearwater (Ronconi et al. 2010b) but whether these behavioural patterns are common across the range, including other non-breeding areas, remains unknown.

The main objective of my thesis was to investigate whether and how similar species, partition resources and coexist during their non-breeding season in an environment with highly variable prey biomass. The thesis is divided into four chapters (in manuscript format), which present data on the coexistence of the two sympatric shearwater species. **Chapter 1** investigates the spatial distribution (and degree of overlap) of great and sooty shearwaters on the northeast

Newfoundland coast (study area), as well as compares the most important bio-physical variables underlying each species' distributional patterns using at-sea surveys conducted over eight years (2007, 2009-2012, 2014-2016) during the summer. **Chapter 2** quantifies the dietary niche breadth and extent of overlap of great and sooty shearwaters among and within years (2014-2016), prior to arrival and throughout the summer in the study area using stable isotope ratios from blood as a proxy of dietary niche breadth. **Chapter 3** investigates shearwater and fulmar species interactions and responses to supplemental food under changing prey availability, using a behavioural experiment in the study area. **Chapter 4** investigates the importance of the study area as moulting areas for both great and sooty shearwaters and compares moult patterns, as well as temporal and spatial overlap of moulting using moult scores and stable isotope ratios from primary (flight) feathers.

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## **Chapter 1: Non-breeding distributional patterns and association of shearwaters and prey on the northeastern Newfoundland coast**

### **Abstract**

In the marine environment, prey aggregations are not uniformly distributed, driving predator species to aggregate in specific areas of high food availability. On the east coast of Newfoundland, capelin (*Mallotus villosus*), a small forage fish, move inshore to spawn during the summer, providing abundant food for marine predators. During this period, great and sooty shearwaters (*Ardenna gravis* and *A. grisea*), long-distance migratory seabirds, aggregate in coastal Newfoundland, but it is unknown whether they aggregate together. Using at-sea surveys, we investigated shearwater distribution and their association with prey aggregations and with each other during July-August, 2007, 2009-2012 and 2014-2016 on the northeast Newfoundland coast. The distributional and density patterns of great and sooty shearwaters were mainly influenced by the other sympatric shearwater species, suggesting that they benefit from foraging in close association. Contrary to our prediction, fish density had little influence on the distributional and density patterns of both species, but depth was more influential, whereby shearwaters were mainly found in shallow areas (< 50 m). As capelin spawning sites and migratory routes to spawning sites are mostly located in shallow areas (< 40 m) along the coast, depth (or distance from shore) is likely an important proxy of high prey availability during the summer capelin spawning season in the study area.

**Key-words:** seabird distribution; shearwater; local enhancement; capelin; predator-prey

## Introduction

Areas of high productivity are not uniformly distributed in the marine environment. As a result, predator species tend to concentrate in specific areas where environmental factors are favourable, such as patches of high food availability (Hunt et al. 1999). The Ideal Free Distribution model predicts, however, that patches of high food availability decline in profitability as the number of conspecific and/or heterospecific competitors increase in a patch. Indeed, spatial segregation is one of the mechanisms species may use to minimize competition within a prey patch, thereby allowing the coexistence of sympatric species within a region (Navarro et al. 2009, Quillfeldt et al. 2013, Clay et al. 2016). When food resources are abundant, however, species might benefit from foraging in association with other species (Hoffman et al. 1981, Clua and Grosvalet 2001, Goyert et al. 2014). For instance, species that consume similar prey types and size might cue to the foraging activities of each other (i.e. local enhancement) to minimize the time and energy spent searching for prey (Silverman et al. 2004, Thiebault et al. 2014, Bairos-Novak et al. 2015), thereby maximizing net energy gain and increasing patch profitability.

To understand the mechanisms driving seabird distributions at sea, researchers commonly integrate data from at-sea surveys and/or tracking devices with biological factors such as prey density and ocean productivity (e.g. chlorophyll A) as well as physical factors that are both static (e.g., bathymetry, distance to colony) and dynamic (e.g., sea surface temperature, salinity; Ainley et al. 2005, Nur et al. 2011). Some studies have direct measures of prey distribution and density (e.g., Ainley et al. 2009, Goyert et al. 2018); however, often researchers rely on bio-physical factors as proxies of prey habitat to explain predator distributional patterns (e.g., Ainley et al. 2005, Amorim et al. 2009). In many cases, these proxies can effectively predict predator species

distribution when prey distribution is not properly assessed or unknown (Torres et al 2008). In addition, predators may also influence the distributional patterns of other predators by enhancing their capacity to locate prey (e.g. local enhancement; Silverman et al. 2004, Thiebault et al. 2014) as well as capture prey (e.g. prey herding; Evans 1982, Ballance et al. 1997, Clua and Grosvalet 2001, Hebshi et al. 2008, Goyert et al. 2014). For instance, surface-feeding seabirds may rely on sub-surface predators, such as tuna (Hebshi et al 2008) or diving seabirds (e.g. Hoffman et al 1981), to drive prey to the ocean surface, thereby enhancing prey accessibility and capture. In contrast, predator species might compete with each other for prey (either through indirect or direct competition), resulting in avoidance and, ultimately, spatial segregation (Hoffman et al. 1981, Ballance et al. 1997, Maniscalco et al. 2001).

Great shearwaters (*Ardenna gravis*) and sooty shearwaters (*Ardenna grisea*) are trans-equatorial migrants and, while they breed in large colonies in different areas of the south Atlantic, they have a sympatric distribution during the non-breeding season in the North Atlantic (Brooke 2004). During non-breeding, both species appear to have a similar diet, based on stomach content analysis (e.g., euphausiids, capelin, squid, herring; Brown et al. 1981) as well as stable isotope and fatty acid signatures (Ronconi et al. 2010; Chapter 2, 4). Both species are also present in large, non-breeding aggregations within coastal regions of the North Atlantic (e.g., Gulf of Maine, Bay of Fundy and Newfoundland), which are often associated with high-density prey aggregations (Brown et al. 1981, Ronconi et al. 2010, Hedd et al. 2012, Davoren 2013a, Powers et al. 2017). In coastal Newfoundland, capelin (*Mallotus villosus*) is a key forage fish and, thus, is the main prey of many predators (Carscadden et al. 2002, Burke and Montevecchi 2008, Krumsick and Rose 2012, Chapter 2). Capelin migrate from offshore wintering areas to coastal regions to spawn during the summer (Davoren et al 2006), resulting in highly abundant

pulsed source of prey near-shore, which is associated with the arrival of non-breeding great and sooty shearwaters (Davoren 2013).

The objective of this study was to describe the distributional patterns of great and sooty shearwaters in a coastal area of northeastern Newfoundland during the capelin spawning season (i.e. high prey availability) and examine the important bio-physical variables underlying these patterns. Specifically, we test the hypothesis that aggregations of both shearwater species are primarily influenced by capelin density and distributional patterns within this non-breeding foraging area. In addition, based on the high abundance of capelin and the energetic benefits of local enhancement (Grünbaum and Veit 2003, Silverman et al. 2004, Thiebault et al. 2014), we hypothesized that great and sooty shearwater aggregations would influence each other and, thus, predicted that the distributions of these two species would be highly associated at sea. Testing this hypothesis will determine whether these two species are spatially segregated or overlapped, thereby suggesting mechanisms underlying distributional patterns.

## **Methods**

### *Study area*

The study was conducted in the northeast coast of Newfoundland (49-50°N; 54-53°W; Fig. 1.1). In the study area, spawning capelin migrate toward the coast in a deep-water (> 200 m) trench (~Line 1; Fig. 1.1), where they remain in a pre-spawning staging area close to the coast to complete gonadal development throughout July (Davoren et al. 2006). Spawning capelin then move northward along the coast in shallow areas (i.e. < 50 m) to spawn on beaches and at demersal (15-40 m) sites during mid-late July (Davoren et al 2006; Davoren 2013). A biological 'hotspot', where high abundances of many marine predator species aggregate, forms over a cluster of annually persistent demersal spawning sites (inshore section of Line 3, Fig. 1.1; Penton

and Davoren 2012; Davoren 2013). Within this hotspot, great and sooty shearwaters represent two of the most abundant species present during the summer, together with breeding common murre (*Uria aalge*) and northern gannets (*Morus bassanus*; Davoren 2007, 2013).

#### *At-sea surveys*

At-sea surveys were repeatedly conducted on 10-14 m commercial fishing vessels during late-July to early-August of 2007, 2009-2012, and 2014-2016 (Table 1.1). The survey timing coincided with the capelin spawning season, when capelin was highly abundant in the study area. The survey consisted of nine transects across the shelf (east-west) and one transect along the coast (south-north; Fig. 1.1). All lines were not conducted annually due to limited ship time, resulting in 200-450 km surveyed each year (Fig. 1.1, Table 1.1). During the surveys, seabird numbers were continuously recorded within a 300 m strip off the port side of the vessel from the bridge of the ship (method Ib, Tasker et al. 1984) at a speed of 9 and 11 km/h. Based on early surveys (2000-2003) in the study area (Davoren 2007), we determined that the probability of detecting birds at sea decreased at distances beyond 300 m, similar to other studies (Barbraud and Thiebot 2009). Therefore, we counted birds within the 300 m strip only to ensure consistency among observers across years. We recorded the number of each species directly into a laptop (Birds and Beast Counter, 1998; D. Senciall, Fisheries and Oceans Canada, version 1.0), along with behavioural descriptions (on water or flying). The software appended a latitude, longitude and time to each count entered. Capelin density was quantified simultaneously using a Biosonics DTX 6000 (BioSonics Inc., Seattle, Washington) scientific echosounding system, whereby the transducer was towed along the starboard side at a depth of ~1 m below the surface, as described in Davoren et al. (2006). In brief, the sounder was operated through a 70 kHz split-beam transducer (5.5° full narrow beam width, 15° full wide beam width) calibrated with a

tungsten carbide sphere and mounted in a towed body. The sounder was operated at 1 ping  $s^{-1}$  and pulse duration of 0.4 ms. Raw high resolution hydroacoustic data ( $s_v$ , volume backscattering coefficients) were continuously acquired above a threshold of -90 dB. Echoview software (version 4, SonarData, Myriax Software Pty. Ltd., Hobart, Tasmania) was used to omit acoustic signals within 0.5 m of the seabed if they could not be distinguished from the seafloor (e.g. side-lobing; Simmonds & MacLennan 2005). To quantify acoustic biomass (area backscattering coefficient, or  $s_a$ ,  $m^2 \cdot m^{-2}$ ; (MacLennan et al. 2002), we integrated acoustic signals using a minimum  $s_v$  threshold of -80 dB in 100 m segments along the survey. Using a published target strength-length relationship for capelin (Rose 1998) along with the mean length of capelin collected in the study area each year,  $s_a$  was converted into the number of the individuals per  $m^2$  of capelin present in each 100 m segment during each survey.

Seabird counts were merged with capelin density within each 100 m segment along each survey. Some bird species fly faster than vessels during surveys, increasing their encounter rates (Spear et al. 1992) and, thus, we only considered the number of shearwaters on the water to avoid overestimating the number of birds in the area. Bathymetry (Depth, m), sea surface temperature (SST,  $^{\circ}C$ ) and chlorophyll A concentration (CHL A,  $mg/m^3$ ) were added to the bird counts (individuals) and fish density (individuals/ $m^2$ ) dataset to examine the most important variables underlying the distribution of each shearwater species in the study area. Bathymetry data (100 m resolution) were obtained from the Canadian Hydrographic Service (CHS), while satellite-derived SST and CHL A data (MODIS Aqua 4 km) were downloaded from Goddard Earth Sciences Data and Information Services Center (GES DISC) at the National Aeronautics and Space Administration (NASA) website [<https://disc.gsfc.nasa.gov>]. We downloaded the mean SST and CHL A during the period that surveys were conducted (July 19-August 13) in

each year. The spatial resolution available for SST and CHL A was 4 km<sup>2</sup> and, thus, all data were merged into each 4 km<sup>2</sup> bin within the study area using ArcGIS Desktop 10.3 ESRI® (Spatial Join tool). When the environmental data (SST and CHL A) were missing in a particular 4-km<sup>2</sup> bin, values from the nearest bin were used. Fish density was calculated as an average of the fish density (individuals/m<sup>2</sup>) over all 100 m survey segments in each 4-km<sup>2</sup> bin. The same calculation was used for the depth. Finally, for the maps (Fig 1.2-1.5) and table (Table 1.1), bird densities were calculated as the total number of each shearwater species on the water in each 4 km<sup>2</sup> bin divided by the total area surveyed within that bin (i.e. the number of 100 m survey segments multiplied by 0.03 km).

### *Statistical analysis*

All statistics analyses were performed using R software (version 3.4.0 Development Core Team 2014). Environmental data were examined for differences among years using non-parametric Wilcoxon tests. The number of birds in the 4-km<sup>2</sup> bins contained a large number of zeros (> 70% of bins/year) and, thus, we used a zero-altered (hurdle) negative binomial model (*pascal* package; Zeileis et al 2008) to determine the important predictor variables underlying the distribution of each shearwater species, similar to Nishizawa et al. (2015) and Goyert et al. (2018). The hurdle model is composed of two parts: a binomial-based part (zero), which identifies factors explaining the presence (i.e. number of birds greater than zero) versus absence (i.e. number of birds equal to zero), and the count-based part, which identifies the factors explaining the number of birds (density) where the birds were present (Zuur et al. 2009). For these models, the total number of great or sooty shearwaters within each 4 km<sup>2</sup> bin was used as the response variable. Each 4 km<sup>2</sup> bin had a different survey effort (i.e. number of 100 m survey

segments) and, therefore, we added the survey effort as an offset within the model. The predictor (explanatory) variables used in both the presence-absence and density models consisted of biotic factors (i.e., fish density, CHL A) and abiotic factors (i.e., SST, depth). Fish density was log transformed to allow a normal distribution. We also included the number of the other shearwater species on the water as a predictor variable to test our second hypothesis and identify whether these two shearwaters species were highly associated (Goyert 2014). All predictor variables were z-scored (standardized) to allow comparison among these variables with different scales and to determine which predictors had the most influence on presence/density of each shearwaters species in the model (Zuur et al. 2007).

Prior to running models, we examined correlations (Spearman) between the covariates and found that depth was highly correlated with CHL A ( $r > 0.7$ ). We only included depth during model selection, as spawning sites of capelin are located in shallow areas (<40 m; Penton and Davoren 2012) and, thus, depth is more indicative of distributional patterns of both shearwaters (Davoren 2013) and capelin (prey; Davoren et al. 2006). We also initially ran the full model (i.e. all predictor variables included) for each shearwater species with year as random variable; however, all predictors were significant. Therefore, to examine if predictor variables explaining the presence and number of great and sooty shearwaters differed among years, separate models were run by year to examine inter-annual differences. Within each year, we used Akaike's Information Criteria corrected for small sample size ( $AIC_c$ ) to select the best ( $\Delta AIC_c = 0$ ) and competitive models ( $\Delta AIC_c < 2$ ). The model averaged parameter estimates for each predictor variable along with its relative importance were then calculated across all competitive models (*MuMIn* package; Barton, 2015). The relative importance (RI) of each predictor variable was

calculated by summing the Akaike weights of all competitive models in which that variable was present (Burnham and Anderson 2002).

In survey-based species distributions, spatial autocorrelation can violate the assumption of independence between samples (Dormann 2007), where samples closer in space will be more similar relative to samples farther apart. By combining survey data into 4 km<sup>2</sup> bins, we reduced the spatial correlation among nearby observations during the survey. In addition, we calculated Moran's I (*ape* package, Paradis et al 2004) for surveys in each year to test for spatial correlation (Dormann 2007, Nishizawa et al. 2015). Although values were mostly statistically significant ( $p < 0.05$ ), indexes were lower than 0.1, indicating a lower spatial correlation within each year's dataset for great and sooty shearwater.

## **Results**

In total, 2,643 km were surveyed during the summer (July-August) in coastal Newfoundland with 7,743 great shearwaters (GRSH) and 12,114 sooty shearwaters (SOSH) counted on the water (Table 1.1). Other common species present on the water during the surveys in relatively high numbers were breeding species, including common murres (*Uria aalge*), northern gannets (*Morus bassanus*) and northern fulmars (*Fulmarus glacialis*) with 13,512, 657 and 655 individuals, respectively, as similar to previous studies (Davoren 2007, 2013). The ratios of great to sooty shearwaters and densities of the two shearwaters species varied widely among years. Higher densities of great relative to sooty shearwaters were observed during 2012, 2014 and 2016, whereas the opposite was the case during 2010, 2011 and 2015 (Table 1.1). The percentage of 4-km<sup>2</sup> bins that sooty shearwaters were present with great shearwaters (and vice versa) varied between 43-94% (Table 1.1).

### *Environmental data*

Environmental conditions varied significantly among years (Table 1.2). Indeed, the annual average SST ranged from 9.94-16.69 °C and differed significantly among years ( $\chi^2=690.98$ ,  $p<0.0001$ ). The warmest years surveyed were 2012 and 2014, whereas the coldest years were 2011 and 2015 (Table 1.2). The annual average fish density also varied significantly among years ( $\chi^2=41.19$ ,  $p<0.001$ ), with higher densities in 2016 and lower in 2010 and 2011 (Table 1.2). In addition, depth ranged from 10 to 320 m in the area surveyed.

### *Shearwater presence and numbers*

The number of other shearwater species on the water was present as a predictor variable in all zero (presence/absence) and count (numbers) components of the hurdle models for both species in all years with high relative importance ( $RI > 0.7$ ), although this predictor variable was not statistically significant in a few years for GRSH (count: 2009, 2011, 2015; zero: 2014) and SOSH (count: 2009, 2011, 2012; zero: 2010, 2011, 2016; Table 1.3). In all cases, there was a positive relationship between the presence and number of one shearwater species with the other and for most models, this predictor variable explained more of the variation in presence/number than other predictors (i.e. higher estimates; Table 1.3). Indeed, aggregations of both species were overlapped or in close proximity (Fig. 1.2-1.5). The relative importance of SST was typically low (mostly  $RI < 0.4$ ) and was only present, statistically significant and with high relative importance ( $RI=1$ ) within the 2010 model for both species (count component), in 2009 for SOSH (count component; Table 1.3) and in 2011 for GRSH (zero component). In general, when present in the model, there was a negative relationship between SST and GRSH numbers, where higher

GRSH numbers occurred at lower temperatures (Table 1.3). In contrast, the relationship was positive for SOSH, with higher SOSH numbers associated with higher temperatures (Table 1.3). The relative importance of depth was higher than SST (mostly  $RI > 0.7$ ), but was only present, statistically significant and with high relative importance ( $RI = 1$ ) within a few models for GRSH (count: 2007, 2014; zero: 2011) and SOSH (count: 2009, 2015; zero: 2007, 2011, 2015; Table 1.3). Shallow areas had higher numbers and presence of both shearwater species (except for SOSH, count: 2015). Finally, the relative importance of fish density (logfish) was typically low (mostly  $RI < 0.4$ ), but fish density (logfish) was present and statistically significant and with high relative importance ( $RI = 1$ ) in models from only one year for GRSH (count: 2016; Table 1.3), where high density of GRSH on the water were associated with high fish density. Similarly, positive relationships were observed between fish density and SOSH density, but fish density was only present and statistically significant for SOSH in two years (count: 2009, 2015; Table 1.3).

## **Discussion**

Although predator species that consume similar prey types and sizes may partition these resources if prey abundance is low (i.e. niche partitioning, Schoener 1974), our results revealed that the at-sea density and distributional patterns of two similar shearwater species were highly overlapped and the number of the other shearwater species influenced the presence and numbers of each shearwater species in all years of our study. This was predicted because the inshore migration of spawning capelin acts as a pulsed resource of high abundance prey for marine predators, which leads to dietary shifts of multiple marine predators to a higher reliance on capelin during spawning (Piatt 1990, Carscadden et al. 2002, Regular et al. 2009, Gulka et al.

2017) as well as multi-species aggregations at and nearby persistent capelin spawning sites (biological hotspot, Davoren 2013a). This suggests limited spatial segregation in the area, although we cannot preclude niche partitioning in other niche dimensions. Surprisingly, fish density had little influence on shearwater distributional and density patterns in the survey area, although shearwater presence and numbers were significantly higher in areas of high fish density in a few years. Similarly, sea surface temperature had minimal and varied influence on shearwater numbers and presence among years, possibly because SST varied little in the study area (i.e. 2-6°C per year) when averaged over the survey period. Alternately, depth was important in explaining the presence and numbers of both shearwater species in more years, with both species being more associated with shallow (< 50 m) areas close to the coast (Fig 1.2-1.5).

The high overlap of both shearwater species and the high variation explained by the other shearwater species, along with multi-species aggregations at and nearby capelin spawning sites (Davoren 2013a) all suggest that there are little costs to foraging in close association with other predators when spawning capelin are highly abundant inshore. Indeed, there may actually be benefits to foraging together. For instance, the use of local enhancement, or cueing to the foraging activities of seabirds, can increase foraging success while reducing the time spent searching for food as it is easier to detect feeding individuals than aggregations of undetected prey (Grünbaum and Veit 2003, Thiebault et al. 2014). As great and sooty shearwaters appear to feed on similar prey types during the non-breeding season in coastal Newfoundland (Brown et al. 1981, Chapter 2) and other regions (Ronconi et al. 2010), these species may cue to the foraging activities of each other to locate prey. Evidence for local enhancement in seabirds may be from species associations at sea, such as positive associations of Pink-footed *Puffinus creatopus* and sooty shearwaters in the Pacific (Briggs et al. 1987, Ainley et al. 2009), as well as multi-species

feeding flocks of taxonomically-related seabirds within the same guild in coastal Chile (Anguita and Simeone 2016). Additionally, high abundances of common terns (*Sterna hirundo*) predicted high abundances of roseate tern (*Sterna dougallii*) and vice-versa (Goyert 2014) and marine mammals are often good predictors of seabird distributions (e.g., Goyert et al. 2018). Another study experimentally showed in the study area that seabirds cue to decoys (i.e. plastic birds) within the study area (Bairos-Novak et al. 2015), but do so to a lesser extent during high capelin biomass relative to low biomass, suggesting that local enhancement may not be the only explanation for multi-species shearwater aggregations. Instead, birds may simply aggregate together within larger areas of high fish density.

Interestingly, fish density did not appear to directly influence the density and distributional patterns of either shearwater species to a great extent, but instead distributional patterns appeared to be mainly influenced by depth. Indeed, shearwater species were primarily aggregated together in shallow (< 50 m) areas along the coast. Similarly, seabird distribution has been explained by depth in other studies, with some species using shallow, coastal areas (e.g., sooty shearwaters in the Pacific, Ainley et al 2009) and others using slope areas (e.g. Yen et al. 2004, Nur et al. 2011), indicating that bathymetry features may be important in explaining seabird and cetacean distribution in some regions. In our study area, depth is important for predicting capelin distribution (Davoren et al. 2006). Indeed, persistent demersal spawning sites are located in shallow waters (< 40 m; Penton and Davoren 2012) and capelin aggregate nearby persistent spawning beaches prior to and during spawning (Davoren et al 2006), again supporting that shallow areas have higher capelin density. In addition, ephemeral schools of maturing capelin move northward along the coast in shallow regions (< 50 m) to locate suitable spawning habitat both within the study area and other regions of coastal Newfoundland (Nakashima 1992,

Davoren 2013b). If shearwater species use other features, such as distance to shore (a proxy of depth in our study area), to find predictable areas where ephemeral capelin schools are abundant, this might explain shearwater density and distributional patterns being more influenced by depth than fish density. The minimal influence of fish density on shearwater distributional and density patterns may also be related to the spatial scale (i.e. 4 km<sup>2</sup>) of our study, as the spatial scale at which prey-predator associations are examined will influence the strength of correlations observed and reported (Schneider and Piatt 1986). Indeed, distributional maps in this study illustrate that 4 km<sup>2</sup> cells with high densities of shearwaters were often found nearby cells with high densities of fish aggregations, suggesting that the spatial correlation between prey and predators would increase with the scale studied, as observed in other studies (Rose and Leggett 1990, Fauchald et al. 2000).

Other studies have found that sea surface temperature can predict seabird aggregations (Hyrenbach et al. 2006, Nishizawa et al. 2015), especially in frontal zones (Abrams 1985, Begg and Reid 1997), which was not the case in this study. In our study area, the average sea surface temperature does not vary substantially during the period surveyed and fronts driving prey distribution did not appear to present, as documented in other areas (Hoefer 2000, Bost et al. 2009, Scales et al. 2014, Cox et al. 2016). In contrast, capelin aggregates mostly near the seabed during the inshore spawning migration (Mowbray 2002) and during the spawning season (Davoren et al. 2006), suggesting that capelin distribution would be more correlated with bottom temperature than sea surface temperature. Indeed, bottom temperature is a key habitat feature of suitable capelin spawning habitat (Penton and Davoren 2012; Crook et al. 2017). As the thermocline occurs between 30-50 m in our study area (Davoren et al. 2006; Penton and Davoren

2008), sea surface temperature likely would not be a good proxy of bottom temperature and, thus, capelin habitat.

Overall, spatial segregation driven by interspecific competition does not appear to play an important role in influencing the density and distributional patterns of two similar shearwater species in coastal Newfoundland during their non-breeding season, likely due to the high abundance of prey. In addition, the overlap and associations of the two species suggest that there are little costs and potentially benefits, such as local enhancement, from foraging in close association. Using proxies of depth, such as distance to shore, to predict high concentrations of capelin schools, either spawning or moving along the coast during the summer, may explain the limited influence of fish density and the high influence of depth on shearwater density and distributional patterns. Future experimental studies will be needed, however, to examine the costs and benefits of foraging in close association by these two similar shearwater species.

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**Table 1.1** Dates, lines surveyed, and total distance covered within each annual survey conducted during the summer (Jul-Aug) on the northeastern Newfoundland coast, along with the percentage of 4 km<sup>2</sup> bins in which sooty shearwaters were present (i.e. overlap) with great shearwaters (and vice versa), the average density (minimum and maximum) of shearwaters on the water in 4 km<sup>2</sup> bins when birds were present, and the ratio of great to sooty shearwaters observed during each survey. Note the survey lines are the same as in Fig. 1 (CL= Coastal line, L1-9 = Lines 1-9).

| Year           | Dates                  | Lines surveyed | Total distance surveyed (km) | GRSH                  |   | SOSH                  |   | Ratio of GRSH / SOSH |
|----------------|------------------------|----------------|------------------------------|-----------------------|---|-----------------------|---|----------------------|
|                |                        |                |                              | Overlap with SOSH (%) | Bird density bird/km <sup>2</sup> (Min - Max) | Overlap with GRSH (%) | Bird density bird/km <sup>2</sup> (Min - Max) |                      |
| 2007           | Jul 24-26; Jul 29-31   | CL; L1, 3-7, 9 | 403.6                        | 73%                   | 20.3<br>(0.5-107.8)                           | 78%                   | 37.7<br>(0.5-288.9)                           | 0.68                 |
| 2009           | Jul 31; Aug 7, 9-10.   | CL; L1 - 9     | 453.1                        | 68 %                  | 21.3<br>(0.7-440.1)                           | 73%                   | 42.4<br>(0.7-734.9)                           | 0.57                 |
| 2010           | Jul 31-Aug 3; Aug 7    | CL; L1-2, 4-8  | 388.7                        | 90%                   | 10.5<br>(2.22-22.9)                           | 60%                   | 168.5<br>(1.1-625.0)                          | 0.05                 |
| 2011           | Jul 27, 29-30; Aug 2-3 | CL; L1-4, 6-8  | 361.7                        | 94%                   | 4.5<br>(0.9-13.8)                             | 52%                   | 62.6<br>(0.5-333.3)                           | 0.05                 |
| 2012           | Jul 29 - Aug 2         | CL; L1-4, 6-8  | 355.5                        | 59%                   | 34.6<br>(0.5-217.4)                           | 76%                   | 35.0<br>(0.4-133.8)                           | 1.45                 |
| 2014           | Jul 27 – 28, 31; Aug 4 | CL; L1-4, 7-8  | 259.4                        | 57%                   | 79.3<br>(1.1-895.7)                           | 77%                   | 72.3<br>(0.5-425)                             | 1.62                 |
| 2015           | Jul 31; Aug 2, 15      | CL; L1,3-4     | 212.1                        | 43%                   | 3.2<br>(1.0-13.3)                             | 45%                   | 25.9<br>(0.9-94.4)                            | 0.11                 |
| 2016           | Aug 8-10, 12           | CL; L1,3-4, 6  | 209.1                        | 64%                   | 77.4<br>(1.1-506.1)                           | 69%                   | 49.1<br>(0.8-326.7)                           | 1.86                 |
| Total/<br>Mean |                        |                | 2,643.2                      | 66%                   | 31.2 ±90.3                                    | 68%                   | 54.8 ±107.4                                   | 0.64                 |

**Table 1.2** Mean  $\pm$  SD of sea surface temperature (SST; °C), and fish density (individual/m<sup>2</sup> x10<sup>3</sup>) in each survey year on the northeast coast of Newfoundland during the survey period (17 Jul-12 Aug). Significantly different values ( $P < 0.05$ ) among years 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.

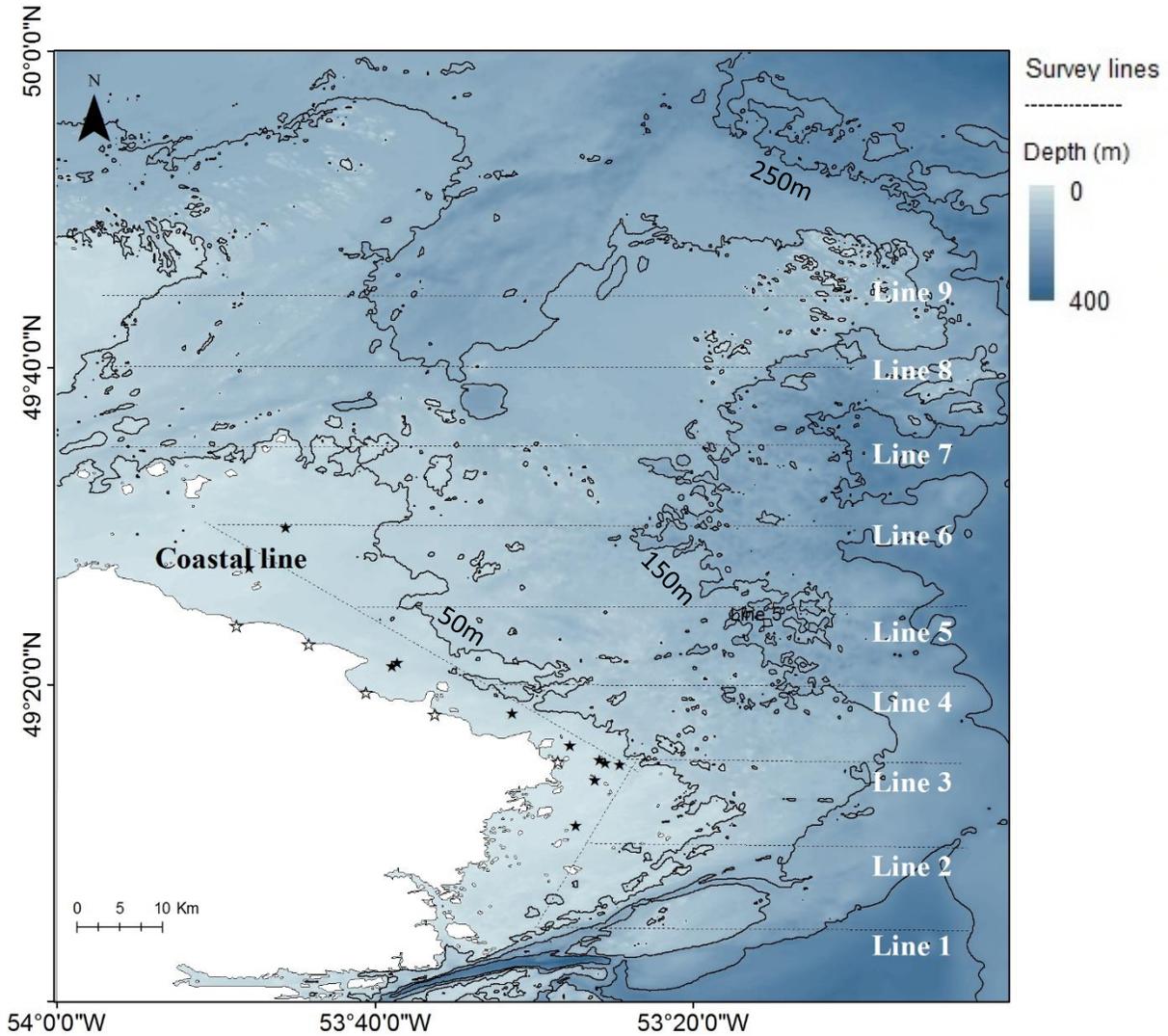
| <b>Year</b> | <b>SST (°C)</b>                | <b>Fish density (ind/m<sup>2</sup> x10<sup>3</sup>)</b> |
|-------------|--------------------------------|---|
| 2007        | 13.27 $\pm$ 1.23 <sup>e</sup>  | 0.31 $\pm$ 2.56 <sup>ab</sup>                           |
| 2009        | 13.77 $\pm$ 0.49 <sup>de</sup> | 0.26 $\pm$ 1.89 <sup>ab</sup>                           |
| 2010        | 13.82 $\pm$ 0.51 <sup>d</sup>  | 0.19 $\pm$ 0.94 <sup>b</sup>                            |
| 2011        | 9.94 $\pm$ 0.55 <sup>g</sup>   | 0.16 $\pm$ 0.65 <sup>b</sup>                            |
| 2012        | 15.81 $\pm$ 0.91 <sup>b</sup>  | 0.15 $\pm$ 0.72 <sup>ab</sup>                           |
| 2014        | 16.69 $\pm$ 1.89 <sup>a</sup>  | 1.90 $\pm$ 11.03 <sup>ab</sup>                          |
| 2015        | 11.93 $\pm$ 1.73 <sup>f</sup>  | 0.23 $\pm$ 1.72 <sup>ab</sup>                           |
| 2016        | 14.38 $\pm$ 0.83 <sup>c</sup>  | 2.88 $\pm$ 18.08 <sup>a</sup>                           |

**Table 1.3** Model averaged estimates of the predictor variables (parameters) from the zero-altered models (count and zero) for the distribution of great and sooty shearwaters in coastal Newfoundland during July-August, 2007, 2009-2012, 2014-2016, with relative importance (RI; sum of Akaike weights) and number of competitive models present (n). Predictor variables that significantly influenced bird numbers and presence (\*p<0.05 \*\*p<0.01 \*\*\*p<0.0001) and were present in all competitive models (RI =1.00) are bolded (continues).

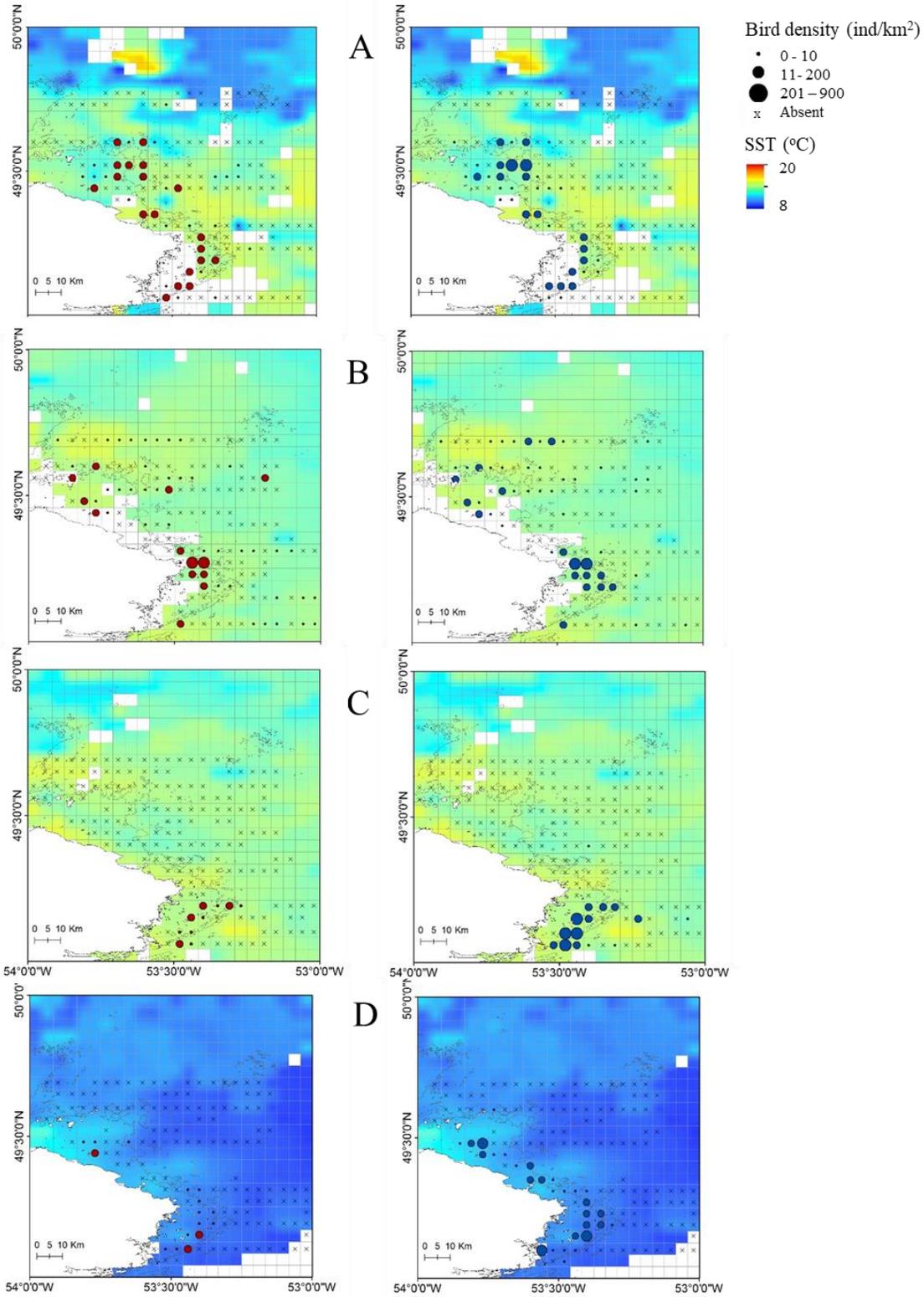
| Species | Model | Parameter | 2007             |             |          | 2009             |             |           | 2010            |             |          | 2011            |             |           | 2012            |             |           |
|---------|-------|-----------|------------------|-------------|----------|------------------|-------------|-----------|-----------------|-------------|----------|-----------------|-------------|-----------|-----------------|-------------|-----------|
|         |       |           | Estimate         | RI          | n        | Estimate         | RI          | n         | Estimate        | RI          | n        | Estimate        | RI          | n         | Estimate        | RI          | n         |
| GRSH    | Count | Intercept | -2.13            |             |          | -4.29            |             |           | -0.61           |             |          | -8.13           |             |           | -2.37           |             |           |
|         |       | SST       | -0.05            | 0.22        | 1        | 0.30             | 0.22        | 3         | <b>-12.73</b>   | <b>1.00</b> | <b>7</b> | -0.80           | 0.36        | 4         |                 |             |           |
|         |       | Depth     | <b>-0.99</b> **  | <b>1.00</b> | <b>3</b> |                  |             |           | 0.07            | 0.31        | 2        | -3.75           | 0.76        | 8         | -1.23           | 1.00        | 3         |
|         |       | logfish   | 0.01             | 0.21        | 1        | 0.86 **          | 0.85        | 8         | 0.06            | 0.42        | 3        | -0.17           | 0.38        | 5         |                 |             |           |
|         |       | Other shw | <b>2.08</b> ***  | <b>1.00</b> | <b>3</b> | 0.57             | 1.00        | 10        | <b>0.72</b> *** | <b>1.00</b> | <b>7</b> | 0.24            | 0.46        | 6         | <b>2.12</b> *   | <b>1.00</b> | <b>3</b>  |
|         | Zero  | Intercept | 7.94             |             |          | 2.5              |             |           | -6.49           |             |          | -19.49          |             |           | -2.76           |             |           |
|         |       | SST       |                  |             |          | 0.55             | 0.37        | 4         |                 |             |          | <b>-6.60</b> ** | <b>1.00</b> | <b>11</b> |                 |             |           |
|         |       | Depth     |                  |             |          | 0.43 *           | 0.90        | 9         | -0.22           | 0.21        | 2        | <b>-4.68</b> ** | <b>1.00</b> | <b>11</b> | -0.62 *         | 0.81        | 2         |
|         |       | logfish   |                  |             |          | 0.11             | 0.28        | 3         | 0.03            | 0.09        | 1        |                 |             |           | -0.21           | 0.38        | 1         |
|         |       | Other shw | <b>97.38</b> *** | <b>1.00</b> | <b>3</b> | <b>52.58</b> *** | <b>1.00</b> | <b>10</b> | <b>11.24</b> *  | <b>1.00</b> | <b>7</b> | <b>4.12</b> *   | <b>1.00</b> | <b>11</b> | <b>17.71</b> *  | <b>1.00</b> | <b>3</b>  |
| SOSH    | Count | Intercept | -2.23            |             |          | -3.05            |             |           | -0.46           |             |          | -1.55           |             |           | -0.82           |             |           |
|         |       | SST       | 0.24             | 0.31        | 2        | <b>3.81</b> *    | <b>1.00</b> | <b>5</b>  | <b>7.23</b> *** | <b>1.00</b> | <b>6</b> |                 |             |           | 0.07            | 0.13        | 2         |
|         |       | Depth     | -1.14            | 0.85        | 4        | <b>-0.80</b> **  | <b>1.00</b> | <b>5</b>  | -0.02           | 0.11        | 1        | -1.49 **        | 0.76        | 4         | -0.17           | 0.28        | 4         |
|         |       | logfish   |                  |             |          | <b>0.80</b> **   | <b>1.00</b> | <b>5</b>  | 0.22            | 0.47        | 3        | 0.17            | 0.29        | 2         |                 |             |           |
|         |       | Other shw | 2.50 *           | 0.77        | 4        | 0.41             | 1.00        | 5         | 4.48 *          | 0.85        | 5        | 5.19            | 0.51        | 3         | 0.37            | 0.94        | 10        |
|         | Zero  | Intercept | 1.10             |             |          | 1.25             |             |           | 13.36           |             |          | -0.14           |             |           | -2.45           |             |           |
|         |       | SST       |                  |             |          | 0.91             | 0.52        | 3         |                 |             |          |                 |             |           | -0.18           | 0.17        | 2         |
|         |       | Depth     | <b>-1.98</b> **  | <b>1.00</b> | <b>5</b> | -0.43            | 0.81        | 4         | 0.11            | 0.26        | 2        | <b>-3.46</b> ** | <b>1.00</b> | <b>6</b>  | -0.83           | 0.81        | 9         |
|         |       | logfish   | 0.04             | 0.14        | 1        | -0.11            | 0.31        | 2         |                 |             |          | <b>0.86</b> *   | <b>1.00</b> | <b>6</b>  | 0.43            | 0.57        | 6         |
|         |       | Other shw | <b>61.00</b> **  | <b>1.00</b> | <b>5</b> | <b>50.49</b> *** | <b>1.00</b> | <b>5</b>  | 160.23          | 1.00        | 6        | 57.99           | 1.00        | 6         | <b>29.45</b> ** | <b>1.00</b> | <b>11</b> |

**Table 1.3** (continued)

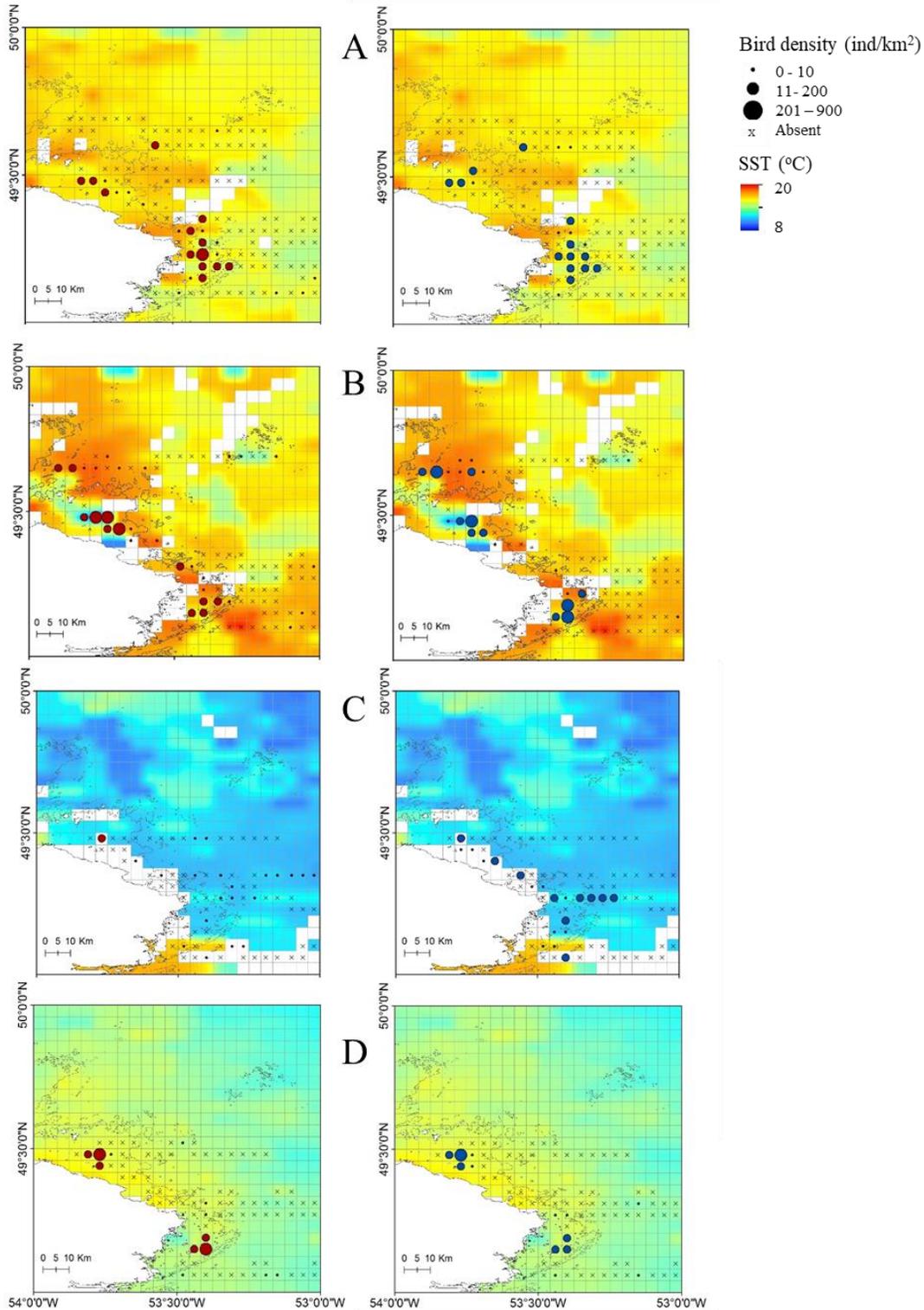
| Species | Model | Parameter | 2014                |             |           | 2015                |             |           | 2016            |             |          |
|---------|-------|-----------|---------------------|-------------|-----------|---------------------|-------------|-----------|-----------------|-------------|----------|
|         |       |           | Estimate            | RI          | n         | Estimate            | RI          | n         | Estimate        | RI          | n        |
| GRSH    | Count | Intercept | -2.92               |             |           | -3.52               |             |           | -2.84           |             |          |
|         |       | SST       | -0.16               | 0.32        | 2         | -0.22               | 0.33        | 6         | 0.17            | 0.16        | 1        |
|         |       | Depth     | <b>-2.25</b><br>*** | <b>1.00</b> | <b>6</b>  | -0.12               | 0.29        | 5         | -0.05           | 0.15        | 1        |
|         |       | logfish   | 0.55                | 0.68        | 4         | -0.05               | 0.01        | 2         | <b>2.02</b> *** | <b>1.00</b> | <b>4</b> |
|         |       | Other shw | <b>1.09</b> *       | <b>1.00</b> | <b>6</b>  | 0.37                | 0.30        | 5         | <b>3.64</b> *** | <b>1.00</b> | <b>4</b> |
|         | Zero  | Intercept | -2.67               |             |           | -3.88               |             |           | 20.30           |             |          |
|         |       | SST       | -0.05               | 0.22        | 2         |                     |             |           |                 |             |          |
|         |       | Depth     | -0.24               | 0.51        | 3         | 0.09                | 0.29        | 6         |                 |             |          |
|         |       | logfish   |                     |             |           | -0.09               | 0.19        | 4         | -0.29           | 0.31        | 1        |
|         |       | Other shw | 11.89               | 1.00        | 6         | <b>6.06</b> *       | <b>1.00</b> | <b>17</b> | <b>189.55</b> * | <b>1.00</b> | <b>4</b> |
| SOSH    | Count | Intercept | -5.32               |             |           | 3.02                |             |           | -14.85          |             |          |
|         |       | SST       | 0.60 *              | 0.63        | 9         | -0.59 *             | 0.84        | 3         | 3.59            | 0.18        | 1        |
|         |       | Depth     | -2.73 *             | 0.89        | 12        | <b>1.97</b> ***     | <b>1.00</b> | <b>4</b>  | -8.12           | 0.82        | 2        |
|         |       | logfish   | -0.46               | 0.28        | 4         | <b>0.80</b> **      | <b>1.00</b> | <b>4</b>  | -2.12           | 0.82        | 2        |
|         |       | Other shw | 0.75 *              | 0.58        | 8         | <b>27.43</b><br>*** | <b>1.00</b> | <b>4</b>  | <b>2.66</b> *   | <b>1.00</b> | <b>3</b> |
|         | Zero  | Intercept | -4.24               |             |           | 0.64                |             |           | -0.81           |             |          |
|         |       | SST       |                     |             |           | 0.10                | 0.21        | 1         |                 |             |          |
|         |       | Depth     | -0.11               | 0.25        | 4         | <b>-2.15</b> **     | <b>1.00</b> | <b>4</b>  |                 |             |          |
|         |       | logfish   | 0.04                | 0.15        | 3         | 0.07                | 0.19        | 1         | 0.23            | 0.38        | 1        |
|         |       | Other shw | <b>7.35</b> *       | <b>1.00</b> | <b>14</b> | <b>52.35</b> *      | <b>1.00</b> | <b>4</b>  | 40.31           | 1.00        | 3        |



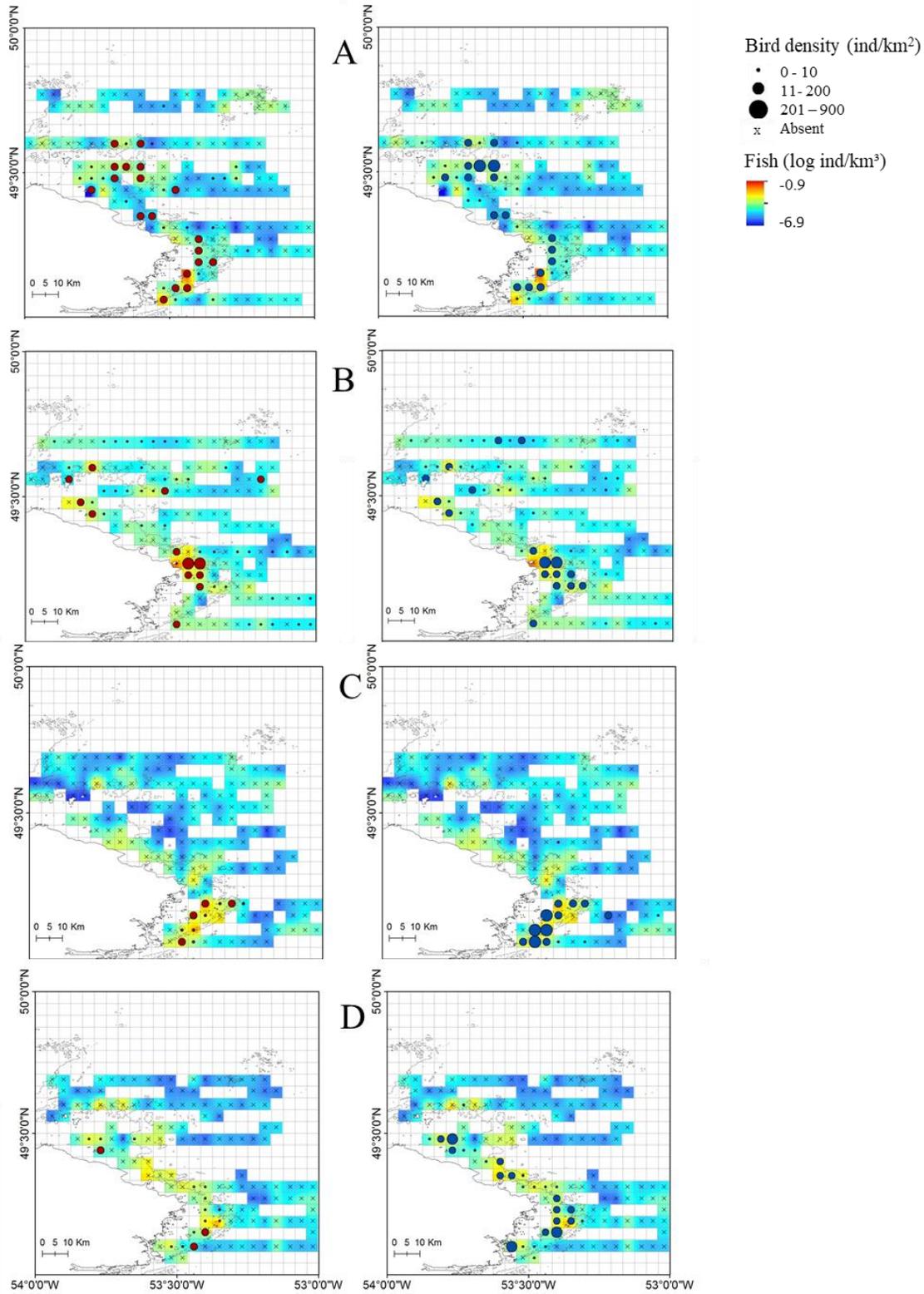
**Figure 1.1** The study area on the northeastern coast of Newfoundland, highlighting survey lines (coastal line and lines 1-9) and known capelin spawning sites at beaches (empty stars) and in deeper water (black stars). 50, 150 and 250 m depth contours are shown on the map.



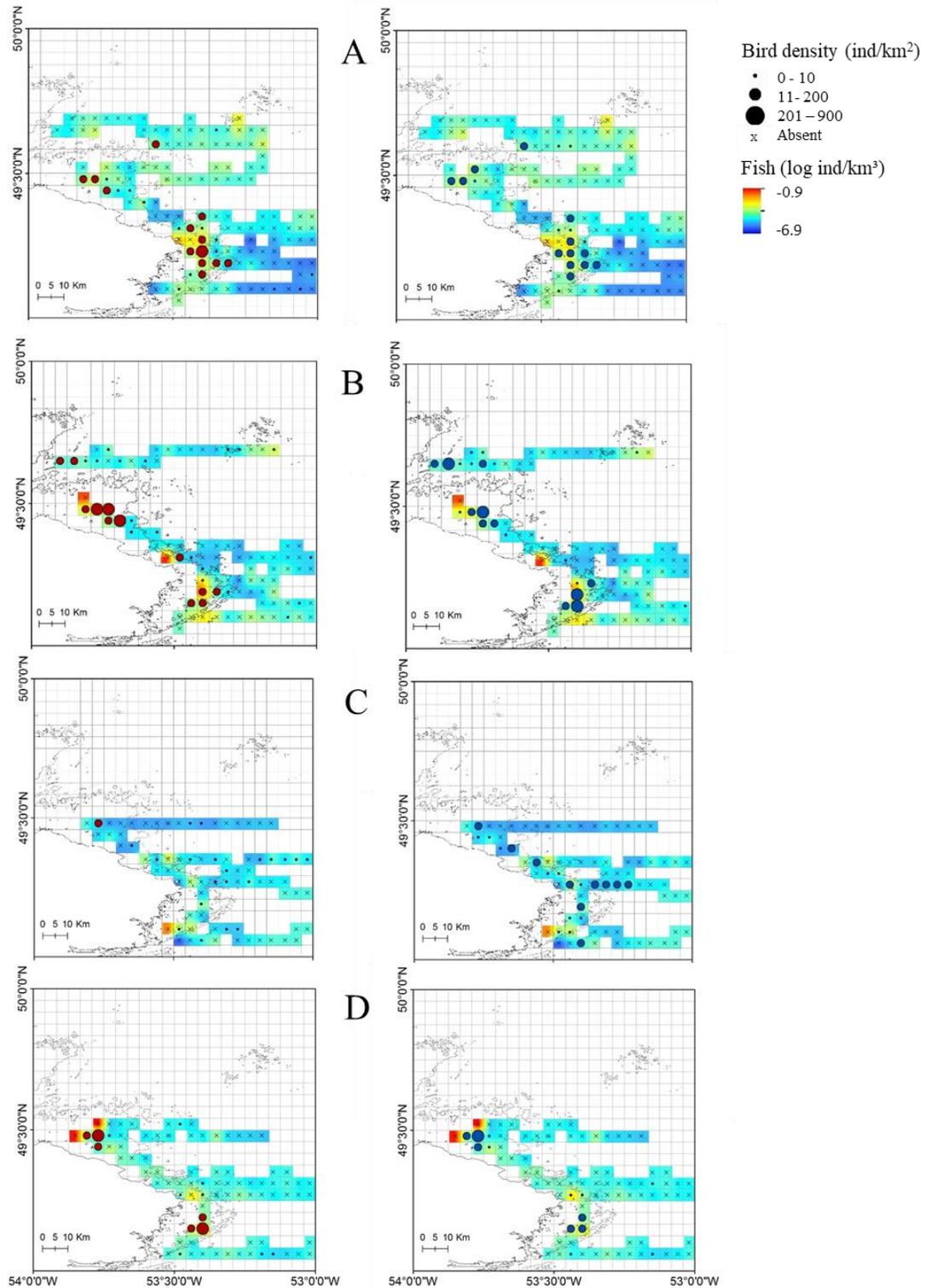
**Figure 1.2.** Great (left) and sooty shearwaters (right) density (ind/km<sup>2</sup>) and sea surface temperature (°C) during the summer on the northeast coast of Newfoundland in 2007(A), 2009(B), 2010(C) and 2011(D). Note that the 50 m depth contour is shown on the maps.



**Figure 1.3** Great (left) and sooty shearwaters (right) density (ind/km<sup>2</sup>) and sea surface temperature (°C) during the summer on the northeast coast of Newfoundland in 2012(A), 2014(B), 2015(C) and 2016(D). Note that the 50 m depth contour is shown on the maps.



**Figure 1.4** Great (left) and sooty shearwaters (right) density (ind/km<sup>2</sup>) and fish density (log ind/km<sup>2</sup>) during the summer on the northeast coast of Newfoundland in 2007(A), 2009(B), 2010(C) and 2011(D). Note that the 50m depth contour is shown on the maps.



**Figure 1.5** Great (left) and sooty shearwaters (right) density(ind/km<sup>2</sup>) and fish density (log ind/km<sup>2</sup>) during the summer on the northeast coast of Newfoundland in 2012(A), 2014(B), 2015(C) and 2016(D). Note that the 50m depth contour is shown on the maps.

## **Chapter 2: Inter-annual variation of dietary niche breadth and overlap of sympatric non-breeding shearwaters under varying prey availability**

### **Abstract**

Variation in prey availability can cause changes in species interactions among predators. Foraging theory predicts that niche breadth will expand when resources become limited, possibly leading to higher niche overlap as the niches broaden; however, a species' niche can become constrained by interactions with other similar species, resulting in an inability to shift niche breadth or niche position. In coastal Newfoundland, capelin is the main forage fish species and its availability (i.e. presence and biomass) during the summer varies both within and among years. Large aggregations of great and sooty shearwaters (*Ardenna gravis* and *A. grisea*) aggregate at annually persistent capelin spawning sites during their non-breeding season. We used stable isotope ratios ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) to investigate variation in isotopic niche breadth of the two shearwater species as well as isotopic niche overlap during 2014, 2015 and 2016. Although capelin availability varied among years, niche overlap between great and sooty shearwaters was consistently high, contradicting competition theory and niche partitioning under limited prey availability. However, as predicted by foraging theory, during lower capelin availability, both shearwater species expanded their niche breadth similarly, suggesting the incorporation of alternative prey types into their diet. My findings suggest that both shearwaters are flexible foragers and can modify their diet during the non-breeding season to accommodate fluctuations in prey availability.

**Key-words:** niche overlap; niche breadth; stable isotope; competition; foraging; shearwaters

## Introduction

Each species has a set of resources and environmental conditions (niche) that individuals require to grow, survive and reproduce (Hutchison 1957). For species with a similar life history and foraging guild, the potential for interspecific competition, represented by the degree of niche overlap, is more pronounced. As food resources are often distributed in an unpredictable and patchy manner in the marine environment, high abundances of multiple predator species tend to concentrate in areas where prey aggregates, resulting in biological hotspots (e.g., Ainley et al. 2009, Davoren 2013). Interspecific competition may occur within hotspots if prey availability becomes limited over time (Begon et al. 2006), thereby influencing a species' niche breadth (Kowalczyk et al. 2015, Yurkowski et al. 2016). Foraging theory predicts that as prey availability becomes limited, individual predators will shift from incorporating primarily preferred prey types in the diet to incorporating a higher variety of less preferred prey types (Pike et al. 1977), thereby resulting in niche expansion (Svanback and Bolnick 2007). Under limited resources, however, a species' niche can become constrained by interactions with other similar species, resulting in an inability to shift niche breadth or niche position. Similar species may only coexist by partitioning the limited resources (niche partitioning; Tokeshi 1999, Begon et al. 2006), resulting in reduced niche overlap between species (Colwell and Futuyma 1971, Holbrook and Schmitt 1989). Indeed, resource partitioning is thought to allow the coexistence of sympatric seabird species by foraging in different locations (Phalan et al. 2007, Navarro et al. 2009, 2013, Linnebjerg et al. 2013, Quillfeldt et al. 2013), periods (e.g. nocturnal vs. diurnal; Navarro et al. 2013), depths in the water column (Ballance et al. 1997), or on different prey types (prey specialisation; Mancini et al. 2014). Although interspecific competition in seabirds is thought to be highest during the breeding period, when multiple species are aggregated at breeding colonies

and have limited foraging areas around the colony (central-place foragers), competition also might occur if prey become limited on the non-breeding grounds.

Stable isotopes have been used to describe the trophic niche breadth of a species (Bearhop et al. 2004). By combining carbon and nitrogen stable isotope ratios, researchers can quantify the isotopic niche breadth of a species, which is defined as an area (in  $\delta$ -space) with isotopic values ( $\delta$ -values, usually  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) as coordinates (Newsome et al. 2007). Using a multi-species approach, niche breadth can be used to determine the degree of isotopic niche overlap, which may represent resource partitioning between sympatric species (Suryan and Fischer 2010, Young et al. 2010, Linnebjerg et al. 2013) and seabird assemblages (Forero et al. 2004, Cherel et al. 2008, Mancini et al. 2014). Nitrogen isotope ratios ( $^{15}\text{N}/^{14}\text{N}$ , or  $\delta^{15}\text{N}$ ) are thought to indicate the trophic position of a species, while carbon isotope ratios ( $^{13}\text{C}/^{12}\text{C}$ , or  $\delta^{13}\text{C}$ ) reflect basal food sources. In the marine environment, the latter can be used to discriminate food obtained from coastal and oceanic areas, high and low latitude regions, and pelagic and benthic areas (Cherel et al. 2005, Quillfeldt et al. 2005). Moreover, stable isotopes of different tissues can be used to evaluate niche breadth and niche overlap on multiple temporal scales, as each tissue has a characteristic isotopic turnover rate (Hobson and Clark 1993, Evans Ogden et al. 2004). For instance, different blood components can give dietary information from two distinct periods, with the red blood cells (RBCs) representing diet over the past few weeks while the plasma represents diet over the past few hours or days (Hobson and Clark 1993, Hahn et al. 2012, Barquete et al. 2013)

In the North Atlantic, non-breeding great and sooty shearwaters (*Ardenna gravis* and *Ardenna grisea*) are among the main consumers of forage fish during the summer (Barrett et al. 2006). Both species appear to occupy a similar trophic niche when they have a sympatric

distribution during the non-breeding season, as evidenced by similar diets (e.g., euphausiids, capelin, squid, herring) from stomach content analysis (Brown et al. 1981) as well as stable isotope and fatty acid signatures (Ronconi et al. 2010c). Despite considerable overlap in diet, there is some indication of subtle resource partitioning between species during their non-breeding season in the Bay of Fundy, with great shearwaters feeding at higher trophic levels (i.e. higher  $\delta^{15}\text{N}$ ) over five years relative to sooty shearwaters (Ronconi et al. 2010c). In addition, sooty shearwaters appeared to feed on different prey sources, represented by a higher  $\delta^{13}\text{C}$  compared to great shearwaters (Ronconi et al. 2010c). In the southern hemisphere, great shearwaters are known to follow boats and feed on discards from fisheries (Olmos 1997, Bugoni et al. 2010), as do sooty shearwaters, but to a lesser extent (Jackson 1988, Wood 1993). When feeding on discards, the larger great shearwater has been reported to displace the slightly smaller sooty shearwater (Ronconi et al. 2010b).

On the northeast Newfoundland coast, great and sooty shearwaters aggregate on spawning sites of a key forage fish (capelin *Mallotus villosus*; Davoren 2013). Capelin is a key prey species for top predators in the Northwest Atlantic, especially when they migrate into coastal regions of Newfoundland to spawn during July and August. Prior to capelin arrival inshore, sandlance (*Ammodytes* sp) is commonly used as food resource by predators in coastal Newfoundland, including breeding seabirds (Burke and Montevecchi 2008). However, the inshore arrival of spawning capelin acts as a pulsed resource, shifting the prey base of marine predators from lower abundance (i.e. pre-spawning) to higher abundance (i.e. spawning). This results in substantial variation of capelin availability throughout the summer (Davoren et al. 2006, 2012). Additionally, the timing of capelin arrival inshore, as well as the inshore spawning biomass shows high inter-annual variation (Davoren et al. 2012, Crook et al. 2017). Therefore,

among and within year variation in capelin availability likely influence interactions among closely related species, such as great and sooty shearwaters, coexisting in the area.

The main objective of this study was to investigate the variation in isotopic niche breadth and overlap between great and sooty shearwaters under varying capelin availability while they co-occur during their non-breeding season in coastal Newfoundland. We hypothesized that isotopic niche breadth of each species and niche overlap between species will vary with capelin availability. We predicted that isotopic niche breadth will be narrower for both species and niche overlap will be higher when capelin biomass is higher, relative to a wider niche breadth and low overlap when capelin biomass is lower. This study will add to our knowledge of how sympatric species partition their niche under varying prey availability.

## **Methods**

### *Prey (capelin) biomass*

A fine-scale (~25 km) survey was conducted every 3-5 days in the study area on northeast Newfoundland coast during July-August 2014-2016. The survey route was centered over a cluster of persistently used deep-water spawning sites of capelin (Penton and Davoren 2012) on which a biological hotspot forms annually (Davoren 2013). Capelin biomass at these spawning sites reflects the timing of arrival of spawning capelin inshore and capelin biomass in the larger study region (Davoren et al. 2006). Along the survey line, seabird densities and capelin biomass were continuously and simultaneously recorded using standard strip-transect methods (method Ib, Tasker et al. 1984) and using a scientific echosounder, respectively. The survey with peak capelin biomass ( $\text{g/m}^2$ ) within a year was used to examine inter-annual variation in capelin biomass and arrival of capelin inshore. Along with the surveys, these deep-water spawning sites

were monitored for the presence of sediment with adherent capelin eggs in early developmental stages by collecting sediment with a 0.3 m<sup>2</sup> Ponar Benthic Grab System, thereby quantifying the timing and duration of spawning, following methods described in previous studies in the study area (Penton and Davoren 2012; Davoren et al. 2012; Davoren 2013; Crook et al. 2017). The timing and duration of capelin spawning was used as a measure of the duration capelin was available within the study area within each year.

### *Sample collection*

Great and sooty shearwaters were captured at sea during the night (July-August 2014-2016) from a commercial fishing boat (*Lady Easton II*) using a spotlight and a long-handled, large dip-net (Whitworth et al. 1997, Ronconi et al. 2010b). For each bird, blood samples (1-3 mL) were collected using a 3-5 mL syringe with 21-25-gauge needle from the tarsal vein. The blood was stored in EDTA tubes (Becton-Dickinson Vacutainer®) and left on ice (approximately 8 hours) until centrifuged to separate the plasma and red blood cells (RBCs). Blood components were frozen separately for stable isotope analysis. Although the anticoagulant (EDTA - Ethylenediaminetetraacetic acid) may affect the stable isotope ratios of blood (Lemons et al. 2012), all samples were treated in the same way and the effect should not influence population-level metrics of isotopic niche breadth and overlap. In addition, EDTA did not influence stable isotope signatures of RBCs on other seabird species (Käkelä et al. 2007) as well as shearwaters (Ronconi unpubl. data).

We opportunistically collected capelin (2014: n=15; 2015: n=20; 2016: n=20) and sand lance (*Ammodytes* sp, 2014: n=7; 2015: n=8; 2016: n=2), the two main forage fish (prey) in the

study area. Approximately 1-2 g of dorsal muscle tissue (without the skin) was collected from each fish and frozen for stable isotope analysis.

### *Stable isotope analysis*

Stable isotope ratios of carbon ( $^{13}\text{C}/^{12}\text{C}$ ) and nitrogen ( $^{15}\text{N}/^{14}\text{N}$ ) were quantified for RBCs and plasma. Each blood component sample was freeze-dried for 48 h. Lipids are depleted in  $^{13}\text{C}$ , resulting in  $^{13}\text{C}/^{12}\text{C}$  ratios that do not necessarily reflect dietary sources (Post et al. 2007). Lipids typically remain in the plasma after centrifuging and, thus, lipids were removed only from plasma samples using petroleum ether in a Soxhlet for approximately 8 h and subsequently oven dried ( $60^\circ\text{C}$ ) for 48 h. Fish muscle (capelin, sandlance) was processed similarly, including lipid extraction. Each sample was homogenized, and a sub-sample (0.4 - 0.8 mg) was weighed and placed in a tin capsule. Samples were shipped to the Chemical Tracers Lab (University of Windsor) where stable carbon and nitrogen isotopes 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 international standards, including Pee Dee Belemnite (PDB) for carbon ( $\delta^{13}\text{C}$ ) and atmospheric air for nitrogen ( $\delta^{15}\text{N}$ ), according to the following equation:  $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$ , where X is  $^{15}\text{N}$  or  $^{13}\text{C}$  and R is the ratio between the heavier and lighter isotopes (i.e.  $^{15}\text{N}/^{14}\text{N}$  or  $^{13}\text{C}/^{12}\text{C}$ ). Precision was assessed as the standard deviation of replicate analyses and was  $\leq 0.19\%$  for  $\delta^{15}\text{N}$  and  $\leq 0.17\%$  for  $\delta^{13}\text{C}$ . Mean instrumental accuracy was  $\leq 0.24\%$  for  $\delta^{15}\text{N}$  and  $\leq 0.06\%$  for  $\delta^{13}\text{C}$ .

### *Data analysis*

The stable isotope ratios for both carbon and nitrogen on the plasma and RBCs were not normally distributed. Therefore, we used the non-parametric Kruskal-Wallis and post-hoc Steel-Dwass test to investigate mean differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  between species within the same year, as well as within the same species among years for both plasma and RBCs. For the prey,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were normally distributed and differences between years (2014-16) were tested using ANOVA and post-hoc Tukey HSD.

The isotopic niche breadth of each species and niche overlap between species in each year was calculated using Stable Isotope Bayesian Ellipses in R (*SIBER* downloaded May 2017; Jackson et al. 2011) for both great and sooty shearwaters and RBCs and plasma separately during the summers of 2014-2016. Traditionally, studies have used standard ellipse area, defined as the standard deviation around the bivariate mean encompassing ~40% of the data, as a measure of isotopic niche breadth (Jackson et al. 2011). However, we used the 95% prediction ellipse, encompassing ~95% of the data points, to represent a more comprehensive population-level niche breadth. The Bayesian approach provides a range of values of 95% prediction ellipse areas by calculating the posterior distribution, consisting of the values from 10,000 iterative calculations. We used the most likely 95% prediction ellipse area (i.e. mode of the distribution) and variation around the most likely ellipse area (i.e. 95% credible intervals) to represent isotopic niche breadth. In addition, we used the Bayesian approach to determine the probability of one isotopic niche breadth being larger than another, by calculating the posterior distribution resulting from 1,000 iterations. The isotopic niche overlap of both species in each year was calculated as the percent overlap of the niches (i.e. most likely, or mode of the distribution, of 95% prediction ellipse area) of great and sooty shearwaters using the overlapped area divided by

the sum of the 95% prediction ellipse area for both species minus the overlapped area, all multiplied by 100.

For the within year analysis, the isotopic niche breadth was calculated using plasma only (representing short-term diet) during two periods: early, when prey biomass was low, and late, when prey biomass was higher. For this analysis, great and sooty shearwater species were pooled together due to low species-specific sample sizes in each period within years (see Results).

## **Results**

### *Capelin biomass, timing and duration of presence and spawning*

During 2014, peak capelin biomass in the study area was higher (0.254 g/m<sup>2</sup>) and occurred earlier (July 14) compared to 2015 (0.126 g/m<sup>2</sup>, July 20) and 2016 (0.027 g/m<sup>2</sup>, July 14). The period of capelin presence and the timing and duration of spawning in the study area varied among years, being earlier in 2014 (presence: July 4-25; spawning: July 16-24) and later in 2015 (presence: July 20-August 12; spawning: July 20-23) and 2016 (presence: July 15-August 16; no spawning). Shearwater blood samples were collected between Jul 14-Aug13 in 2014; Jul 16-Aug 17 in 2015 and Jul 21-Aug 16 in 2016.

### *Stable isotope*

#### *Prey*

Capelin carbon and nitrogen stable isotope ratios did not differ among years ( $\delta^{13}\text{C}$ :  $F_{2,54}=1.66$ ,  $p=0.20$ ;  $\delta^{15}\text{N}$ :  $F_{2,54}=1.51$ ,  $p=0.23$ ). Sandlance carbon and nitrogen stable isotope ratios, however, differed among years ( $\delta^{13}\text{C}$ :  $F_{2,16}=4.26$ ,  $p=0.036$ ;  $\delta^{15}\text{N}$ :  $F_{2,16}=3.90$ ,  $p=0.045$ ). Post-hoc results showed that  $\delta^{13}\text{C}$  were lower in 2014 relative to 2015 ( $p=0.03$ ) but similar to 2016

( $p=0.47$ ), while 2015 and 2016 had similar  $\delta^{13}\text{C}$  ( $p=0.77$ ). For  $\delta^{15}\text{N}$ , the values were lower in 2014 relative to 2015 ( $p=0.04$ ) but similar in 2016 ( $p=0.88$ ), while 2015 and 2016 had similar  $\delta^{13}\text{C}$  ( $p=0.41$ ; Table 2.1).

### *Plasma*

Carbon and nitrogen stable isotope ratios ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) of plasma did not differ between great and sooty shearwaters in the same year (Table 2.2), but both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  within a species differed among years (2014-2016; Table 2.2). Post-hoc tests revealed that carbon and nitrogen stable isotope ratios for both species were higher in 2014 relative to 2015 (GRSH,  $\delta^{13}\text{C}$ :  $Z=-5.00$   $p<0.001$  and  $\delta^{15}\text{N}$ :  $Z=-5.71$   $p<0.001$ ; SOSH,  $\delta^{13}\text{C}$ :  $Z=-4.00$   $p<0.001$  and  $\delta^{15}\text{N}$ :  $Z=-4.01$   $p<0.001$ ) and 2016 (GRSH,  $\delta^{13}\text{C}$ :  $Z=-5.15$   $p<0.001$  and  $\delta^{15}\text{N}$ :  $Z=-5.12$   $p<0.001$ ; SOSH,  $\delta^{13}\text{C}$ :  $Z=-5.09$   $p<0.001$  and  $\delta^{15}\text{N}$ :  $Z=-5.01$   $p<0.001$ ), but did not differ between 2015 (GRSH,  $\delta^{13}\text{C}$ :  $Z=-0.46$   $p<0.89$  and  $\delta^{15}\text{N}$ :  $Z=0.59$   $p=0.83$ ; SOSH,  $\delta^{13}\text{C}$ :  $Z=-0.99$   $p=0.58$  and  $\delta^{15}\text{N}$ :  $Z=0.51$   $p=0.86$ ), and 2016 (Table 2.2).

The isotopic niche breadth (95% ellipse area) was the narrowest in 2014 for both great and sooty shearwaters. In 2015, 95% ellipse area was four times wider than 2014 and in 2016 the niche breadth was double the value of 2014 (Table 2.2). Indeed, the probability of 95% ellipse area in 2014 being smaller than 2015 was 100% for both species and >94% than 2016 for both species. In addition, the probability of 95% ellipse area in 2015 being smaller than 2016 was <4% for both species. The probability of isotopic niche overlap between species within each year was high for all years ranging from 56 to 60% (Fig. 2.1).

By combining the half-life from plasma (~2.9 days; Hobson and Clark 1993), dates of blood sample collection, and presence of capelin in the study area, we divided each year into

early (i.e. pre-spawning, low biomass) and late (i.e. spawning, high biomass) periods so as to examine within year variation (Fig. 2.2). The timing of early and late seasons varied among years, due to different timing of capelin spawning and peak biomass in the study area, with 2014 season being earlier (early:  $\leq$  July 13; late:  $\geq$  July 14) than 2015 and 2016 (early:  $\leq$  July 30; late:  $\geq$  July 31). During 2014 and 2015, niche breadth (95% ellipse area) was wider in early (0.89 and 2.93, respectively) relative to the late season (0.43 and 1.31; Fig. 2.2). In contrast, 2016 had a narrower niche breadth earlier in the season (1.08) than later (1.23; Fig. 2.2). The probability of 95% ellipse area in early season being smaller than late season was 99% in 2014, 98% in 2015 and 39% in 2016.

#### *Red blood cells*

Carbon and nitrogen stable isotope ratios of RBCs did not differ significantly between great and sooty shearwaters within the same year and within species among years; however,  $\delta^{15}\text{N}$  differed among years for great shearwaters, with lower  $\delta^{15}\text{N}$  in 2015 relative to 2014 (Table 2.2).

The isotopic niche breadth (95% ellipse area) was variable among years for both great and sooty shearwaters (Table 2.2). In 2015, 95% ellipse area was wider than 2014 and 2016 for both species (Table 2.2). Indeed, the probability of 95% ellipse area in 2014 being smaller than 2015 was 98% for both species. In addition, the probability of 95% ellipse area in 2015 being smaller than 2016 was  $<26\%$  for both species. The isotopic niche overlap between species within each year was ranged from 44 to 63% (Fig. 2.3).

## Discussion

In contrast to our predictions, niche overlap between non-breeding great and sooty shearwaters remained consistently high under varying prey (capelin) availability in all three years. Together with similar shifts in the dietary niche of both species with varying capelin availability among years, findings suggest that these species share the same trophic niche in the study area. Although high niche overlap suggests a high potential for competition between these species during the summer in coastal Newfoundland, the decline in prey abundance was not enough to result in niche partitioning. As predicted by foraging theory, the isotopic niche breadth of each species expanded during 2015 and 2016 (especially for plasma), which was consistent with shearwaters feeding on alternative prey when capelin arrived late and abundance was lower after arrival relative to 2014. Similarly, isotopic niche breadth of both species combined within years tended to be higher during lower (early) relative to higher (late) capelin availability, suggesting that shearwaters consume a variety of prey types prior to capelin presence in the study area (i.e. pre-spawning) but switch to a more capelin-based diet once it arrives inshore to spawn and becomes the dominant prey in the area. Niche breadth did not vary throughout the season during 2016, likely because individuals sampled during the pre-spawning period were caught in the southern part in the study area where capelin was already present.

Similar stable isotope ratios and overlapping isotopic niches suggest that great and sooty shearwaters fed on similar prey and did not partition their dietary niches under the range of capelin availability in our study. Similar to our findings, stomach contents previously revealed that both species feed on similar prey types in the Northwest Atlantic (e.g., capelin *Mallotus villosus*; squid *Illex illecebrosus*; herring *Clupea harengus*; euphausiids *Meganyctiphanes norvegica*), with some differences associated with variation in dive capacity and bill morphology

(Brown 1981). Similarly, great and sooty shearwaters shared the same dietary niche over five years in the Bay of Fundy; however, subtle differences in isotopic ratios indicated that great shearwaters consistently fed at a higher trophic level (higher  $\delta^{15}\text{N}$ ) and different food sources (lower  $\delta^{13}\text{C}$ ) relative to sooty shearwaters (Ronconi et al. 2010c). High niche overlap has been reported among other similar seabird species while coexisting in the same area. For instance, multiple species (i.e. five cormorant and three tern species) breeding sympatrically on the Argentinean Patagonia shelf had high niche overlap and coexistence was thought to be possible because of high food availability or distinct foraging strategies (Forero et al 2004, Barger and Kitaysky 2012). In the Bering Sea (Alaska), however, two sympatrically breeding auk species had overlapping dietary niches when food availability was high, but segregated niches when food resources were low (Barger and Kitaysky 2012). As niche partitioning is predicted under limited prey (Schoener 1974), differences between studies are probably related to the magnitude of variation in prey availability, thereby likely determining whether dietary niche overlap shifted as prey availability varied.

High isotopic niche overlap, however, does not indicate that species do not partitioning their niche in other ways. For instance, Franco-Trecu et al. (2017) found that two dolphin species had high isotopic niche overlap, but were spatially segregated during foraging. In our study, however, both shearwater species were caught in mixed-species flocks at the same locations on the same nights, illustrating that they were not spatially or temporally segregated. Additionally, both species are known to feed diurnally, being more active during dawn and dusk (Shaffer et al. 2009, Ronconi et al. 2010a). Although the dive capacity varies between species, with sooty shearwaters able to dive deeper (up to 70 m, Weimerskirch and Sagar 1996, Shaffer et al. 2009) than great shearwaters (up to 19 m, Ronconi et al. 2010a), both species usually perform shallow

dives (great: <10 m; sooty: <30 m; Shaffer et al. 2009, Ronconi et al. 2010a) and were captured typically in <40 m in the study area. Therefore, partitioning the water column seems unlikely. As great and sooty shearwaters can travel several hundred kilometers per day (Shaffer et al. 2009, Ronconi et al. 2010a, Powers et al. 2017), it is possible that one or both species are able to depart and return to the study the area as prey availability fluctuates. In addition, niche partitioning may occur through different prey capture strategies at the same foraging sites, as shown in Chapter 3.

Great and sooty shearwaters expanded their isotopic niches during 2015 and 2016 relative to 2014, which were associated with altered mean isotopic ratios. Although these inter-annual differences in stable isotope ratios may result from shifts in the isotopic baseline of the food web (Solomon et al. 2008), both capelin and the primary alternate prey species (sandlance) showed no or minimal differences in isotopic ratios throughout the three years of this study. This suggests that great and sooty shearwaters consumed a wider range of prey during years when capelin was less available in the area (i.e. 2015, 2016). This is predicted by foraging theory, whereby the absence of preferred prey or limited food resources can lead to individuals incorporating alternative prey into their diet, resulting in niche expansion within a population (Svanback and Bolnick 2007, Ceia et al. 2014). Indeed, switching to more available, abundant and energy-dense prey types within seasons has been reported in other seabird species (Abraham and Sydeman 2006, Ito et al. 2009, Kowalczyk et al. 2015). Similar annual changes in prey availability also were associated with shifts in niche breadth for breeding little penguins (*Eudyptula minor*) and yellow-legged gulls (*Larus michahellis*), whereby niche breadth broadened for both species when a preferred prey type was less available (Ceia et al. 2014, Kowalczyk et al. 2015).

Under limited prey, interspecific competition may cause species to partition their niche (dietary, spatially or temporally). The high degree of isotopic niche overlap between great and

sooty shearwaters and similar shifts in niche breadth during the summer in coastal Newfoundland suggests that, although prey availability varied, it did not become a limiting resource. Future work, however, should examine daily turnover rates and movement patterns of individual shearwaters within and outside of the study area under varying prey availability to test whether individuals depart the study area, thereby spatially segregating their non-breeding habitats, when prey abundance become lower.

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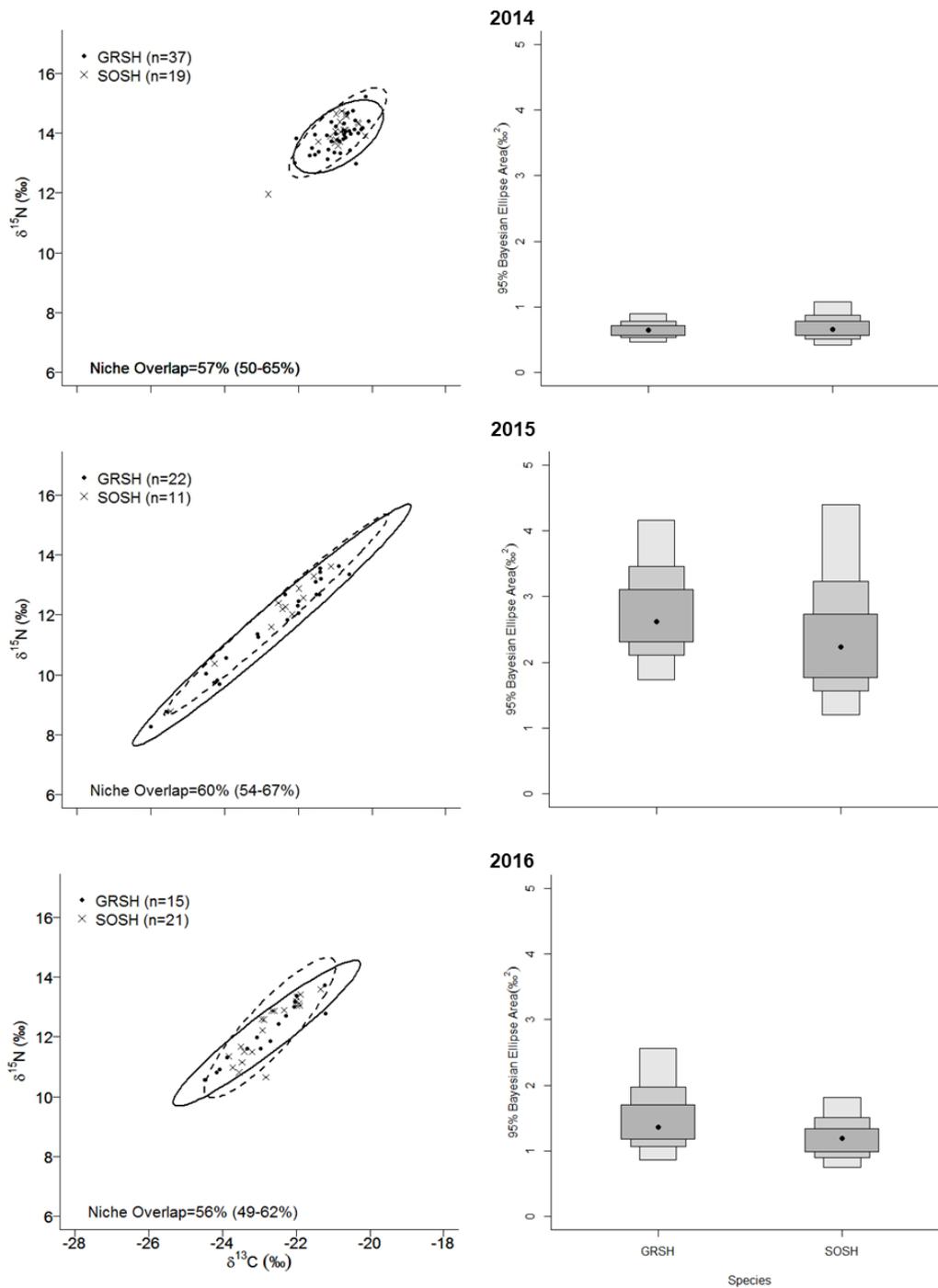
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**Table 2.1** Stable isotope ratios ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , mean  $\pm$  SD) of capelin and sandlance (lipid-extracted muscle tissue) sampled opportunistically in coastal Newfoundland during the summer (2014, 2015 and 2016).

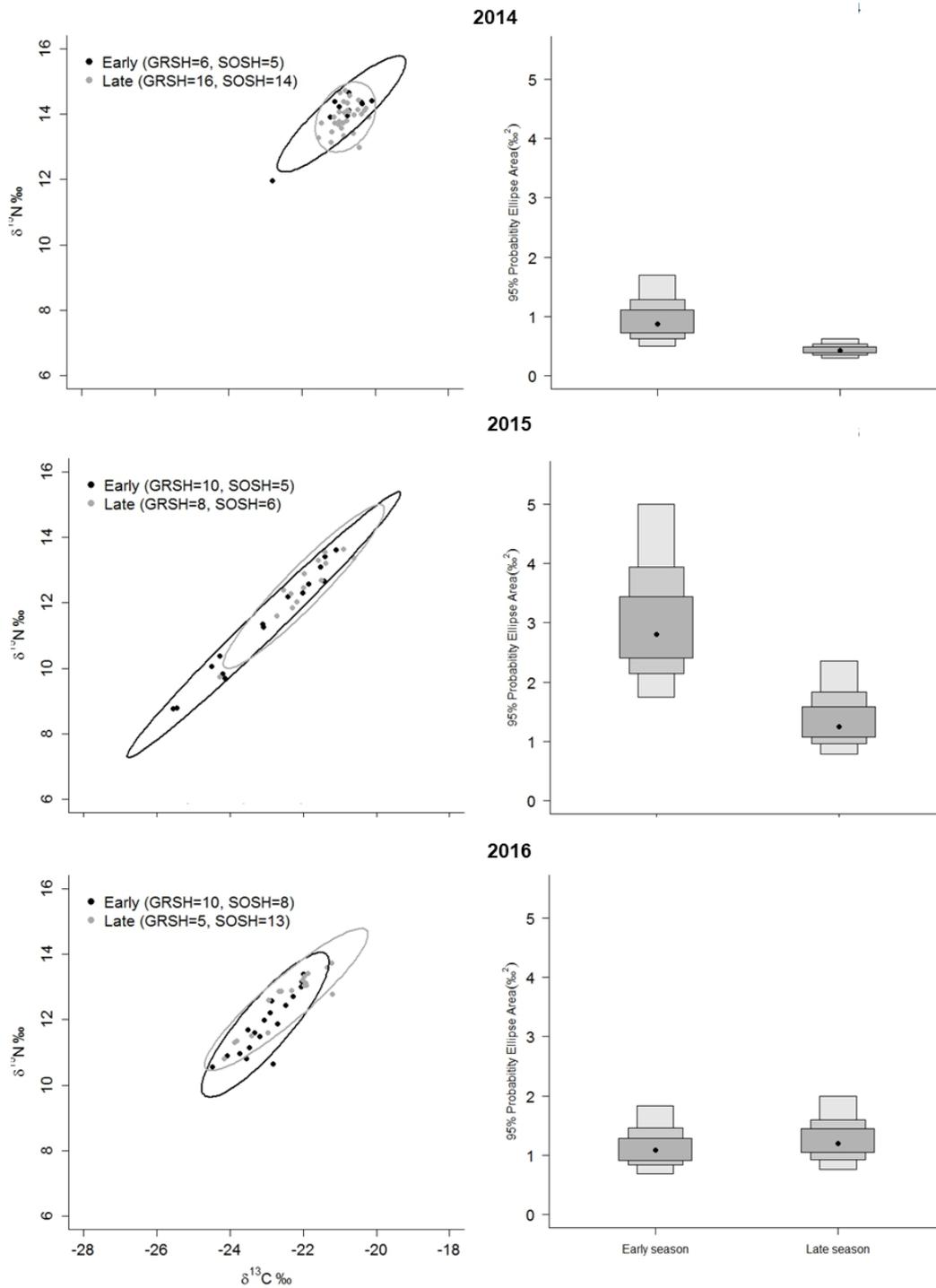
|                  |                           | <b>2014</b>       | <b>2015</b>       | <b>2016</b>       |                             |
|------------------|---------------------------|-------------------|-------------------|-------------------|-----------------------------|
| <b>Capelin</b>   | $\delta^{13}\text{C}$ (‰) | -20.39 $\pm$ 0.50 | -20.17 $\pm$ 0.34 | -20.17 $\pm$ 0.34 | $F_{2,54}=1.66$ , $p=0.20$  |
|                  | $\delta^{15}\text{N}$ (‰) | 12.02 $\pm$ 0.62  | 12.21 $\pm$ 0.42  | 12.21 $\pm$ 0.42  | $F_{2,54}=1.51$ , $p=0.23$  |
| <b>Sandlance</b> | $\delta^{13}\text{C}$ (‰) | -20.86 $\pm$ 0.39 | -20.46 $\pm$ 0.09 | -20.61 $\pm$ 0.42 | $F_{2,16}=4.26$ , $p=0.036$ |
|                  | $\delta^{15}\text{N}$ (‰) | 10.6 $\pm$ 0.31   | 11.17 $\pm$ 0.46  | 10.76 $\pm$ 0.42  | $F_{2,16}=3.90$ , $p=0.045$ |

**Table 2.2** Stable isotope ratio ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , mean  $\pm$  SD) and isotopic niche breadth (mode of Bayesian ellipse areas and 50% credible intervals) from plasma and red blood cells (RBCs) of great shearwaters (GRSH) and sooty shearwaters (SOSH) sampled on the northeast Newfoundland coast during July-August 2014, 2015 and 2016. The statistical results between years (bottom) and species (side) are shown in the table.

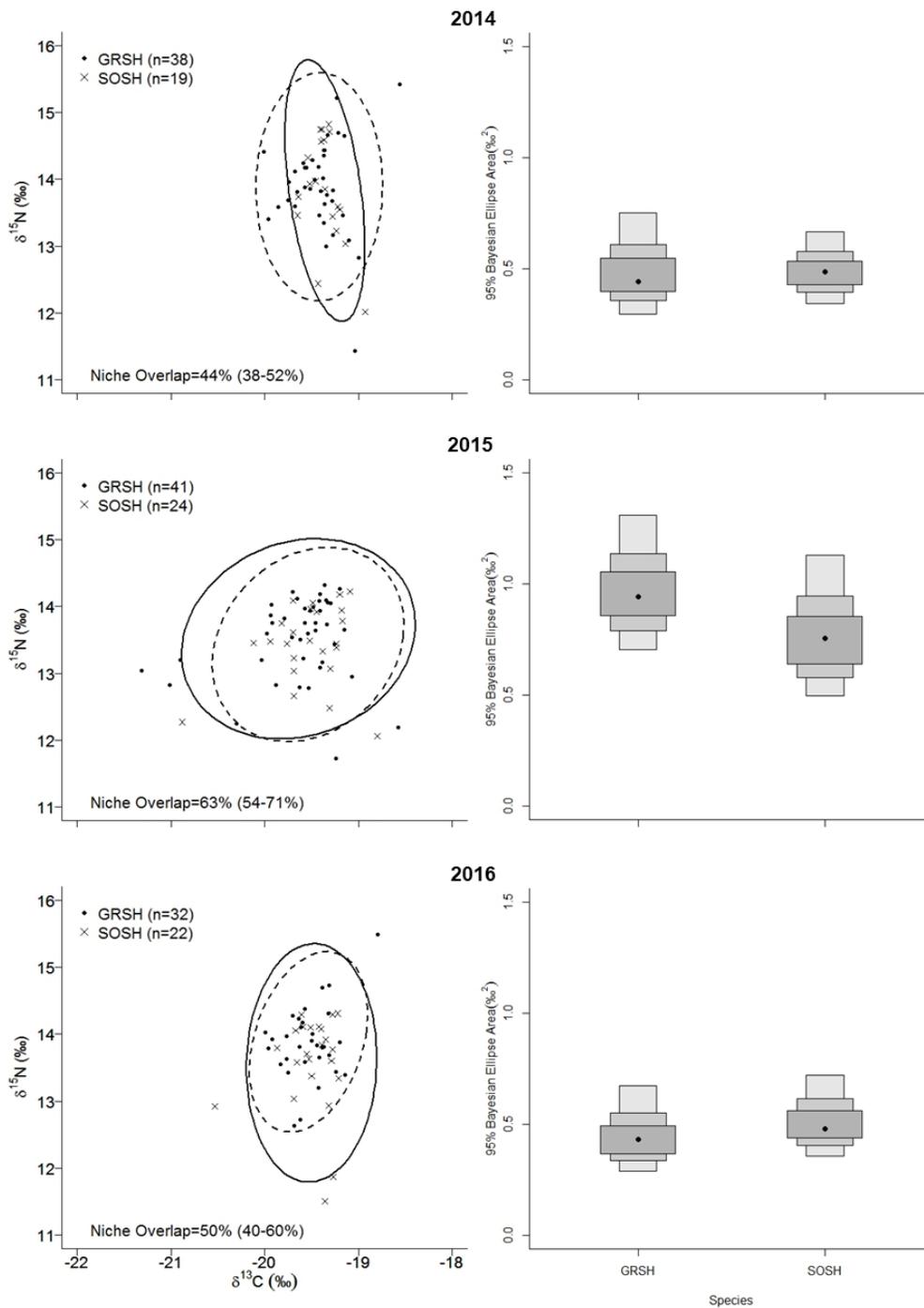
|               |             | $\delta^{13}\text{C}$ (‰) |                            | $\delta^{15}\text{N}$ (‰)  |                            | Niche breadth (‰ <sup>2</sup> ) |                          |                     |                     |
|---------------|-------------|---------------------------|----------------------------|----------------------------|----------------------------|---------------------------------|--------------------------|---------------------|---------------------|
|               |             | GRSH                      | SOSH                       | GRSH                       | SOSH                       | GRSH                            | SOSH                     |                     |                     |
| <b>Plasma</b> | <b>2014</b> | -20.91<br>$\pm 0.50$      | -20.92<br>$\pm 0.54$       | $\chi^2=0.002$<br>p=0.97   | 13.88<br>$\pm 0.50$        | 14.01<br>$\pm 0.61$             | $\chi^2=1.41$<br>p=0.24  | 0.65<br>(0.58-0.72) | 0.66<br>(0.57-0.79) |
|               | <b>2015</b> | -22.71<br>$\pm 1.54$      | -22.59<br>$\pm 1.24$       | $\chi^2=0.04$<br>p=0.83    | 11.66<br>$\pm 1.65$        | 12.00<br>$\pm 1.37$             | $\chi^2=0.09$<br>p=0.76  | 2.57<br>(2.28-3.07) | 2.22<br>(1.78-2.76) |
|               | <b>2016</b> | -22.80<br>$\pm 1.04$      | -22.71<br>$\pm 0.73$       | $\chi^2=0.22$<br>p=0.64    | 12.12<br>$\pm 1.00$        | 12.30<br>$\pm 0.96$             | $\chi^2=0.35$<br>p=0.55  | 1.42<br>(1.20-1.71) | 1.15<br>(1.00-1.33) |
|               |             |                           | $\chi^2=38.99$<br>p<0.0001 | $\chi^2=30.71$<br>p<0.0001 | $\chi^2=44.78$<br>p<0.0001 | $\chi^2=30.07$<br>p<0.0001      |                          |                     |                     |
| <b>RBC</b>    | <b>2014</b> | -19.42<br>$\pm 0.28$      | -19.36<br>$\pm 0.17$       | $\chi^2=0.76$<br>p=0.38    | 13.89<br>$\pm 0.70$        | 13.83<br>$\pm 0.80$             | $\chi^2=0.006$<br>p=0.94 | 0.59<br>(0.53-0.66) | 0.39 (0.33-0.46)    |
|               | <b>2015</b> | -19.64<br>$\pm 0.51$      | -19.54<br>$\pm 0.42$       | $\chi^2=0.69$<br>p=0.41    | 13.52<br>$\pm 0.61$        | 13.43<br>$\pm 0.59$             | $\chi^2=0.52$<br>p=0.47  | 0.95<br>(0.85-1.06) | 0.76<br>(0.66-0.88) |
|               | <b>2016</b> | -19.53<br>$\pm 0.26$      | -19.49<br>$\pm 0.29$       | $\chi^2=1.98$<br>p=0.16    | 13.88<br>$\pm 0.55$        | 13.60<br>$\pm 0.73$             | $\chi^2=1.03$<br>p=0.31  | 0.41<br>(0.33-0.46) | 0.62<br>(0.54-0.72) |
|               |             |                           | $\chi^2=5.80$<br>p=0.05    | $\chi^2=2.69$<br>p=0.26    | $\chi^2=7.38$<br>p=0.03    | $\chi^2=4.00$<br>p=0.14         |                          |                     |                     |



**Figure 2.1** The isotopic biplot of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for great (GRSH) and sooty shearwaters (SOSH) on the left and the Bayesian ellipse areas estimates (isotopic niche breadth) on the right for plasma sampled on eastern Newfoundland coast during 2014-2016. The percent niche overlap (mode and credible intervals) of isotopic niches between species are presented in each panel. On the boxplots (right), the point represents the mode estimates and the boxes indicate the Bayesian credible intervals at 50 % (dark gray), 75 % (medium gray), and 95 % (light gray).



**Figure 2.2** The isotopic biplot of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for great and sooty shearwaters (pooled) on the left and the Bayesian ellipse areas estimates (isotopic niche breadth) on the right for plasma sampled on eastern Newfoundland coast during early and late season in 2014-2016. On the boxplots (right), the point represents the Bayesian mode estimates and the boxes indicate the Bayesian credible intervals at 50 % (dark gray), 75 % (medium gray), and 95 % (light gray).



**Figure 2.3** The isotopic biplot of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for great (GRSH) and sooty shearwaters (SOSH) on the left and the Bayesian ellipse areas estimates (isotopic niche breadth) on the right for RBCs sampled on eastern Newfoundland coast during 2014-2016. The percent niche overlap (mode and credible intervals) of isotopic niches of great and sooty shearwaters are presented in each panel. On the boxplots (right), the point represents the Bayesian mode estimates and the boxes indicate the Bayesian credible intervals at 50 % (dark gray), 75 % (medium gray), and 95 % (light gray).

### **Chapter 3: Procellarids interactions and responses to supplemental food during varying natural prey availability**

#### **Abstract**

Multiple species tend to concentrate in areas with high prey availability and, thus, competition may occur if resources become limited. Competition occurs when individuals directly interact to prevent each other from exploiting resources (interference), or when individuals do not directly interact but respond to a decreased level of a limited resource after exploitation by others (exploitative). In coastal Newfoundland, capelin (*Mallotus villosus*) is the main forage fish, upon which most top predators rely as prey; however, availability varies drastically throughout the summer. We investigated the interactions and responses of non-breeding great and sooty shearwaters (*Ardenna gravis* and *A. grisea*) and northern fulmars (*Fulmarus glacialis*) to supplemental food under this changing prey availability. We conducted an at-sea experiment where supplemental food was offered during higher and lower prey availability. Shearwaters were mainly attracted to the supplemental food offered during the experimental period, while northern fulmars seem to be attracted to the experimental platform during the control period (i.e. before supplemental food offerings). Shearwater numbers were higher when prey availability was lower, but the opposite response was observed for fulmars, suggesting that shearwaters relied less on supplemental food when natural prey availability was higher, while northern fulmars relied on supplemental food regardless of natural prey availability. Overall, my findings suggest that shearwaters will be more reliant on fisheries discards when availability of natural prey decreases, possibly leading to higher by-catch and mortality. This result is particularly important, given current global exploitation rates of important forage fish.

**Key-words:** supplemental food; prey availability; shearwater; fulmar; discard; competition

## Introduction

In the marine environment, areas of high productivity are not uniformly distributed. As a result, mixed-species feeding assemblages of marine predators tend to concentrate in areas where environmental factors are favourable, such as high food availability (Hunt et al. 1999, Worm et al. 2003, Davoren 2013, Lewison et al. 2014). High abundance aggregations of multiple species, however, can lead to interspecific interactions that limit an individual's or a species' access to prey during prey capture (Schoener 1983, Begon et al. 2006). Interspecific competition is traditionally classified as either exploitative or interference competition (Park 1962, Schoener 1983). The former occurs when there are no direct interactions among individuals or species, but availability of a resource decreases through exploitation (Schoener 1983). This type of competition is more likely to occur when resources are scarce and dispersed (Maurer 1984). In contrast, interference competition occurs when individuals directly interfere with each other during prey capture to prevent an individual or a species from exploiting resources (Schoener 1983) and usually occurs when resources are more concentrated (Maurer 1984). One of the most common types of interference competition is encounter competition, which can be observed in the form of aggression among competitors, displacement of competitors, or simply avoidance (Schoener 1983).

As marine predators, seabird foraging behaviour can be influenced by the presence of other competitor species (Paredes et al. 2008, Navarro et al. 2013), in conjunction with prey type, density and distribution (Regular et al. 2010, Garthe et al. 2011). Evidence for interference competition is reported in studies examining mixed-species feeding flocks mainly feeding on natural prey. For instance, Glaucous-winged gulls (*Larus glaucescens*) hindered prey capture by Black-legged kittiwakes (*Rissa tridactyla*) by forming high-density aggregations on the water

directly over prey patches in Alaska (Maniscalco et al. 2001). Similarly, brown noddies (*Anous stolidus*) interfere with roseate terns (*Sterna dougalli*) by obstructing access to prey and reducing feeding attempts (Shealer and Burger 1993). Although some pursuit-diving species (i.e. alcids) can enhance foraging efficiency of other species by forcing tight prey schools to the surface (Hoffman et al. 1981, Grover and Olla 1983, Chilton and Sealy 1987, Camphuysen and Webb 1999), other pursuit-plunging (e.g. shearwaters) and plunge-diving (e.g. gannets) species might disperse and force prey to move further from the surface, thus, reducing the foraging efficiency of non-diving species (Hoffman et al. 1981). Evidence of interference competition has been reported when seabird species aggregate to feed on fisheries discards (Hudson and Furness 1988a, Oro and Ruiz 1997, Arcos and Oro 2002, Bugoni et al. 2010). When feeding on discards, species composition, behaviour and aggressiveness greatly influence seabird feeding success (Garthe and Hüppop 1998), as larger and more aggressive species have been reported to displace and/or steal (kleptoparasitism) discards from smaller and less aggressive species (Jiménez et al. 2011). For instance, smaller seabird species (i.e., northern fulmars *Fulmarus glacialis*, herring gulls *Larus argentatus* and black-legged kittiwakes *Rissa tridactyla*) were displaced by larger species (i.e., great blacked-back gulls *Larus marinus*, great skuas *Stercorarius skua* and northern gannets *Morus bassanus*) when feeding on discards from whitefish trawlers around Shetland (Hudson and Furness 1988b). These interactions, however, can also be influenced by the type of fish remains discarded at sea (i.e. whole fish or offal) and the fishery (i.e. species composition discarded) owing to species-specific prey preferences (González-Zevallos and Yorio 2011).

On the northeast coast of Newfoundland, a small forage fish, capelin (*Mallotus villosus*), is the main natural prey source of most marine predators (Carscadden et al. 2002, Burke and Montevecchi 2008, Davoren 2013). Capelin migrates inshore during the summer to spawn on

beaches and also at deep-water sites (15-40 m; Davoren et al. 2012; Penton and Davoren 2012). Associated with the deep-water spawning sites, breeding and non-breeding seabirds and whales aggregate in high abundances to feed on spawning capelin (Davoren 2013). After spawning, capelin either die (mostly males) or migrate back to offshore areas near the shelf break (Davoren et al. 2006). As such, capelin availability varies substantially throughout the summer, transforming the foraging habitat for seabird predators from lower (i.e. during capelin spawning) into higher food supply (i.e. pre- and post-spawning). In this context, interspecific competition and interactions among species might vary throughout the summer. In addition, historically, the Atlantic cod (*Gadus morhua*) has been the main target species for fisheries during the summer in coastal Newfoundland and the discard of this fishery activity can be used as alternative food source for seabirds in the area, including breeding and non-breeding species. Among the non-breeding seabirds, three species of procellarids are present, including great shearwaters (*Ardenna gravis*), sooty shearwaters (*Ardenna grisea*) and northern fulmars (*Fulmarus glacialis*). Although northern fulmars breed and are resident in the area, most of the individuals observed are moulting flight feathers (primaries), suggesting that they were failed or non-breeders as primary feather moult and breeding do not overlap for fulmars (Allard et al. 2008). In contrast, great and sooty shearwaters are trans-equatorial migrant and are non-breeders during the summer in the North Atlantic (Howell 2010). In general, the three procellarid species appear to similarly concentrate their foraging activity during dawn and dusk (Garthe and Furness 2001, Raymond et al. 2010, Ronconi et al. 2010a). The feeding behaviour of both shearwaters species is similar, whereby they typically feed by surface-seizing, pursuit-plunging and pursuit-diving (Ashmole 1971). Maximum dive depths, however, differ between species, with sooty shearwaters having deeper maximum dive depths (up to 69 m, Shaffer et al. 2009) than great shearwaters (up to 19

m, Ronconi et al. 2010a). Despite this, both species most often perform shallow dives (<10 m; Raymond et al. 2010; Ronconi et al. 2010a). Northern fulmars typically feed by surface-seizing, surface-filtering, scavenging and, to a lesser extent, pursuit-diving (Ashmole 1971). Diving in northern fulmars is rarely observed and reported on a few occasions while feeding on natural prey or discards (Wahl 1984); however, frequent shallow (<1 m) dives with a maximum depth of 2.6 m have been reported for this species (Garthe and Furness 2001). Great shearwater, sooty shearwater and northern fulmar are reported to consume fisheries discards as food resource (Hudson and Furness 1988b, Jackson 1988, Wood 1993, Olmos 1997, Bugoni et al. 2010). When feeding on discards, however, species-specific temperament seems to differ. Great shearwaters are reported to be a bolder species, displacing even larger species by outnumbering other species at resource patches as well as aggressive behaviours (Olmos 1997). Similarly, northern fulmars are reported to displace larger species, but mainly by outnumbering other scavenging species (Camphuysen and Garthe 1997). In contrast, sooty shearwaters have not been reported to displace other species through direct interactions or high numbers while feeding on fisheries discards.

The main objective of this study was to examine fine-scale foraging behaviour and interactions among individuals of three procellariid species (great and sooty shearwaters and northern fulmars) under changing natural prey (capelin) availability during their non-breeding season off the northeast coast of Newfoundland. To do this, we conducted an at-sea experiment, whereby supplemental food was offered during periods of lower and higher capelin availability. We first hypothesized supplement food offerings will influence the response of all three species, regardless of variation in natural capelin availability because all three species use fisheries discard and offal as alternative food source (H1). We predicted that higher numbers of birds of

each species will be observed nearby the experimental platform when supplemental food was offered, relative to the control periods, when supplemental food was not offered. We also hypothesised, however, that variation in capelin availability throughout the summer will influence the responses of each species to supplemental food (H2). For all three species, we predicted that a higher number of birds and a higher proportion of birds on the water relative to flying would be observed nearby the experimental platform when capelin availability was lower in the study area, but that a lower number of birds and a higher proportion of birds flying relative to on the water would be observed when capelin availability was higher. Based on previous studies, we also hypothesized species will influence responses to supplemental food (H3). We predicted that larger and more aggressive species, specifically great shearwaters and northern fulmars, will directly interact with other individuals (i.e. fight) to capture supplemental food items (i.e. interference competition), while the less aggressive and smaller species, sooty shearwaters, will avoid direct interactions with other species.

## **Methods**

The study was conducted on the northeast coast of Newfoundland during July-August of 2015 and 2016. The timing of capelin spawning in the study area can vary up to four weeks (Davoren et al. 2012) and, thus, timing was determined each year by monitoring spawning sites (see Crook et al. 2017). The timing and duration of spawning was used to distinguish between periods of high (i.e. during spawning) and low prey availability (i.e. during pre- and post-spawning). In coastal Newfoundland, Atlantic cod (*Gadus morhua*) is one of the main target species for fisheries during the summer and, thus, Atlantic cod offal (liver) was used as supplemental food in our at-sea experiment. The at-sea experiments were conducted during both

periods (low and high prey availability), with the period of capelin spawning representing lower food supply conditions and pre- and post-spawning periods representing higher food supply conditions within the study area.

The experimental design involved conducting a ‘trial’, whereby one trial was 30 min, which was divided in three 10 minutes periods: pre-control, experimental and post-control. We recorded video throughout each 30 min trial using a GoPro® (Hero 4) camera attached to a pole on one side of the experimental platform (i.e. 5 m open boat) to further quantify behaviour (Fig. 3.1). Prior to each trial, we chose a location within 1-2 km of a cluster of persistent deep-water spawning sites of capelin nearby shearwaters aggregations and the boat motor was turned off to reduce any influence of motor noise on bird behaviour. Weather variables, including sea state, visibility and wind speed and direction, were recorded. These variables did not vary much across, however, as good weather conditions were required to conduct trials. During the pre-control period within a trial, we did not offer supplemental food to quantify the number and species composition of birds that were simply attracted to the boat. During the experimental period within a trial, we offered supplemental food (offal), simulating fisheries, by manually throwing one 30-40 g piece of cod liver ~1-2 m from the boat every 30 s for 10 min (Fig. 3.1). We used cod offal to simulate gutting and cleaning cod at-sea, as traditionally occurred in the study area. After the experimental period within a trial, we conducted a post-control period, where we remained in the same location for another 10 min without providing supplemental food. We conducted up to three trials per day (i.e., trial 1, trial 2 and trial 3) in different locations (~1 km apart).

### *Video and behavioural analysis*

All videos were processed to record species composition and abundances of each species. We focused on species known to respond to fisheries discards in the study area, including procellarids (great shearwaters: GRSH, sooty shearwaters: SOSH and northern fulmar: NOFU) and larids (herring gull, great black-backed gull, and immature gull species). Occasionally other species were also recorded and reported in the results. At the beginning of each video and every 30 s until the end of the 30 min trial, the number of birds on the water of each species within the camera's field of view was counted and recorded. For the procellarids, we also recorded the number of individuals of each species near (< 5 m) and far (> 5 m) from the experimental platform (Fig. 3.1). We also continuously recorded the number of flying procellarids of each species, as well as the number of birds per species that landed on the water, performed a dive (shearwaters) and fought for supplemental food items (experimental period only). When a dive was observed, the duration of the dive was recorded when possible.

### *Data analysis*

Within each 10 min period per trial (i.e. pre- and post-control and experimental period), we quantified two response variables: the maximum number of individuals of each species observed on the water (near and far combined) and the sum of flying birds for each species. During each experimental period, we also calculated the proportion of birds on the water for each species using the maximum number of birds on the water (near and far combined) divided by the total number of birds from the same species recorded during the experimental period (flying and on the water). A high proportion of birds on the water relative to flying was used as a proxy of the level of response, whereby a higher proportion of flying birds represented a lower response to

the supplemental food. We only used the first and second trials for these counts, as individuals tended to follow the boat after the second trial, resulting in much higher numbers of birds during the third trial and, thus, biasing the experimental results.

For each procellariid species, we first tested whether the number of birds on the water and flying separately was higher during the experimental period relative to the control periods (pre- and post-control; H1) to determine if birds were responding to the supplemental food or simply to the experimental platform. To do this, we used non-parametric Wilcoxon tests and post-hoc Steel-Dwass tests for multiple comparisons. Second, we used a generalized linear model to test whether prey (capelin) availability influenced the number of birds of each species during the experimental period (H2). For each species, we ran a model for the birds on the water and another for flying birds as response variables. The fixed predictor variables were year (2015 and 2016), trial (1 and 2) and prey availability (low and high). As the response variables were count data with a high number of zeros (overdispersed data), we used a negative binomial distribution to fit our models. We performed model selection using Akaike Information Criteria (AIC), whereby predictor variables were eliminated sequentially resulting in a model with the lowest AIC, which were then reported in the results. Analyses were performed in R (version 3.4.2) using the *MASS* package (Venables and Ripley, 2002).

Finally, we used the presence and absence of a number of behaviours during the experimental period to examine for different responses of the three species to the supplemental food (H3) using logistic regressions. These behaviours included landing on the water, attempting to capture supplemental food items, diving and proximity to the experimental platform. A higher presence of landing on the water by a species was used as a proxy of the level of response, whereby more birds landing on the water represented a higher response to the supplemental food.

In addition, the higher presence of attempts to consume, involving a scramble (or ‘fight’) among multiple individuals for the supplemental food items, was used as a proxy of boldness, whereby a higher presence of attempts represented a more bold species. In contrast, a higher presence of diving behaviour (shearwaters only), presumably to capture sinking food items solitarily rather than fighting with other individuals to capture items at the surface, was used as a proxy of avoidance of other species, whereby a higher presence of diving represented a higher level of displacement or avoidance of other species. In addition, proximity to the experimental platform (i.e. near and far) for birds on the water was used as a proxy of the level of response by each individuals/species to the supplemental food and also as a proxy of boldness, whereby a higher presence of birds residing in the area near the experimental platform represented a higher response to the supplemental food and bolder behaviour. The fixed predictor variables for the logistic regressions for each behaviour were species (great shearwater, sooty shearwater and northern fulmar) and prey availability (low and high). When significant differences were observed ( $p < 0.05$ ) in the logistic regressions, odd ratios were computed to determine the magnitude of the effect on the seabird behavioural responses (land on the water, attempt to consume food item, proximity to experimental platform).

## **Results**

Over all trials, the total number of birds observed on the water consisted of 71.2% gull species (56% herring gull, 5.2% great blacked-back gull, 10% immatures from both species), 16.8% great shearwaters, 9.0% northern fulmars and 2.3% sooty shearwaters. Species sighted occasionally (i.e.  $< 5$  individuals over all trials) flying or on the water during the experiment were common tern (*Sterna hirundo*), Pomarine jaeger (*Stercorarius pomarinus*) and Manx shearwater

(*Puffinus puffinus*). Other species common in the area observed flying by (i.e. typically did not land) during the experiment were common murre (*Uria aalge*), razorbills (*Alca torda*), and northern gannets (*Morus bassanus*).

Owing to our focus on the procellarids, trials in which procellarid species were not observed were deleted from the analysis (n=3). During 2015, trials were conducted August 2-14 (n=13), with four trials during high capelin availability (Aug 8, 9) and nine during low capelin availability (Aug 2-3, Aug 11-18). During 2016, trials were conducted July 16-August 17 (n=12), with six trials during high capelin availability (Jul 25-Aug 4) and six conducted during low capelin availability (Jul 16, Aug 12-17). In total, 438 food items (i.e. pieces of cod liver) were offered during experimental periods in 2015 and 2016 during low (n=229) and high (n=209) capelin availability.

The capture success of food items varied across species and between capelin availability periods (Fig. 3.2). During low prey availability, 6% of the food items offered were not consumed (i.e. 'ignored'), whereas 26% were not consumed during high prey availability (Fig. 3.2). The majority of food items was consumed by gull species, including herring gull, great blacked-back gull and immature gulls of both species, during both prey availability periods, followed by northern fulmars and great shearwaters, while sooty shearwaters only consumed cod liver once during low prey availability (Fig. 3.2).

The mean number of birds (all species, including gulls species) on the water and flying were higher during the experimental period (i.e. when cod liver was offered) than during the pre-control period (water:  $Z=3.19$ ,  $p=0.004$ ; flying:  $Z=4.51$ ,  $p<0.001$ ), but did not differ from the post-control period (H1; water:  $Z=-0.34$   $p=0.94$ ; flying:  $Z= -1.81$ ,  $p=0.17$ ). Each species responded similarly to supplemental food, with significantly higher numbers of great shearwaters

(flying and on the water) and sooty shearwaters (flying) during the experimental period relative to the pre-control (GRSH flying:  $Z=4.52$ ,  $p<0.0001$ ; GRSH water:  $Z=3.58$ ,  $p=0.001$ ; SOSH flying:  $Z=4.17$ ,  $p<0.0001$ ), but not relative to the post-control (GRSH flying:  $Z=-1.74$ ,  $p=0.19$ ; GRSH water:  $Z=-1.59$ ,  $p=0.25$ ; SOSH flying:  $Z=-2.25$ ,  $p=0.06$ ; Fig. 3.3). A similar trend was observed for northern fulmars (flying and on the water) and sooty shearwaters (on the water), but the numbers of birds did not differ significantly between the experimental period and both the pre-control (NOFU water:  $Z=1.60$ ,  $p=0.25$ ; SOSH water:  $Z=1.60$ ,  $p=0.25$ ; NOFU flying:  $Z=1.81$ ,  $p=0.17$ ) and the post-control periods (NOFU water:  $Z=0.09$ ,  $p=0.99$ ; SOSH water:  $Z=0.09$ ,  $p=0.99$ ; NOFU flying:  $Z=-0.41$ ,  $p=0.91$ ; Fig. 3.3).

We used only the experimental period to test species responses to the supplemental food under varying prey availability (H2). For great shearwaters, the number of birds on the water was mainly explained by prey availability, being higher when prey availability was low (Fig. 3.4a, Table 3.1). Although flying birds showed a similar trend (Fig. 3.5a), the number of flying birds was not significantly explained by prey availability (Table 3.1). For sooty shearwaters, the number of birds flying was mainly explained by prey availability (Table 3.1), with higher number of individuals flying when prey availability was low (Fig. 3.5b). Similarly, the number of sooty shearwaters on the water was higher when prey availability was low (Fig. 3.4b), but this was not significant (Table 3.1). Interestingly, the mean number of great and sooty shearwaters on the water and flying reached a peak earlier in the experimental period (~14-16 min) during low prey availability compared to high prey availability (peak ~17-19 min; Fig 4ab, 5ab). For northern fulmars, the number of birds on the water was explained by prey availability, year and trial. These patterns showed an opposite trend to the shearwaters, being higher during high prey availability, but also higher during 2015 relative to 2016 and during the second relative to the

first trial (Table 3.1; Fig 3.4c). Interestingly, the number of flying fulmars was not explained by prey availability, but was higher during 2015 relative to 2016 and during the second relative to the first trial (Table 3.1; Fig 3.5c).

During the experimental period, great shearwaters were 5.9 times (CI=1.2-29.8;  $p=0.03$ ) more likely to land on the water than sooty shearwaters, but the likelihood of northern fulmars landing did not differ from great shearwaters ( $p=0.35$ ) or sooty shearwaters ( $p=0.19$ ). Out of all great shearwaters and northern fulmars observed during the experimental period, 18% and 11%, respectively, were recorded on the water with the rest flying. In contrast, out of all the sooty shearwaters observed during the experimental period, only 2.8% were observed on the water. In addition, during low prey availability, all three species combined were 6.3 times (CI= 1.6-24.6;  $p=0.008$ ) more likely to land on the water than during high prey availability. In support, 26% ( $\pm 7.0$ ) of the great shearwaters were observed on the water during low prey availability, but only 8% ( $\pm 2.5$ ) during high prey availability. For northern fulmars, 37% ( $\pm 15.1$ ) were observed on the water during low and 28% ( $\pm 8.2$ ) during high prey availability. Sooty shearwaters followed the same trend, but with lower numbers on the water during low ( $3.3 \pm 1.6\%$ ) and high ( $2.6 \pm 1.5\%$ ) prey availability.

When on the water, logistic regression revealed that great shearwaters were 28.5 times (CI=5.6-145.4;  $p<0.0001$ ) more likely to occur close to the experimental platform (i.e.  $<5$  m; often  $< 2$  m away) than sooty shearwaters. Indeed, 97.0% of great shearwaters on the water were observed near the experimental platform, while 53.6% of the sooty shearwaters on the water remained far (i.e.  $>5$  m). Northern fulmars were also more likely to occur (8.2 times; CI=1.8-37.9;  $p=0.007$ ) closer to the experimental platform ( $<5$  m) than sooty shearwaters, but did not differ from great shearwaters ( $p=0.09$ ). For all species combined, the proximity to the

experimental platform did not vary between low and high prey availability ( $p=0.36$ ). Great shearwaters were 47.4 times (CI=7.5-298.6;  $p<0.0001$ ) more likely to fight over food items than sooty shearwaters, while northern fulmars were 17.8 times (CI=3.0-104.1,  $p=0.001$ ) more likely to fight over food items than sooty shearwaters, but did not differ from great shearwaters ( $p=0.18$ ). Indeed, when present, one or more great shearwaters attempted to catch and consume a food item 91.1% of the times cold liver was thrown during the experimental period, and were successful in 26.0% of these attempts. During 68.6% of the experimental periods when fulmars were present on the water, one or more fulmars attempted to catch the food item, and were successful 66.8% of the attempts. Interestingly, fulmars did not always try to consume the cod liver, even when they were the only species present during a trial. In contrast, sooty shearwaters only attempted to catch and consume a food item 27.4% of the times experimental discards were thrown (mostly one individual, during one trial) when present on the water, during which sooty shearwaters were successful only once (4.3%).

Although sooty shearwaters were not significantly more likely to dive than great shearwaters ( $\chi^2=0.30$ ,  $p=0.58$ ), sooty shearwaters tended to dive more often (40% of the trials) than great shearwaters (22% of the trials). Sooty shearwaters also had significantly longer dive durations ( $7.0 \pm 5.3$  s) than great shearwaters ( $2.2 \pm 1.5$  s;  $Z=5.18$   $p<0.001$ ). When diving, sooty shearwaters often traveled underneath the birds fighting for the food item (i.e. hatched circle in Fig. 3.1), possibly attempting to catch any sinking pieces. Indeed, we often saw individuals of sooty shearwaters coming to the surface and diving again. In addition, sooty shearwaters did not stay longer than ~30 s after landing on the water and often dove immediately upon landing on the water and took off flying immediately upon surfacing. Dive behaviour for northern fulmars was not observed during the trials or in the study area.

Interestingly, although kleptoparasitism is commonly observed among seabird species in mixed-species assemblages, only three events were observed during the trials. In two cases, a herring gull stole a food item from a northern fulmar and from a great shearwater, while during the other event, a great shearwater stole the cod liver from a northern fulmar.

## **Discussion**

Shearwater species were attracted to the supplemental food, with higher numbers of birds during the experimental period relative to the pre-control period, as predicted. This result is not surprising, as the use of discards and offal by procellariids as the main or alternative food resource has been observed worldwide in different types of fisheries (Navarro et al. 2009, Bugoni et al. 2010). In contrast, the number of fulmars associated with the experimental platform was similar during the experimental and control periods, suggesting that fulmars were attracted to the experimental platform throughout the trial. The number of shearwaters attracted to the supplemental food during the experimental period varied with natural prey availability, with higher numbers of birds attracted to the experimental platform during low relative to high prey availability for great (birds on water) and sooty shearwaters (flying birds), again as predicted. Interestingly, fulmars showed the opposite trend. This suggests that when natural prey was abundant in the area (during spawning), other food resources, such as discards and offal, were less important to obtain energy for shearwaters but not for fulmars. Finally, species differed in their responses to the supplemental food when present at the experimental platform, with great shearwaters and northern fulmars, the larger more aggressive species, directly fighting over supplemental food items during capture, while sooty shearwaters, the less aggressive and smaller species, did not, possibly to avoid direct interactions with other species during prey capture.

These species-specific responses to supplemental food under varying prey availability highlight possible mechanisms underlying variation in discard and offal use among procellarids in different regions and times of year.

In contrast to shearwaters, fulmars appeared to be attracted to the experimental platform more than the supplemental food, suggesting that fulmars rely on alternative food sources (fisheries discards and offal) regardless of natural prey availability in the area. Further evidence for high reliance on offal was that fulmars tended to follow and stay close to the experimental platform, as evidenced by the second trial per day having a higher number of fulmars, while shearwater species did not. In support, northern fulmars are known to be more commonly present at seabird feeding assemblages associated with fishing vessels than with natural prey (Camphuysen and Webb 1999). This high reliance on discards may be related to the minimal dive capacity of fulmars relative to the shearwaters in the study area (Garthe and Furness 2001), which presumably reduces their ability to capture natural prey such as capelin. Fulmars also differed in their response to capelin availability relative to shearwaters, with higher numbers of birds (on water) during high relative to low capelin availability. This further suggests that fulmar foraging behaviour is not tightly linked to capelin availability, but rather that they may be responding to lower numbers of other seabird species at the experimental platform during high capelin availability. In support, fulmars were highly successful in consuming discards from trawlers in the North Sea when they outnumbered other scavenger species, but foraging success declined when the relative abundance of other species was higher (Camphuysen and Garthe 1997, Garthe and Hüppop 1998 Maynard 2018). Among the procellarids in the study area, fulmars had lower relative abundances compared to other species during the experiment, as they are generally present in lower numbers in the study area during the summer (Davoren 2013).

In contrast to fulmars, shearwaters were attracted to the supplemental food (i.e. experimental period). Indeed, discards may be an important source of energy when natural prey availability varies, as evidenced by the high number of shearwaters associated with the experimental period relative to the control period as well as during low relative to high prey availability. In the study area, capelin is usually highly accessible to most sub-surface predators, as high abundance aggregations form in shallow areas (<40 m) to spawn (Davoren et al. 2008). Therefore, the use of alternative food resources, such as fishery discards or offal, may not be exploited to a high degree during these periods. On the other hand, when capelin availability is low, shearwaters might use other methods to find prey, such as cueing to the foraging activities of other seabirds (local enhancement; Thiebault et al. 2014, Bairos-Novak et al. 2015). In support, the number of shearwaters had a higher peak and peaked earlier in the experimental period during low compared to high capelin availability, suggesting that more birds took less time to cue to the supplemental food when capelin availability was low in the study area. Indeed, searching for patches of natural prey during low capelin availability may result in high energy expenditure, which may be minimized by cueing to fisheries activities. Indeed, shifting between natural prey and discards or offal under varying prey availability has been shown in other shearwater species (Navarro et al. 2009). Balearic shearwaters *Puffinus mauretanicus*, shifted their diet through the breeding season from demersal fish derived from trawling discards to mainly feed on pelagic fish (anchovies) as the abundance of this natural prey varied along with energy requirements over the breeding season (Navarro et al. 2009).

When present at the experimental platform, great shearwaters and northern fulmars appeared to display a higher response to the supplemental food than sooty shearwaters. This higher response was illustrated by the higher numbers of individuals on the water (relative to

flying), primarily occupying the area closer (<5 m) to the experimental platform, as well as a higher proportion of attempts to capture supplemental food items, resulting in direct interactions primarily with larger gull species. Indeed, great shearwaters tried to consume supplemental food items the majority of the times when present, suggesting that they are not intimidated by larger species, such as herring and great black-backed gulls. This bold behaviour of great shearwaters has been observed in other studies. For instance, great shearwater is a common species associated with longline fishing vessels off the Brazilian coast (Olmos 1997) and has been reported to approach larger species (e.g. albatross species) by lunging at them and, in a few occasions, stole food from Pomarine jaegers (Olmos 1997). Although great shearwaters and northern fulmars were similarly likely to fight over supplemental food items, fulmars attempted less but successfully consumed more cod liver. This suggests that fulmars may be less bold than great shearwaters. This is corroborated by the lack of fulmars displaying aggressive behaviour, while one of the three kleptoparasitism events observed was by a great shearwater towards a northern fulmar. In general, a lower number of kleptoparasitism events was observed in this study relative to others (Hudson and Furness 1988a, Camphuysen and Garthe 1997, Garthe and Hüppop 1998, González-Zevallos and Yorio 2011). This difference may be related to the characteristics of the supplemental prey (Camphuysen and Garthe 1997), whereby more kleptoparasitic events were observed with larger prey discarded (e.g. whole fish; Hudson and Furness 1988a, González-Zevallos and Yorio 2011), as individuals will usually take longer to manipulate larger prey before swallowing them. In contrast, the small, soft food items offered in this study were easily and quickly swallowed. Overall, the more bold tendencies of fulmars and great shearwaters result in their close proximity approaches to boats and, thus, are often captured at-sea (Bugoni et al. 2008, Carvalho unpublished, Ronconi et al. 2010b, Wakefield unpublished).

In contrast to great shearwaters and fulmars, sooty shearwaters are often displaced (i.e. observed farther from boats) by other seabird species and, thus, harder to catch at-sea (Bugoni et al. 2008b, Ronconi et al. 2010b). Indeed, sooty shearwaters displayed a lower response to the supplemental food, illustrated by the higher proportion of birds flying relative to on the water, occupying the area farther (>5 m) from the experimental platform and avoiding direct interactions with other birds, primarily by diving to capture supplemental food items. These behavioural tendencies to stay farther from the boat and dive more frequently to capture discards have been documented in other studies (Bugoni et al. 2008, Ronconi et al. 2010b). Although sooty shearwaters seem to use fisheries discards and offal as an important food resource, their distribution on the Northwest Pacific was more likely associated with natural prey, such as euphasiids and anchovies, than fishing vessels (Wahl and Heinemann 1979). Sooty shearwaters may avoid direct interactions with other species by diving underwater to capture discards. For instance, diving was observed for sooty shearwaters feeding on sinking discards from trawlers in Patagonia (Yorio and Caille 1999). Similarly, other shearwater species (Balearic shearwater) have been observed to dive to capture discards, presumably to reduce interactions with other seabird species (Arcos and Oro 2002). Interestingly, dive durations of other procellariids (*Procellaria sp.*) while feeding on discards averaged 8 s (Olmos 1997), similar to sooty shearwaters in our study. In the present study, the food item (cod liver) offered usually floated on the water (i.e. did not sink) due to its high lipid content, thereby minimizing the capture success of diving sooty shearwaters. In other circumstances, however, sooty shearwaters might have higher success by diving, such as when food items sink (e.g. dead fish), especially when associated with other seabird species with limited or no dive capacity, such as gull species, albatrosses and fulmars. When feeding on natural prey in other regions, sooty shearwaters have

been identified as a more competitive species. For instance, sooty shearwaters were classified as a suppressor species in mixed-species seabird flocks in Alaska when feeding on natural prey, whereby their feeding behaviour by pursuit-diving in groups dispersed the prey and compromised the feeding success of other seabirds (Hoffman et al. 1981). In addition, sooty shearwaters were reported to interfere with the foraging behaviour of surface-feeding Antarctic terns by blocking their access to prey due to their higher numbers on the ocean surface above prey aggregations (Sagar and Sagar 1989). Differences in the competitive nature of sooty shearwaters among studies might be related to variation in prey types (e.g., natural, discards) or prey behaviour (e.g., schooling, dispersed), species composition and relative abundance in mixed-species assemblages.

In conclusion, the attraction and use of fisheries discards and offal as food resources may be important to reduce energy expenditure by procellariid species during the non-breeding season when searching for patches of natural prey that are in low abundance. Although this may be beneficial, attraction to fishing vessels also results in a high mortality through by-catch of seabird species, especially procellariids, in different fisheries, especially long line fisheries, and has become one of the major concerns regarding seabird conservation (Lewison and Crowder 2003, Croxall et al. 2012). Additionally, natural prey of these species, primarily forage fish, currently comprise 37% of the global fish catch (Pikitch et al. 2012). As we continue to overexploit forage fish species, reducing their availability for marine predators, seabird species will rely more on fisheries discards and offal as main food resources, which may in turn increase their chances of by-catch mortality. Findings suggest, however, that species-specific responses to discards by procellariids under varying prey availability, as well as seabird species composition

and relative abundance, will result in varied and episodic by-catch mortality in certain regions and times of year.

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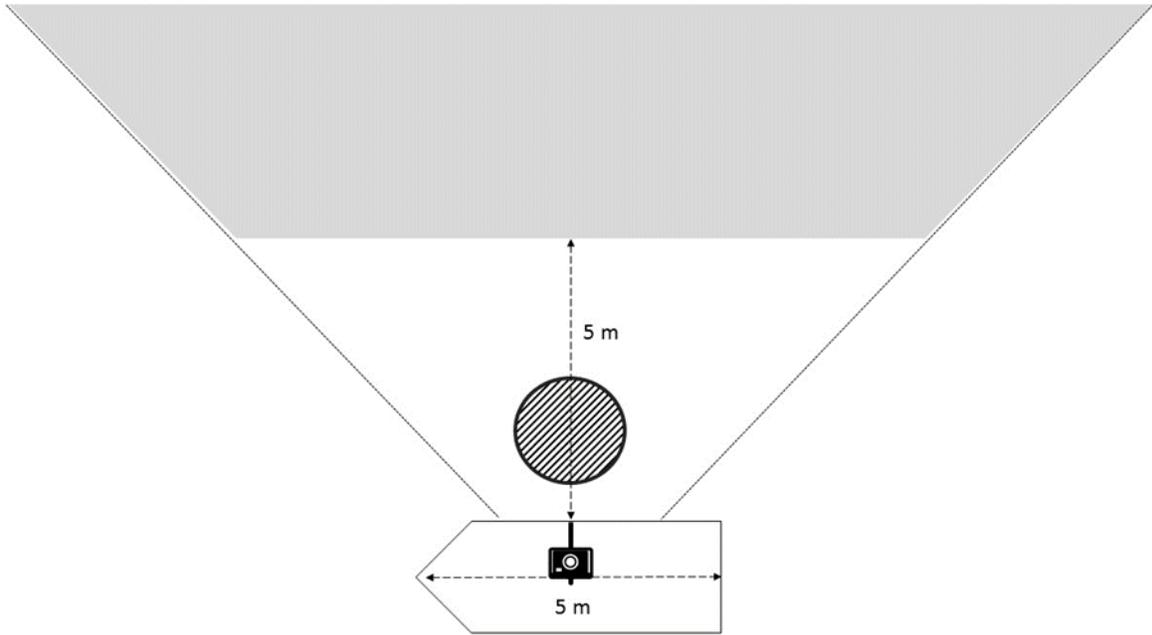
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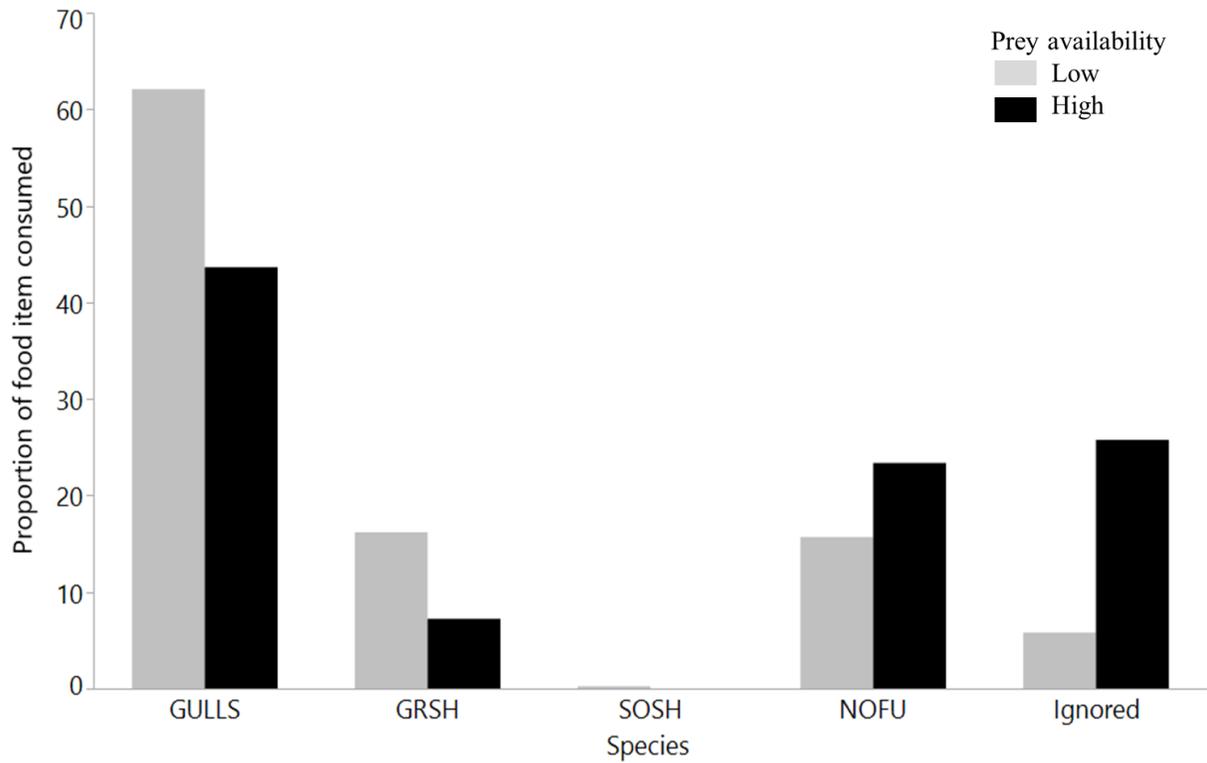
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**Table 3.1** Reduced negative binomial generalized linear models (GLM) for great and sooty shearwaters and northern fulmar flying and on the water recorded during experimental period. Coefficients for each factor ('prey' refers to high and low capelin availability periods; 'trials' refers to the first or second trial conducted in each day; 'year' is the year the trials were conducted), Z test and its p-value are shown in the table.

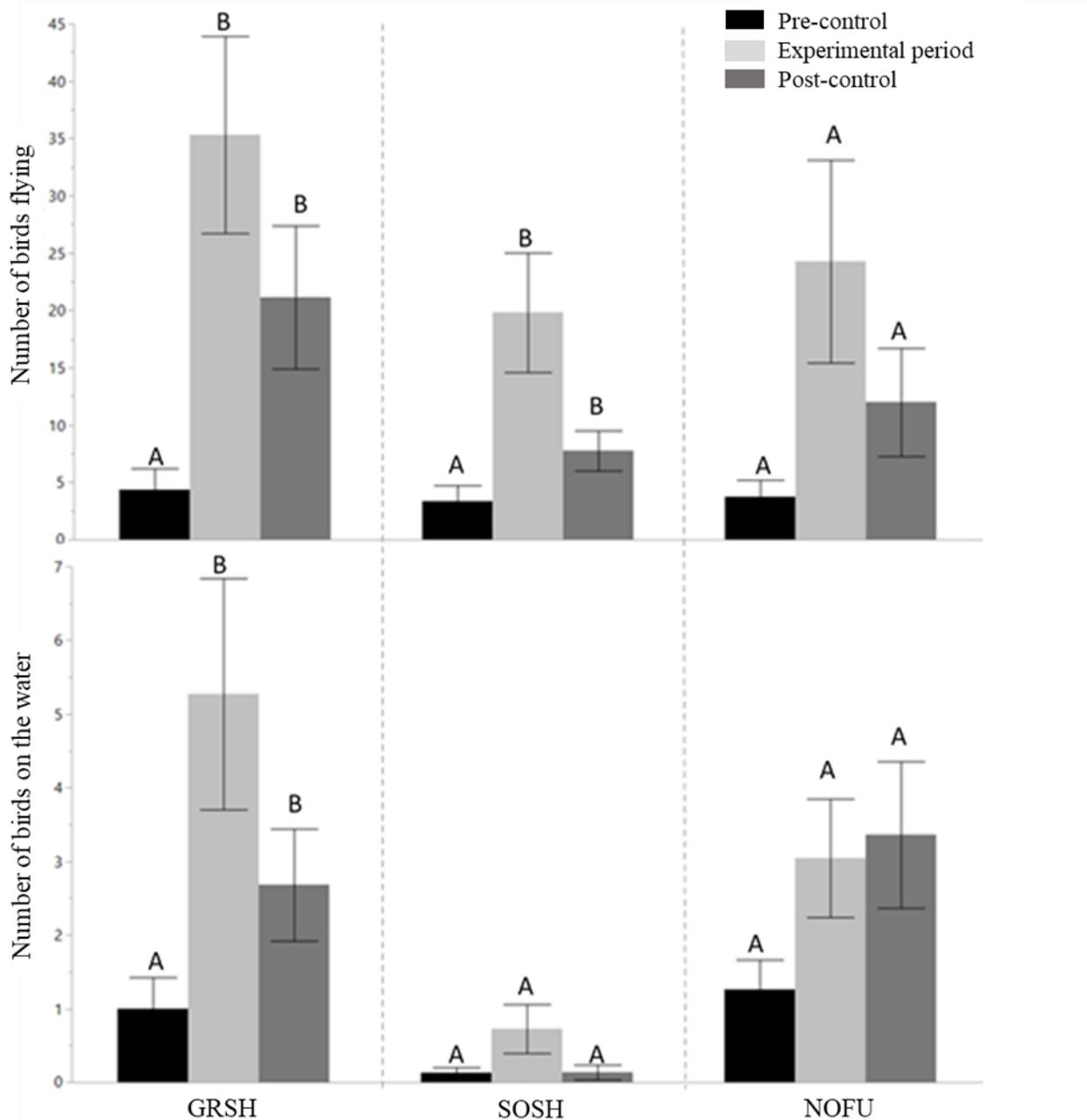
|                 | <b>Factor</b> | <b>Estimate</b> | <b>SE</b> | <b>Z</b> | <b>p</b>         |
|-----------------|---------------|-----------------|-----------|----------|------------------|
| <b>GRSH</b>     |               |                 |           |          |                  |
| <b>Flying</b>   | Intercept     | 3.26            | 0.45      | 7.24     | <b>&lt;0.001</b> |
|                 | Prey          | 0.72            | 0.42      | 1.71     | 0.09             |
| <b>On water</b> | Intercept     | 0.88            | 0.34      | 2.52     | <b>0.01</b>      |
|                 | Prey          | 1.15            | 0.43      | 2.70     | <b>0.007</b>     |
| <b>SOSH</b>     |               |                 |           |          |                  |
| <b>Flying</b>   | Intercept     | 2.40            | 0.31      | 7.69     | <b>&lt;0.001</b> |
|                 | Prey          | 0.89            | 0.42      | 2.13     | <b>0.03</b>      |
| <b>On water</b> | Intercept     | -2.00           | 0.85      | -2.36    | <b>0.02</b>      |
|                 | Trial         | 1.16            | 0.69      | 1.68     | 0.09             |
|                 | Prey          | 1.46            | 0.78      | 1.86     | 0.06             |
| <b>NOFU</b>     |               |                 |           |          |                  |
| <b>Flying</b>   | Intercept     | 3.09            | 0.67      | 4.63     | <b>&lt;0.001</b> |
|                 | Trial         | 1.59            | 0.80      | 1.98     | <b>0.05</b>      |
|                 | Year          | -2.62           | 0.81      | -3.23    | <b>0.001</b>     |
| <b>On water</b> | Intercept     | 0.64            | 0.54      | 1.19     | 0.23             |
|                 | Trial         | 1.97            | 0.53      | 3.73     | <b>&lt;0.001</b> |
|                 | Year          | -1.19           | 0.50      | -2.40    | <b>0.02</b>      |
|                 | Prey          | -1.14           | 0.49      | -2.33    | <b>0.02</b>      |



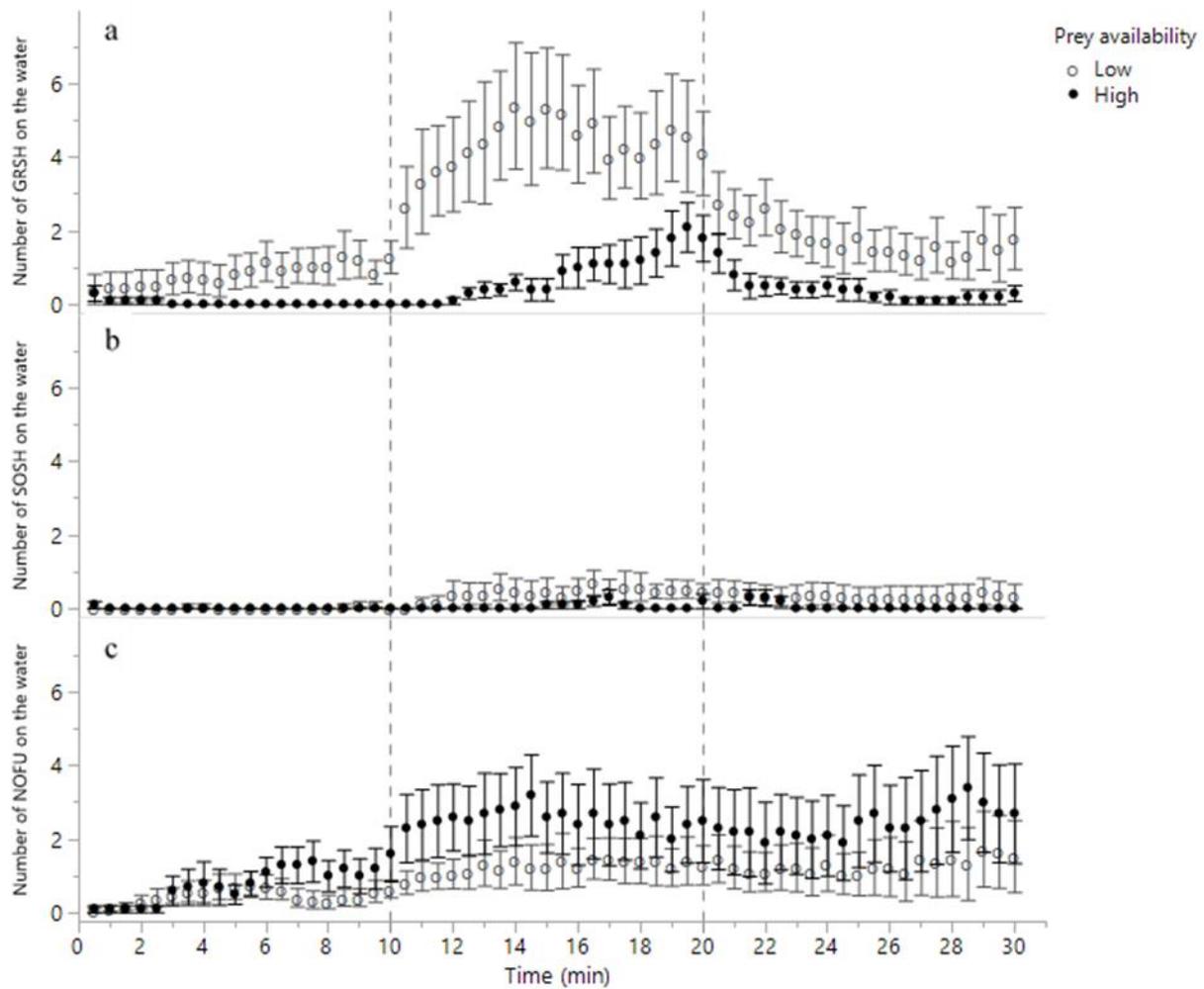
**Figure 3.1** Experimental design showing the near (<5 m from the boat; white area) and the far area (>5 m from the boat; shaded area) where birds were counted on the water. The hatched circle represents the area where the discards were thrown during the experimental period (1-2 m from the boat). The camera (GoPro® Hero 4) was attached to a pole usually in the right side of the boat.



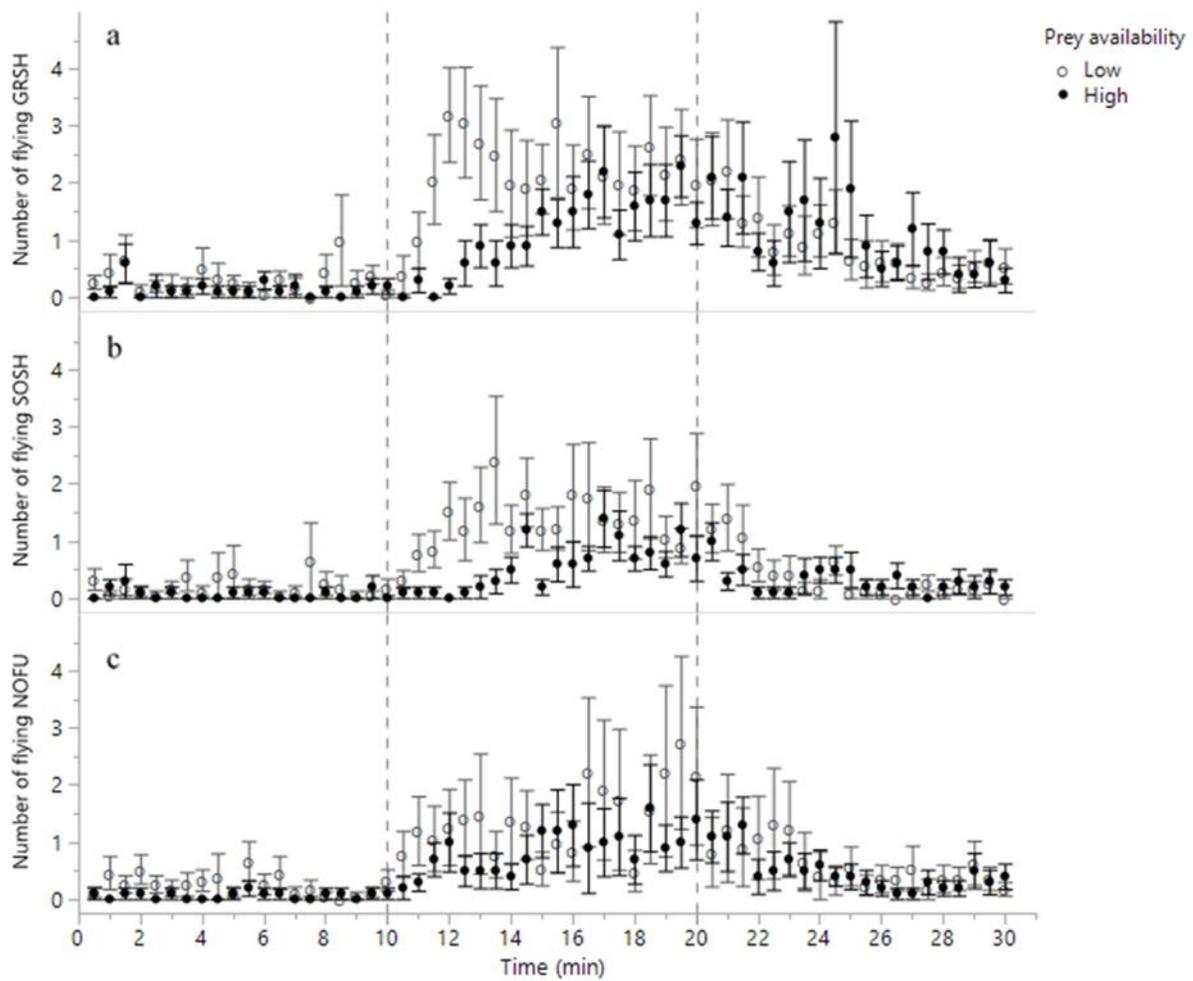
**Figure 3.2** Percentage of supplemental food items (cod liver) consumed by gulls (i.e. herring gull, great blacked-back gull and immatures of both species), great shearwaters (GRSH), sooty shearwaters (SOSH), northern fulmars (NOFU) or ignored during experimental periods conducted during low (gray) and high (black) prey availability in coastal Newfoundland during July-August of 2015 and 2016.



**Figure 3.3** Mean ( $\pm$  SE) numbers of birds flying (top) and on the water (bottom) during pre-control (black), experimental (light gray) and post-control (dark gray) periods for great shearwater (GRSH), sooty shearwaters (SOSH) and northern fulmars (NOFU) during July-August 2015-2016 on the northeast Newfoundland coast. Note the different y-axis scales on the top and bottom graphs.



**Figure 3.4** Mean ( $\pm$ SE) number of birds on the water every 30 s during the 30 min trial for great shearwater (a, GRSH), sooty shearwater (b, SOSH) and northern fulmar (c, NOFU) during low (open circle) and high (closed circle) prey availability during July-August 2015-2016 on the northeast Newfoundland coast. Dashed lines separate the pre-control (0-10 min), experimental (10-20 min) and post-control (20-30 min) periods (n=13).



**Figure 3.5** Mean ( $\pm$ SE) number of flying birds in 30 s intervals during the 30 min trials for great shearwater (a, GRSH), sooty shearwater (b, SOSH) and northern fulmar (c, NOFU) during low (open circle) and high (closed circle) prey availability during July-August 2015-2016 on the northeast Newfoundland coast. Dashed lines separate the pre-control (0-10 min), experimental (10-20 min) and post-control (20-30 min) periods (n=13)

## Chapter 4: Moulting chronology and strategies of sympatric great and sooty shearwaters

### Abstract

Moulting is energetically demanding, during which flight may be compromised and foraging ranges may become constrained. During non-breeding, great (*Ardenna gravis*) and sooty shearwaters (*A. grisea*) migrate from South Atlantic breeding colonies to aggregate at North Atlantic feeding grounds. We investigated whether both shearwaters used coastal Newfoundland as a moulting area and used stable isotope ratios ( $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ ) of primary feathers (P1, P5, P10) to identify moulting location/diet for both species. Moulting scores indicated that both species finished their moulting in coastal Newfoundland, which was further corroborated with similar stable isotope ratios for great ( $\delta^{15}\text{N}=15.17 \pm 1.13 \text{‰}$ ;  $\delta^{13}\text{C}=-18.66 \pm 0.54 \text{‰}$ ) and sooty shearwaters ( $15.54 \pm 0.74 \text{‰}$ ;  $-18.43 \pm 0.78 \text{‰}$ ); however, sooty shearwater moulting was more advanced relative to great shearwater. In contrast, P1 and P5 isotopic ratios (grown before arriving in coastal Newfoundland) differed between and within species, suggesting divergent locations/diet used for early moulting. For great shearwaters, P1/P5 isotopic ratios were more variable (broader niche breadth) than P10, suggesting that some individuals start moulting in the South Atlantic and others in the North Atlantic. Sooty shearwaters had two distinct groupings of isotopic ratios in P1/P5, with one group feeding at lower trophic levels (lower  $\delta^{15}\text{N}$ ) relative to the other. These findings illustrate distinct locations or diets at the start of moulting, both within and between species, but diets converged when aggregated together at the end of moulting. More importantly, we determined the location of an important moulting area for sooty shearwaters in coastal Newfoundland, opposed to previous studies that suggested moulting was completed offshore.

**Key-words:** moulting; stable isotope; feathers; primaries; shearwaters; *Ardenna*

## Introduction

Moult is an important part of the annual cycle of bird species and does not usually overlap with breeding periods because both are energetically demanding activities (Lindström 1993, Howell 2010). As such, the most 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 time of breeding and migration (Langston and Rohwer 1996; Bridge 2006; Rohwer 2009). Indeed, the ‘winter moult’ (i.e. moult on the non-breeding grounds) for trans-equatorial migrants, such as shearwaters, tends to occur in highly productive areas in the opposite hemisphere (Barta et al. 2008), where food availability is high (Brown 1988, Howell 2010). As wing moult affects a bird’s ability to fly (Tucker 1991, Sawdelle et al. 1996), moult tends to occur after migration to the northern hemisphere, 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.

Great shearwaters (*Ardenna gravis*) breed in the South Atlantic (November to April; Tristan da Cunha and Falkland Islands) while sooty shearwaters (*Ardenna grisea*) breed in the South Atlantic Ocean (Falkland Islands) and in higher numbers in the Pacific Ocean. Both species migrate to the North Atlantic during their non-breeding season (May to October), where they have a sympatric distribution (Howell 2012). In the northeast coast of Newfoundland, great and sooty shearwaters aggregate in high abundance near capelin spawning sites, which is their main prey species in the area (Davoren 2007, 2013). Although great and sooty shearwaters share a similar annual cycle, differences in the timing and regions of moult are unclear. Indeed, great

shearwaters are known to undergo flight feather moult in coastal areas of eastern Canada (Brown 1988), while sooty shearwaters appear to moult offshore, based on observations of newly moulted feathers upon arrival in inshore areas (Brown 1988). Both species are attracted to fishing vessels and feed on discards from fisheries, but great shearwaters appear to do this to a greater extent (Olmos 1997, Bugoni et al. 2010) than sooty shearwaters (Wood 1993, Jackson 1988). Both species also forage together 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 2007, 2013). Therefore, it is possible that moulting regions overlap.

As feathers are inert once fully grown, they have been used to estimate dietary composition and/or location during the period of moult using stable isotope ratios (e.g., Cherel et al. 2000; Ramos et al. 2009a, Dehnhard et al. 2011). In the marine environment, carbon stable isotope ratios ( $\delta^{13}\text{C}$ ) are used to indicate foraging areas while nitrogen stable isotope ratios ( $\delta^{15}\text{N}$ ) are used to indicate trophic levels of the 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 changes in prey types during moult (Ramos et al. 2009a). In the southern hemisphere, great and sooty shearwaters are known to feed on fisheries discards, including squid baits and offal from sharks and tunas (Petry et al. 2008, Bugoni et al. 2010), which occupy higher trophic levels (higher  $\delta^{15}\text{N}$ ) relative to natural lower trophic level fish and invertebrate prey that are captured in northern hemisphere (Ronconi et al. 2010a). This suggests the potential to identify distinct moulting areas by sampling a number of feathers.

The main objective of this study was to describe the patterns and chronology of flight feather (i.e., primaries, secondaries) moult of great and sooty shearwaters during the non-

breeding season and examine whether moulting regions overlap between species. Based on similar migratory and distributional patterns, we predicted that the timing and location of flight feather moult and will be similar. As moult represents an energetically demanding part of the annual cycle of avian species, it is critical to determine important the regions used for moulting along with the timing for protection. In addition, a better understanding of moult patterns and stable isotopes signatures from multiple feathers will provide insight into migratory patterns of these similar species during nonbreeding.

## **Methods**

### *Data collection*

Great and sooty shearwaters were captured at sea at night on the northeast coast of Newfoundland from a commercial fishing boat (FV *Lady Easton II*) using a spotlight and a long-handled, large dip-net (Ronconi et al. 2010b) during July and August, 2014 and 2015. Each bird was genetically sexed using a few drops of blood placed on FTA cards (Fridolfsson and Ellegren 1999). Flight feathers (i.e. primaries, secondaries, rectrices) 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 0 to 5 as follow: 0 – old feather; 1 – absence of feather or new feather complete inside of the pin; 2 – new feather emerging from the sheath up to one third grown; 3 – new feather between one to 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, and shearwaters species, is typically symmetrical (Bridge 2006, Ramos et al. 2009b), we scored only the right wing. Finally, a small area (~1 cm<sup>2</sup>) of feathers was sampled from the inner (P1), mid (P5) and outer (P10) primary

feather for stable isotope analysis. When P10 was not available (non-existing or too short to collect, i.e. score 1 or 2), P8 or P9 were collected instead. The moult score dataset was supplemented with great and sooty shearwaters captured in the Bay of Fundy, Nova Scotia (July-September, 2005-2014), Gulf of Maine (July, 2014), Sable Island, Nova Scotia (dead birds, June 2011, 2012) and Brazilian Coast in the South Atlantic (February and April, 2006; Bugoni et al. 2015).

### *Stable isotope analysis*

Stable isotope ratios on primary feathers (P1, P5 and P10) were determined for a subset of individuals sampled within the study area on northeast Newfoundland coast during July-August 2014 (GRSH: n=38; SOSH: n=19) and 2015 (GRSH: n=10; SOSH: n=10). Samples of primary feathers were washed in 0.25M 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 nitrogen isotope ratios ( $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ ) 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 Pee Dee Belemnite (PDB) for carbon ( $\delta^{13}\text{C}$ ) and atmospheric air for nitrogen ( $\delta^{15}\text{N}$ ), according to the following equation:  $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$ , where X is  $^{15}\text{N}$  or  $^{13}\text{C}$  and R is the ratio between the heavier and lighter isotopes (i.e.  $^{15}\text{N}/^{14}\text{N}$  or  $^{13}\text{C}/^{12}\text{C}$ ). Precision was assessed as the standard deviation of replicate analyses of three standards (NIST1577c, tilapia muscle and USGS 41) and was  $\leq 0.21\text{‰}$  for nitrogen and  $\leq 0.14\text{‰}$  for carbon.

### *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. Males and females were pooled in analyses as PMS (GRSH  $Z=-1.59$   $p=0.11$  and SOSH  $Z=0.88$   $p=0.38$ ) and SMS (GRSH  $Z=-1.12$   $p=0.26$  and SOSH  $Z=-0.09$   $p=0.93$ ) did not differ between sexes. We used mixed-effect models to compare stable isotope ratios ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , separately as response variables) between and within species using species (great and sooty shearwaters) and feathers (P1, P5, P10) as fixed factors and individual as a random effect. Post-hoc Tukey HSD tests were conducted using only the fixed effects from the model and  $\alpha$  values were adjusted for multiple comparisons (Bonferroni). Year and sex were not included in the model, because no differences in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  were found between 2014 and 2015 or between males and females.

The isotopic niche breadth for each type of feather (P1, P5, P10) for both species was calculated using Standard Ellipses Area, corrected for small sample size ( $\text{SEAc}$ ; Jackson et al. 2011). The Standard Ellipses Area is considered a standard deviation around the bivariate mean, and encompasses 40% of the data and is used, among other metrics, to represent population niche breadth (Jackson et al. 2011). The isotopic niche overlap between the primaries feathers within and between species was calculated by the area of overlap divided by the sum of the  $\text{SEAc}$  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 collected on the northeastern coast of Newfoundland during July-August, 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 4.1).

### *Moult pattern and chronology*

The moult patterns of flight feathers were similar for great (GRSH) and sooty shearwaters (SOSH). Primary feather moult was sequential, starting with the inner primaries and ending with the outer primary (P10) for both species (Fig. 4.1). The majority of great shearwaters in active moult were moulting one to three primaries simultaneously (86%), whereas approximately 14% were moulting four primaries, few individuals were moulting up to five primaries (<1%) and one individual was moulting seven primaries at once. The majority of sooty shearwaters in active moult were moulting three primaries simultaneously (90%), with few individuals moulting up to four primaries (10%). The number of primary feathers growing simultaneously was inversely related with PMS (GRSH:  $R^2=0.19$ ,  $F_{437}=98.89$ ,  $p<0.001$ ; SOSH:  $R^2=0.23$ ,  $F_{62}=17.72$ ,  $p<0.001$ ). 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. 4.1). The tail (rectrices) moult was variable and asymmetrical and, thus, patterns could not be clearly defined for either species. The majority of great (97 %) and sooty shearwaters (95%) in active moult captured in Newfoundland were also moulting body feathers (contour feathers) while growing flight feathers.

Although both species had similar moult patterns, sooty shearwaters had a more advanced moult on the northeast Newfoundland coast (P1-P6 complete) relative to great shearwaters (P1-P4 complete) when sampled during the first two weeks after arrival in the study

area (July 15-31, 2014 and 2015; Fig. 4.1). Individuals sampled in August were excluded from the moult patterns analysis, since the majority of the birds sampled were great shearwaters and would not be comparable to sooty shearwater in the same time frame. When combining all study locations and years (Table 4.1), moult chronology for both primary and secondary feathers indeed was more advanced in sooty relative to great shearwaters (Fig 4.2). Interestingly, a few great shearwaters caught during the winter in the South Atlantic were moulting (Fig 4.2). Although for both species males seem to have a higher moult score than females (i.e. finish moult earlier), this trend was not statistically significant for either species (GRSH:  $Z=-1.10$ ,  $p=0.27$  and SOSH:  $Z=0$ ,  $p=1.00$ ).

#### *Feather stable isotopes*

Carbon stable isotope ratios ( $\delta^{13}\text{C}$ ) of primary feathers differed between species ( $F_{1,72.6}=15.04$ ,  $p<0.001$ ) and within species ( $F_{2,145.1}=69.48$ ,  $p<0.001$ ) and also when the interaction between species and feather was included in the model ( $F_{2,145.1}=17.22$ ,  $p<0.001$ ). Posthoc 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  $\delta^{13}\text{C}$  than sooty shearwaters ( $p<0.001$ ; Table 4.2.; Fig 4.3). For P5,  $\delta^{13}\text{C}$  was also higher for great relative to sooty shearwaters ( $p<0.001$ ; Table 4.2; Fig 4.3). For the outer primary (P10), which was moulted by both species in the study area, no differences were observed between species ( $p=0.75$ ; Table 4.2; Fig 4.3). For great shearwaters,  $\delta^{13}\text{C}$  was similar for P1 and P5 ( $p=0.36$ ), but P10 was significantly lower than P1 ( $p<0.001$ ) and P5 ( $p<0.001$ ; Table 4.2; Fig. 4.3). In contrast, the carbon isotopic signature for sooty shearwaters did not differ significantly among primary feathers (P1xP5:  $p=0.23$ ; P1xP10:  $p=0.37$ ), with the exception of P5 being higher than P10

( $p < 0.001$ ; Table 4.2; Fig. 4.3). For individuals of both species,  $\delta^{13}\text{C}$  converged on the same general range, but appeared to be more variable for great shearwater during early moult (i.e. P1 and P5) relative to later (i.e. P10). In addition, no differences in  $\delta^{13}\text{C}$  were found between males and females for great ( $Z = -0.58$ ,  $p = 0.56$ ) or sooty shearwaters ( $Z = -0.72$ ,  $p = 0.47$ ).

Nitrogen stable isotope ratios ( $\delta^{15}\text{N}$ ) of primary feathers differed significantly between species ( $F_{1,76.3} = 7.73$ ,  $p = 0.007$ ) but not within species ( $F_{2,148.1} = 0.34$ ,  $p = 0.71$ ). The  $\delta^{15}\text{N}$  differed significantly when the interaction between species and feather was included in the model ( $F_{2,148.1} = 14.18$ ,  $p < 0.001$ ). Post-hoc tests revealed that  $\delta^{15}\text{N}$  was higher for great relative to sooty shearwaters for P1 ( $p < 0.006$ , Table 4.2; Fig 4.3) and P5 ( $p = 0.001$ , Table 4.2; Fig 4.3) but not for P10 ( $p = 0.89$ ; Table 4.2; Fig 4.3). For great shearwaters,  $\delta^{15}\text{N}$  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 4.2; Fig 4.3). For sooty shearwaters,  $\delta^{15}\text{N}$  did not differ significantly among primaries (P1xP5:  $p = 1.00$ ; P1xP10:  $p = 0.11$ ; P5xP10:  $p = 0.12$ ; Table 4.2; Fig 4.3). The  $\delta^{15}\text{N}$  for P1, however, appeared to separate into two distinct groups, with most individuals ( $n = 21$ ) having higher nitrogen isotopic signatures ( $15.81 \pm 0.20\text{‰}$ ), while others ( $n = 8$ ) were lower ( $12.15 \pm 0.25\text{‰}$ ; Fig 4.3B). The same pattern was observed for P5 ( $n = 21$ ,  $12.88 \pm 0.15\text{‰}$  and  $n = 8$ ,  $12.03 \pm 0.19\text{‰}$ ; Fig 4.3B). Individuals with lower  $\delta^{15}\text{N}$ , however, converged to a nitrogen isotopic signature similar to other individuals later during moult (i.e. P10). In summary,  $\delta^{15}\text{N}$  for great shearwaters seemed to be more variable over all primaries relative to sooty shearwaters. No differences in  $\delta^{15}\text{N}$  were found between males and females for great ( $Z = -1.59$ ,  $p = 0.11$ ) or sooty shearwaters ( $Z = -0.74$ ,  $p = 0.46$ ).

For great shearwater, the isotopic niche breadth ( $\text{SEA}_c$ ) was broader before arrival in the study area than while moulting in the study area (Table 4.2). The niche overlap between both species was higher in the study area (P10: 44.4%) but lower before arriving in the study area (P1:

5.8%, P5: 9.3%). Within species, great shearwater had a higher overlap between P1 and P5 (64.8%) and no or almost no overlap between P1 and P10 (0) and P5 and P10 (0.1%). For sooty shearwaters, there was a higher overlap between the primaries (P1-P5: 23.6%, P1-P10: 12.3%; P5-P10: 30.8%).

## **Discussion**

In this study, we describe the patterns of flight feather moult (i.e. primaries, secondaries) of great and sooty shearwaters during the non-breeding season on the northeast coast of Newfoundland. As predicted based on previous literature (Brown 1988), the timing of flight feather moult differed between great and sooty shearwaters in coastal Newfoundland, with sooty shearwaters showing more advanced moult than great shearwaters. In addition, we report for the first time that sooty shearwaters finish their moult in coastal waters, contrary to previous reports (Brown 1988). Also as predicted, distinct stable isotope ratios were found for the inner and mid-primaries (i.e. P1 and P5) of great and sooty shearwaters, suggesting that these species may moult in different locations or consume different prey types during early moult. In contrast, stable isotope ratios feathers grown in the study area (i.e. P10) were similar and showed higher niche overlap, suggesting a similar dietary niche. This may be possible due to high abundance of prey during the summer in the study area, resulting from the inshore migration of spawning capelin (Davoren 2013). Although sex-based differences during moult have been reported for some species, such as Cory's shearwaters (Ramos et al. 2009b), this was not observed in our study for great and sooty shearwaters. Additionally, similar moult timing and stable isotope signatures were observed for both species among years. Inter-annual similarities have been found

for other studies (e.g., black-browed albatross), suggesting a high degree of fidelity on foraging areas (Phillips et al. 2009), which has been found for other Procellariiformes (Cherel et al. 2000).

The moult pattern for both species was similar to patterns reported for other shearwaters and Procellariiformes, with an ascending pattern (starting at inner primaries and finishing with the outer primaries). We were not able to determine whether P2 was moulted before P1 because most individuals were captured in later moult, but this pattern has been already reported for sooty shearwaters and other Procellariiformes (Thompson et al. 2000, Arroyo et al. 2004, Allard et al. 2008). The simultaneous shedding and growth of inner primaries is supported by the higher number of the feathers growing when the primary moult score is low and also by the similar stable isotope ratios ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) for P1 and P5 for both species. 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 (Cory's shearwaters; Ramos et al. 2009b) and Procellariiformes (Northern fulmars; Thompson et al. 2000). This moult pattern may have evolved to minimize gaps in flight feathers and, thus, energetic costs of flight during moult (Hedenström 1991; Lindström et al 1993), as secondaries (S1-S4) adjacent to primaries (P1-P5) moult at different times.

The higher moult score for both primary and secondary feathers in sooty relative to great shearwaters (Fig. 4.2) 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 and Rower 1996). Timing of moult can be influenced by several ecological factors, including breeding status (breeders, non-breeders and failed breeders; Alonso et al. 2009), breeding location (Alonso et al. 2009, Catry et al. 2013), body condition (parasites; Langston and Hillgarth 1995), age class (immature and juveniles; Hower 2010) and intra and inter-specific competition at breeding and

non-breeding site. By one species completing moult in advance of another similar, sympatric species, this species may depart moulting/non-breeding grounds earlier if prey becomes limited. Interestingly, prey becomes lower in the study area once capelin spawning is complete (Davoren et al. 2006), and sooty shearwaters have more advanced moult and, thus, tend to leave the area in early August. In contrast, great shearwaters remain until later in the summer (mid-late August), when they have completed moult (i.e. P8-P10). Interestingly, sooty shearwaters have been noted to be the less competitive species relative to great shearwaters (Ronconi et al. 2010b). Indeed, the species ratio changes in the study area (Carvalho unpublished data), when sooty shearwaters are dominant in early summer (July) and decrease in numbers later in summer (August). A previous study suggested that great shearwaters delay wing-moult until arriving in waters off Canada (Brown 1988). This has been corroborated by reports of individuals observed moulting in the Bay of Fundy (Ronconi et al. 2010a) and also on the coast of Newfoundland (Brown 1988). In contrast, sooty shearwaters in the Atlantic were hypothesized to moult between late April and early June in an offshore area west of the Mid-Atlantic-Ridge (MAR), and to a lesser extent on the southern Grand Bank off Newfoundland (Hedd et al. 2012). In support, sooty shearwaters have been observed with a complete set of new flight feathers on coastal areas of eastern Canada (Brown 1988), suggesting that they may moult prior to arriving in coastal Newfoundland.

The high overlap of isotopic niches for great and sooty shearwater in the study area (i.e. P10) suggests that they feed on similar prey while in the study area, likely the highly abundant spawning capelin. This is corroborated with narrower niche breadth while in the study area as well, likely reflecting a primarily capelin-based diet. Indeed, the niche breadth of both species and other top predator in the study area based on the blood (Chapter 2; Gulka et al. 2017) narrowed their niche breadth throughout the summer season – also suggesting convergence of

both species on a similar prey type/diet. In contrast, distinct stable isotope ratios from inner feathers (P1, P5) of great and sooty shearwaters grown before arriving in the study area suggest that these species were either feeding on different prey types or moulting in different locations before moving to the study area. This is corroborated by both species having wider niche breadth and lower niche overlap between species during early moult (P1 and P5) prior to arriving in the study area. species. When paired with tracking devices, stable isotope ratios identified different locations of moult of seabirds (Hedd et al. 2012, Thompson et al. 2015, Cherel et al. 2016). Indeed, stable isotope ratios from multiple primaries and secondaries reflect different moult locations (and time of simultaneous growth) during migration of Cory's shearwaters (González-Solís et al. 2007; Ramos et al. 2009a) and sooty shearwaters (Hedd et al. 2012). In support, carbon stable isotope ratios ( $\delta^{13}\text{C}$ ) has been used in prior studies to identify spatial segregation between species (Phillips et al. 2009). Similarly, closely related petrel species were shown to be moulting at the same time, but foraging in different areas (spatial segregation), possibly avoiding competition with species with the same feeding habit (Cherel et al. 2006). Although we cannot preclude that both species feed on different prey in the same region, based on the stable isotope data in our study, great and sooty shearwaters seem to have distinct moulting areas in the earlier moult stage (P1-P5) prior arriving in the study area. Carbon stable isotope ratios have been used to identify different foraging areas in Southern Ocean (Cherel and Hobson 2007). Based on our data and our references data, North and South Atlantic seem to have a distinct signature for  $\delta^{13}\text{C}$ , lower and higher signature, respectively.

For great shearwaters, differences in stable isotope signatures (especially in  $\delta^{13}\text{C}$ ) suggest that some individuals may have begun moulting in the South Atlantic (i.e. higher  $\delta^{13}\text{C}$ ). When compared to other published stable isotope ratios of shearwater feathers moulted in different

regions, some great shearwaters had signatures resembling those moulting in the South Atlantic (Brazilian coast) with higher  $\delta^{13}\text{C}$  (Quillfeldt et al. 2008, Bugoni et al. 2010), while others resembled those moulting in the North Atlantic (Bay of Fundy), with lower  $\delta^{13}\text{C}$  (Ronconi unpublished data; Fig. 4.3). In support, some individuals have been observed moulting primary feathers during the breeding season in the south Atlantic and it was hypothesized that those individuals were non-breeding birds (failed breeders or immature birds; Watson 1971; Bugoni et al. 2015). Similarly, great and sooty shearwaters captured and sampled in South Atlantic (Bugoni et al. 2010) have higher blood  $\delta^{13}\text{C}$  than individuals caught in North Atlantic (Ronconi et al. 2010a; Chapter 2).

We also found distinct groupings of stable isotope signatures within sooty shearwaters during early moult (i.e. P1, P5). Sooty shearwaters were previously found to use two distinct feeding areas during moult on the Newfoundland shelf, resulting in different stable isotope ratios within primary feathers (P5; Hedd et al. 2012). Interestingly, one group of individuals started their moult (P1-P5) with similar stable isotope ratios to those found by Hedd et al. (2012) on the mid-Atlantic ridge (i.e. lower  $\delta^{15}\text{N}$ ), whereas the other group started their moult with ratios similar to those found on the Grand Banks (Hedd et al. 2012). Differences in the non-breeding areas has also been reported for sooty shearwaters on the Pacific Ocean, where three distinct areas could be defined using stable isotope signatures and geolocators (Shaffer et al. 2006, Thompson et al. 2015). Overall, this suggests that individuals of sooty shearwaters also may moult in different areas. By the end of the moult (P10), however, stable isotope ratios of most individuals converged, possibly indicating a capelin-based diet (higher  $\delta^{15}\text{N}$ ).

In conclusion, stable isotope ratios can be used to identify distinct moult location or diet of similar species on the non-breeding grounds. Sympatric species might evolve a temporal

and/or spatial segregation to avoid inter-specific competition while moulting, since it is energetically demanding and flight might be constrained or more energetically expensive while growing multiple flight feathers simultaneously, but may converge at the same location at the same time if there is super-abundant prey. There is still a gap of information from the earlier moult stages for both species, since they might start the moult offshore (sooty shearwaters) or prior to migration (great shearwaters). Tracking devices combined with stable isotope ratios of feathers would be useful to identify distinct moulting areas (i.e. South vs. North Atlantic), especially for great shearwaters.

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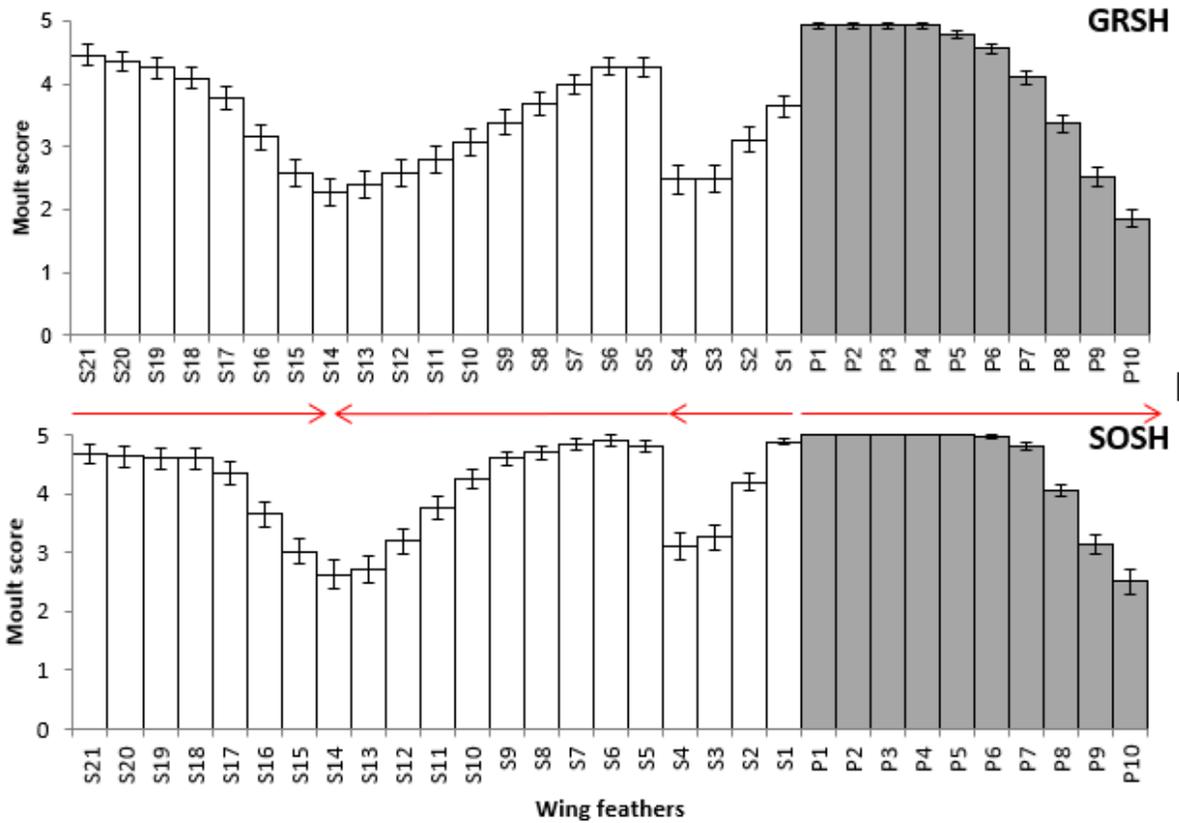
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**Table 4.1** Number of great and sooty shearwaters (range per year shown in brackets) with primary and secondary moult scores recorded within each non-breeding location, along with the years sampled and number of individuals sampled for stable isotope analysis of feathers. Note the \* refers to data derived from Bugoni et al (2015).

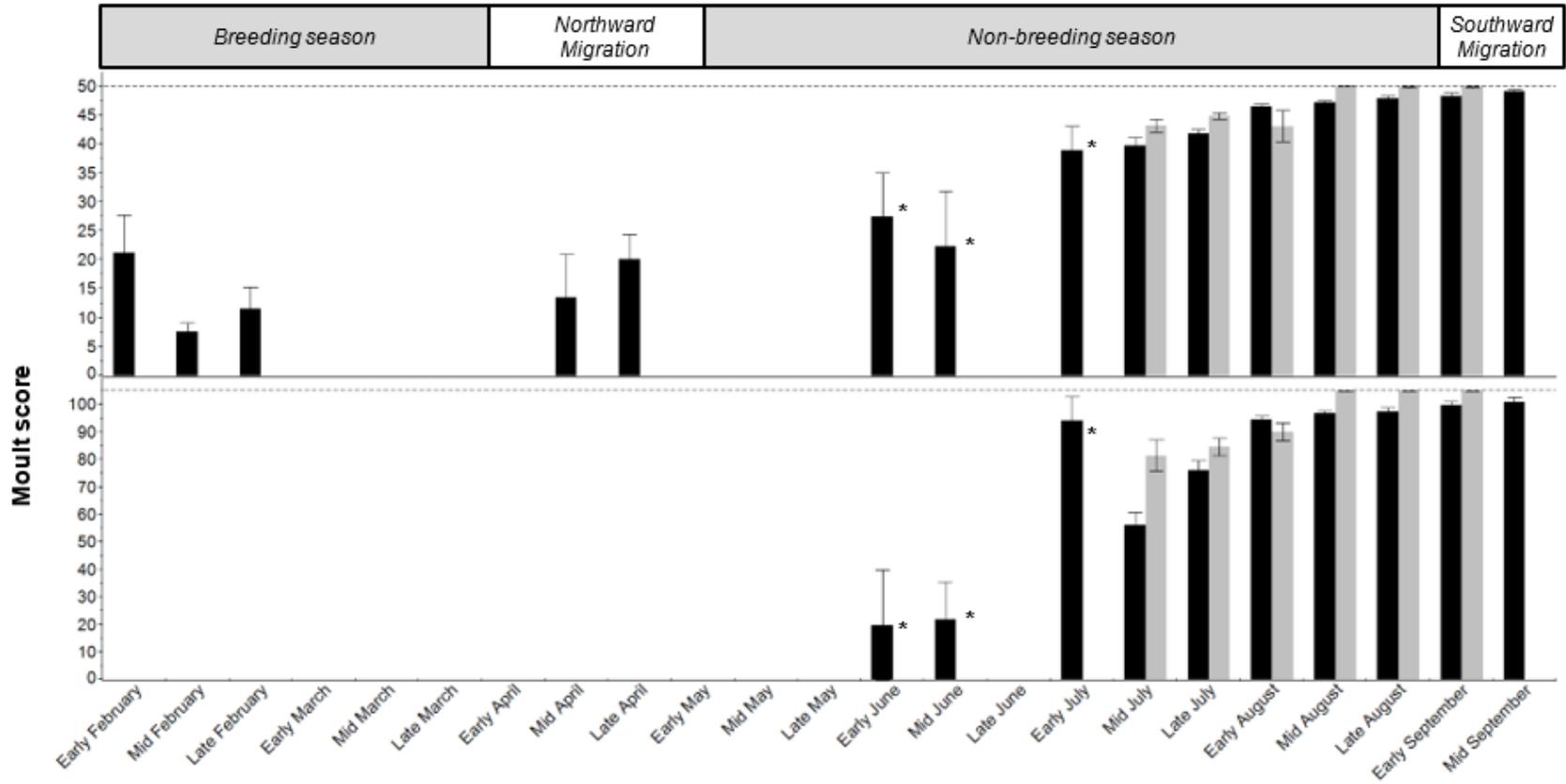
| <b>Species</b>          | <b>Location</b>                      | <b>Years</b>       | <b>Moult score primary</b> | <b>Moult score secondary</b> | <b>Feather Samples</b> |
|-------------------------|--------------------------------------|--------------------|----------------------------|------------------------------|------------------------|
| <b>Great Shearwater</b> | Newfoundland                         | 2014-2015          | 126(51-75)                 | 123(51-72)                   | 48(10-38)              |
|                         | Bay of Fundy                         | 2005-2012,<br>2014 | 381 (16-90)                | 344(16-90)                   |                        |
|                         | Gulf of Maine                        | 2014               | 13                         |                              |                        |
|                         | Sable Island                         | 2011-2012          | 7 (2-5)                    | 7(2-5)                       |                        |
|                         | South Atlantic<br>(Brazilian coast)* | 2006               | 67                         |                              |                        |
|                         | <b>Total</b>                         |                    |                            | <b>594</b>                   |                        |
| <b>Sooty Shearwater</b> | 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<br>(Brazilian coast)* | 2006               | 2                          |                              |                        |
|                         | <b>Total</b>                         |                    | <b>101</b>                 | <b>99</b>                    |                        |

**Table 4.2** Means ( $\pm$  SE) stable isotope ratios ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) and isotopic niche breadth ( $\text{SEA}_c$ ) of the primaries (P1, P5 and P10) from great and sooty shearwaters captured in July-August 2014-2015 on the northeast coast of Newfoundland.

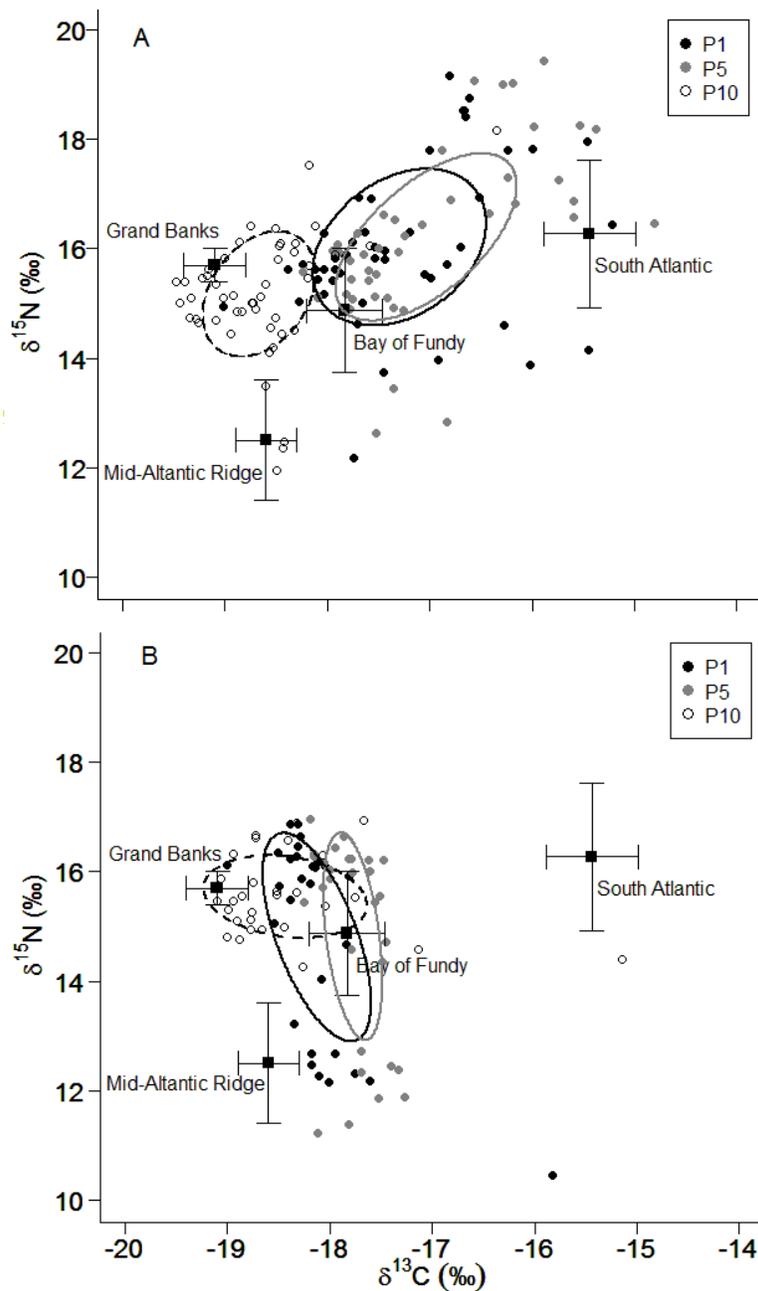
|             |     | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) | Niche breadth<br>$\text{SEA}_c$ (‰ <sup>2</sup> ) |
|-------------|-----|---------------------------|---------------------------|---|
| <b>GRSH</b> | P1  | -17.29 $\pm$ 0.12         | 16.02 $\pm$ 0.20          | 3.61  |
|             | P5  | -17.03 $\pm$ 0.13         | 16.19 $\pm$ 0.23          | 3.36  |
|             | P10 | -18.66 $\pm$ 0.08         | 15.17 $\pm$ 0.16          | 1.87  |
| <b>SOSH</b> | P1  | -18.12 $\pm$ 0.10         | 14.80 $\pm$ 0.35          | 2.48  |
|             | P5  | -17.77 $\pm$ 0.05         | 14.82 $\pm$ 0.34          | 1.55  |
|             | P10 | -18.43 $\pm$ 0.15         | 15.54 $\pm$ 0.14          | 1.85  |



**Figure 4.1** Mean ( $\pm$  SE) moult score of primary (gray bars) and secondary (white bars) feathers of great shearwaters (GRSH, n=118) and sooty shearwaters (SOSH, n=60) captured during their non-breeding season (July 15-31, 2014 and 2015) on the northeast coast of Newfoundland. The moult pattern is indicated by the arrows.



**Figure 4.2** Mean  $\pm$  SE moult score of primary feathers (PMS, top) and secondary feathers (SMS, bottom) for great (black) and sooty (gray) shearwaters during February-September (2005-2015) from all study locations combined (see Table 4.1). Moult scores from dead birds are indicated with an \*. Dashed lines represent the maximum total moult score. Individuals from February and April were captured in the South Atlantic (Bugoni et al. 2015).



**Figure 4.3** Stable isotope ratios ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) and standard ellipse area (SEA) of P1 (black circle; black ellipse), P5 (gray circle; gray ellipse) and P10 (open circle; dotted line ellipse) for great (A) and sooty shearwater feathers (B) collected during July-August on the northeast coast of Newfoundland. Mean  $\pm$ SD stable isotope ratios from feathers (body) from great shearwaters sampled in Bay of Fundy (Ronconi unpublished data) and South Atlantic (Bugoni et al. 2010) and primaries (P5) from sooty shearwaters staging at Grand Banks and Mid-Atlantic Ridge (Hedd et al. 2012) are also indicated.

## General Conclusion

Competition theory states that similar species feeding on similar prey will display niche partitioning to minimize interspecific competition and be able to coexist under limited prey abundance (Schoener 1974, Begon et al. 2006). According to Hutchinson (1957), niche is a  $n$ -dimensional hypervolume which will allow sympatric species to partition their niche. In this thesis, I investigated niche partitioning and overlap between great and sooty shearwaters in the niche dimensions of space (Chapter 1, 3) and time (Chapter 4), as well as diet (Chapter 2, 4), and on a fine-scale during prey capture (Chapter 3) within their non-breeding season in coastal Newfoundland.

I found a high overlap in the isotopic niche breadth (Chapter 2, 4) and density and distributional patterns (Chapter 1) of great and sooty shearwaters during their non-breeding season in coastal Newfoundland. Indeed, the high overlap in isotopic niche between the species in both plasma and red blood cells (Chapter 2), as well as in the primary feathers moulted in coastal Newfoundland (P10; Chapter 4), suggest that both species rely on capelin during their non-breeding season, but also on other similar prey types (e.g. sand lance). The high variation in capelin biomass among years, however, affected the isotopic niche breadth (plasma) of both species. In years when capelin biomass was lower, both species incorporated other similar prey types (niche expansion) without reducing the isotopic niche overlap between species. This suggests that prey biomass in coastal Newfoundland was not limiting even when capelin biomass was low or individuals could leave the study area to minimize competitions, as they can travel long distances. Future studies should focus on investigating the diet of both shearwater species in more detail, perhaps using mixing models while incorporating stable isotope ratios from other

prey types present in the study area to identify subtle partitioning between these two sympatric species.

In addition, both species were observed in mixed-species feeding flocks and assemblages associated with capelin spawning sites in coastal Newfoundland (Chapter 1). Indeed, the density and distributional patterns of both species were highly associated with shallow areas associated with capelin spawning sites and migratory routes to spawning sites and the presence and density of each species was mainly influenced by the other shearwater species (Chapter 1). This suggests that the benefits of foraging together outweigh any costs. For instance, species can use local enhancement to find prey patches, thereby minimizing the time and energy spent searching for prey (Silverman et al. 2004, Thiebault et al. 2014). In addition, as capelin acts as a pulsed resource in coastal Newfoundland, with marine predators shifting their diet to primarily capelin once they arrive inshore (e.g. Gulka et al. 2017), prey biomass is likely unlimited when shearwaters are resident in the study area during the summer. This is supported by the lack of evidence for niche partitioning in multiple dimensions between the shearwater species found in this study. In contrast, divergent stable isotope ratios of primary feathers grown prior to arriving in the study area (P1, P5) as well as different moult timing, suggested a temporal and spatial segregation of great and sooty shearwaters during early moult prior to arriving in coastal Newfoundland. Future studies should use tracking devices to examine the fine-scale spatial overlap between the two shearwater species during and after residence in coastal Newfoundland to further investigate overlap of distributional and density patterns in other regions.

Although we did not observe niche partitioning to a great extent, great and sooty shearwaters displayed different strategies when capturing the same prey items during our behavioural experiment (Chapter 3). Both species were attracted to the supplemental food (cod

liver) offered during the experimental trials in higher numbers during low capelin availability compared to lower numbers during high capelin availability. However, great shearwaters displayed a more bold response, whereby they landed on the water more often and remained closer to the boat during the trials. In contrast, sooty shearwaters displayed a more shy response, whereby they were observed primarily flying and landed only for a few seconds before diving or taking off. In addition, great shearwaters engaged often in disputes for food with other larger species (gulls and northern fulmars), while sooty shearwaters dove more frequently under feeding flocks, presumably to avoid direct interactions with other species. Future studies should further investigate individual behaviour to identify whether these patterns were driven by bold or shy individuals within each species.

Overall, this study not only advances our understanding on competition and coexistence of sympatric species, but also provides valuable information for the conservation of shearwaters species. Currently, the great shearwater is listed as least concern on the IUCN (International Union for Conservation of Nature) Red List of Threatened Species, as its population remains stable (BirdLife International 2018). The sooty shearwater, however, is listed as near threatened on the IUCN Red List due to signs of rapid population decline in recent years (BirdLife International 2018). Many human-induced threats, such as chemical and plastic pollution as well as by-catch in fisheries, are impacting these two species and most other procellariid seabirds (Gaskin et al. 1978, Ogi 1989, Olmos 1997, Uhlmann 2003, Haman et al. 2013). Considering that their response to fisheries offal was dependent on the availability of natural prey (Chapter 3), the current spatio-temporal changes in capelin availability in coastal Newfoundland (DFO 2018) may put both these seabird species and others at higher risk of by-catch as they appear to rely more on supplemental fisheries-based food (i.e. offal and discards) when natural prey availability

is low. In addition, as long-distance migrants, they rely on a global-scale conservation effort. Although much more is known about both species during the breeding season, when they are highly accessible at breeding colonies (e.g., Rowan 1952, Watson 1971, Kitson et al. 2000, Scott et al. 2008, Shaffer et al. 2009, Ronconi et al. 2010a), little is known about their ecology during the non-breeding period where studies are restricted to tracking data and at-sea observations (but see Ronconi et al. 2010b). This study contributed knowledge on the foraging areas and behaviour of both species in an important non-breeding and moulting area. In particular, I determined the location of an important moulting area for sooty shearwaters in coastal Newfoundland, opposed to previous studies that suggested moult was completed offshore, before arriving in coastal areas (Brown 1988; Cooper et al. 1991). In addition, I concluded that both species are highly associated with each other and have flexible diets and foraging behaviour during the non-breeding season to accommodate fluctuations in prey availability. As seabirds have often been used as indicators of changes in their environment (Piatt and Sydeman 2007), understanding and monitoring their ecology in these important foraging/moulting areas will be crucial to evaluate the impacts of future changes in the marine environment on top predators.

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