



Intra- and inter-annual shifts in foraging tactics by parental northern gannets *Morus bassanus* indicate changing prey fields

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ABSTRACT: Seabirds are constrained by central-place foraging during breeding, when the energy obtained from prey must outweigh the costs of travel, search, capture and transport. The distribution and phenology of the cold-blooded marine fishes they exploit are heavily influenced by oceanic climate. Northern gannets, the largest breeding seabird in the North Atlantic, use a generalist foraging strategy, preying on a wide array of pelagic fishes. They employ different foraging tactics for different prey types, with rapid, shallow V-shaped dives used for large, powerful prey such as mackerel, and U-shaped dives for smaller forage fishes like capelin. Here we assess intra- and inter-annual differences in foraging effort and influences of prey availability at the southernmost colony of the species at Cape St. Mary's, Newfoundland, Canada. We compared foraging trip characteristics (total and maximum distance, directness, duration and number of dives) of parental gannets during the breeding seasons of 2019 (n = 10) and 2020 (n = 7) using GPS/time-depth recorders. Individual gannets shifted away from using U-shaped dives in early chick-rearing to primarily V-shaped dives in late chick-rearing. Shifts were abrupt and occurred in mid-August in 2019 and 2020. Maximum and total foraging trip distance and duration were significantly greater during early chick-rearing in 2020 than in 2019. Kernel density 50% utilization distributions were larger and expanded further from the colony during early chick-rearing in 2020 ($7297 \pm 1419 \text{ km}^2$; mean \pm SE) than 2019 ($2382 \pm 797 \text{ km}^2$). Increased foraging effort during early chick-rearing in 2020 was likely due to decreased capelin availability, resulting from earlier spawning, and greater variation in the timing of spawning among sites, which may have been influenced by warmer waters.

KEY WORDS: Northern gannet · Foraging behaviour · Prey availability · Prey switching · Dive profiles · Forage fish

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1. INTRODUCTION

During the breeding season, parental seabirds are central-place foragers and are constrained in their travel to and from the breeding colony due to incubation and chick-rearing requirements. The energetic benefits obtained from their prey must outweigh the

costs associated with locating, capturing and transport to provide for themselves and their offspring (MacArthur & Pianka 1966, Burke & Montevecchi 2009, Elliott et al. 2009).

Prey fields and prey availability in marine environments are dynamic, often shifting substantially annually and during the breeding season based on the

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phenology of different species and environmental conditions (Perry et al. 2005, Pinsky et al. 2013, Henderson et al. 2017). Seabirds shift foraging tactics to cope with inter- and intra-annual variation in environmental conditions and associated differences in prey availability (Montevecchi et al. 2009, Garthe et al. 2011, Botha & Pistorius 2018). Foraging effort (e.g. foraging trip distance and duration, number of dives, time budgets) exhibited by seabirds reflects the abundance, distribution and quality of their prey within their foraging range around the colony (Cairns 1987, Piatt et al. 2007). Differences in foraging effort/behaviour within and between years by seabirds provide proxies for how easily they can locate and capture their prey (Burke & Montevecchi 2009), as well as insight into which prey species they target (Garthe et al. 2000, Elliott et al. 2008).

As the migratory and reproductive strategies of marine fishes rely heavily on ocean temperature, climate anomalies can induce shifts in their horizontal and vertical distributions (Perry et al. 2005, Dulvy et al. 2008, Fincham et al. 2013, McQueen & Marshall 2017). Furthermore, ocean climate anomalies have been linked to declines in standing stock biomass of key prey species for seabirds (Plourde et al. 2015, Buren et al. 2019). These changes in availability can have profound influences on seabirds via increasing effort needed to acquire resources and ultimately inhibiting their ability to successfully rear offspring (Cairns 1987).

In the Northwest Atlantic, key forage fish species, such as capelin *Mallotus villosus* and Atlantic mackerel *Scomber scombrus*, have exhibited dramatic declines in standing stock biomass in recent decades (Buren et al. 2019, DFO 2019). In the case of capelin, a centennially significant cold-water anomaly in the early 1990s induced a 30-fold decline in standing stock biomass; the stock has not recovered and has exhibited delayed spawning in the years since this event (Buren et al. 2019). The Northwest Atlantic mackerel standing stock biomass has also declined precipitously in recent years and is listed in the 'Critical Zone', in which continued fisheries pressure may result in the inability of the stock to maintain itself (DFO 2019). This reduction in available mackerel has also been linked to a climate-driven regime shift associated with warming waters in the Gulf of St. Lawrence (Plourde et al. 2015).

The northern gannet *Morus bassanus*, a large, generalist seabird of the North Atlantic, feeds on a wide array of pelagic fishes during the breeding season, which vary based on prey availability, distribution and quality. Atlantic mackerel, capelin,

Atlantic herring *Clupea harengus*, Atlantic saury *Scomberesox saurus* and shortfin squid *Illex illecebrosus* are important prey during the breeding season in the Northwest Atlantic (Montevecchi 2007, Montevecchi et al. 2009). These forage fishes vary in size and energy content, with mackerel being the largest, most energetically dense option (10.3 kJ g^{-1}) and capelin being the smallest and least energetically dense (4.2 kJ g^{-1} ; Montevecchi et al. 1984). Saury and herring fall between these 2 values, with energetic contents of 6.8 and 4.3 kJ g^{-1} , respectively (Montevecchi et al. 1984). Owing to central-place foraging constraints and the need to balance energy expenditure, it is expected that longer foraging trips will be associated with the larger, more profitable prey species (mackerel), and shorter trips with the smaller, less profitable species (capelin). Thus, distribution and availability of these fishes around the colony alter decision-making and ultimately reproductive success of gannets (Hamer et al. 2007, Warwick-Evans et al. 2016). For instance, if capelin are only energetically profitable within a certain radius around the colony, gannets would need to switch to a larger, more energetically dense fish such as mackerel if capelin availability wanes within this radius.

Due to differences in prey size, burst swimming speed and distribution in the water column, gannets employ different dive behaviours when pursuing different prey species (Garthe et al. 2000). For example, mackerel are larger fish that swim near surface waters and are capable of explosive burst speeds of 18 body lengths per second (Wardle & He 1988). Gannets use shallow, high-speed 'V-shaped' dives with minimal wing-propulsion to capture mackerel (Garthe et al. 2014). In contrast, dives for the smaller, slower capelin (~1.5 to 1.7 body lengths per second swimming speed; Behrens et al. 2006) tend to be deeper, prolonged, wing-propelled 'U-shaped' dives (Garthe et al. 2000, 2011).

In the Northwest Atlantic, gannet population growth has been stagnant and reproductive success has been poor since the early 2010s at the southern limit of their breeding range (d'Entremont et al. 2022). These negative population trends first manifested in 2012, when a marine heatwave coincided with mass colony abandonments and record low reproductive success at 3 colonies (Bonaventure, Great Bird Rocks and Cape St. Mary's; Montevecchi et al. 2021). Additionally, the declines in reproductive success as well as plateaued population growth (Chardine et al. 2013) have been associated with declining forage fish stocks due to fisheries pressure

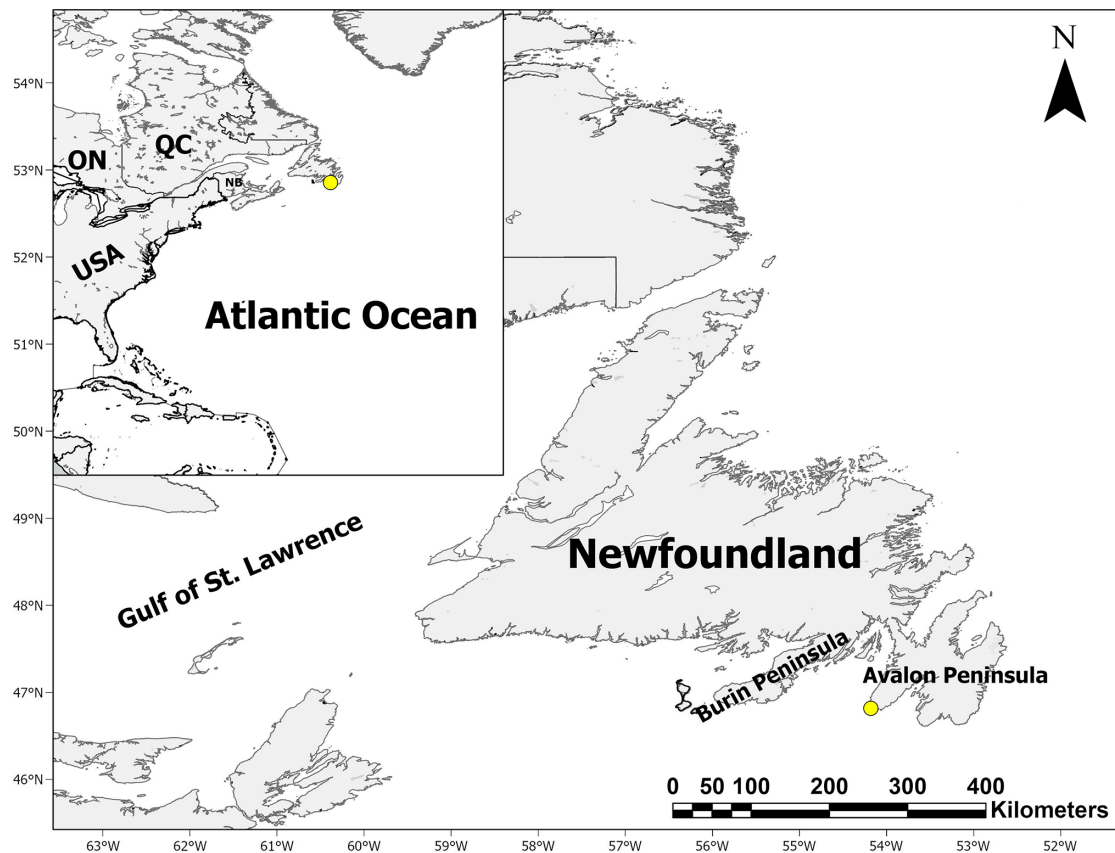


Fig. 1. Location of Newfoundland and Cape St. Mary's (yellow dot) relative to eastern North America

and warming ocean climate (Guillemette et al. 2018, d'Entremont et al. 2022). As these observed declines in reproductive success and population growth appear to be climate driven, it is expected that ocean climate has induced indirect impacts on gannets in the region through alterations in prey availability (Plourde et al. 2015, Buren et al. 2019). Hence, it is critical to assess associations between climate, indicators of prey availability and foraging behaviour to determine whether these observed declines in productivity are a product of alterations in foraging effort.

In the present study, we assess the foraging behaviour of northern gannets at their southernmost colony, Cape St. Mary's, Newfoundland (46.81°N , 54.18°W ; Fig. 1), for the first time. Owing to the geographic location, Cape St. Mary's is likely to be one of the first colonies to experience the negative effects of warming oceanic climate (see Montevecchi et al. 2021, d'Entremont et al. 2022). Our objectives are to assess intra- and inter-annual differences in foraging effort associated with shifts in prey availability and environmental conditions. We hypothesize that gan-

nets will adjust their foraging behaviour (e.g. dive profiles, trip duration, trip distance, number of dives) to cope with (1) intra- and (2) inter-annual variation in the availability of different prey types. We predict that gannets will increase foraging effort (1) intra-annually when available prey shifts from coastally spawning forage fish (capelin) to larger pelagic species (mackerel, saury) and (2) inter-annually if prey availability is lower. This study also provides baseline information regarding the foraging range/behaviour of parental northern gannets at their southernmost colony.

2. MATERIALS AND METHODS

2.1. Study site

Cape St. Mary's is home to 14 598 breeding pairs at last estimate in 2018 (d'Entremont et al. 2022). Approximately half of the gannets at this colony nest on an isolated sea-stack known as Bird Rock, and the remaining half nest on adjacent mainland cliffs.

2.2. GPS tagging

From mainland breeding sites, 10 gannets in 2019 and 7 gannets in 2020 were fitted with either battery ($n = 7$) or solar-powered ($n = 10$) Ecotone Uria 300 GPS with temperature-depth recorder (TDR) loggers. Tags weigh 13.5 g (dimensions: $36 \times 22 \times 12.5$ mm) and were attached dorsally to the 4 innermost rectrices posterior to the uropygial gland with Tesa® tape and cable ties (Wilson et al. 1997). Birds were captured using extending noose poles, weighed with a 5 kg Pesola® spring scale and equipped with Canadian Wildlife Service aluminium bands on their right legs. Tagged gannets in our study had a mass of 3652 ± 423 g (mean \pm SD) and thus, GPS devices were $<0.5\%$ of body mass, where the risk of effects on animal behaviour is minimal (Geen et al. 2019). Tags were set to record the location of each bird every 15 min. Dive depth was recorded every 1 s after submersion during diving bouts. Devices were set to only record GPS locations when away from the colony and out of range of the receiver to conserve battery life. Five devices were deployed on both July 18, 2019 (3 solar-powered, 2 battery-powered) and August 21, 2019 (2 solar-powered, 3 battery-powered). Seven devices were deployed on July 18, 2020 (5 solar-powered, 2 battery-powered). Three individuals were fitted with GPS devices in both 2019 and 2020, allowing for inter-annual comparisons for the same individuals. An Ecotone base station with a directional antenna was deployed in the colony area approximately 25 m away from the tagged birds to remotely upload GPS-TDR data from each equipped bird when it returned to the colony. All tagged birds had chicks that were approximately 2 to 4 wk old when devices were deployed.

2.3. Diet sample collection

To assess intra- and inter-annual changes in dietary composition, regurgitations were collected from roosting gannets above the mainland cliffs on August 4 and 28 in 2019. Though roosting birds are likely non-breeding gannets, they were targeted for diet sample retrieval to impose less disturbance on breeding pairs, and they likely provide an accurate representation of prey fields being exploited by parental gannets during the same period (Kirkham et al. 1985). Diet samples could not be collected from roosting gannets in 2020 due to reduced researcher presence at the study site associated with the COVID-19 pandemic. Prey composition in regurgi-

tates were identified to species and counted. Opportunistic regurgitates were also assessed for prey species composition during the tagging process in 2019 and 2020.

2.4. GPS data processing

Analysis was conducted using R version 4.04 (R Core Team 2021). Distance from the centre of the colony in kilometres was determined for each GPS location using the 'distance' function in the package 'argosfilter' Version 0.63 (Freitas 2015). Individual foraging trips were manually identified using a combination of distance from the colony and tag-base station communications indicating when tagged birds were in range of the base station (i.e. at the colony). Foraging trip duration, maximum foraging trip distance and total trip distance were calculated by using the 'summaryBy' function in the 'doBy' package Version 4.6.11 (Højsgaard & Halekoh 2021). Directness of foraging trips was measured as maximum distance from the colony divided by total distance travelled per trip (Osborne et al. 2020). GPS locations associated with dives were manually assigned by inspecting the raw data for GPS fixes that occurred within 15 (92% of 2725 dive locations) to 30 min (8%) before a recorded dive.

2.5. Dive analysis

Dive depth and duration from foraging trips of tagged gannets were determined using the package 'diveMove' Version 1.5.3 (Luque 2007). The average number of dives, average depth and dive profile type composition per individual trip were assessed throughout the chick-rearing period. All dives that had a bottom time ≥ 3 s and/or total duration >10 s and depth >8 m were classified as 'U-shaped' dives and all dives with a bottom time <3 s and/or total duration <10 s and depth <8 m were classified as 'V-shaped' dives (Garthe et al. 2000). All dives less than 1 m in depth were removed from analysis, as these could have been associated with bathing bouts and were unlikely to be foraging dives. In both 2019 and 2020, a shift away from U-shaped dives to predominantly V-shaped dives occurred during the breeding season. Using this shift in dive profiles, for further analysis we partitioned the chick-rearing stage into (1) early chick-rearing period until August 15 (when U-shaped dives occurred more regularly; 11.9% of dives in 2019 and 22.2% of dives in 2020), and (2) the

late chick-rearing period from August 16 onwards (when U-shaped dives were rare; 2.3% of dives in 2019 and 2.7% of dives in 2020). This division of the chick-rearing period is also consistent with the age of chicks at this time, as most chicks were approximately 7 to 8 wk old on August 15, and the entire chick-rearing period for the species is typically 13 wk (Mowbray 2020).

2.6. Identifying core foraging areas and ranges

Locations associated with dives across all foraging trips for each individual were presented as 50% utilization kernel density distribution maps using the 'adehabitatHR' package Version 0.4.19 (Calenge 2006) to determine core foraging ranges for each individual in 2019 and 2020 and for each chick-rearing period. Kernel density analysis is a non-parametric density estimate that derives a probability density function of habitat use based on location information (Worton 1989) and is commonly used for displaying foraging ranges of seabird species (Perrow et al. 2015, Hedd et al. 2018). ArcGIS Pro version 2.7.26828 was used to display kernel density utilization distributions.

2.7. Behavioural states analysis

Behavioural states analysis was conducted to assess differences in the proportion of time spent in different behavioural states during foraging trips throughout the breeding season and across years. Previous work on gannets has concluded that they exhibit 3 different behavioural states during foraging trips: transit, rest and area-restricted search (ARS; Bodey et al. 2014, Bennison et al. 2018). A variety of methods are utilized to determine the behavioural state associated with GPS fixes from telemetry data, including speed–tortuosity thresholds (Wakefield et al. 2013), first passage time (Hamer et al. 2009) and hidden Markov models (HMM; Zhang et al. 2019), amongst others. Recent efforts, however, have shown that HMM methodology is the most accurate for assessing the behavioural states of GPS data from gannets, with approximately 80% of dives being associated with ARS-defined GPS fixes (Bennison et al. 2018).

We used the package 'momentuHMM' Version 1.5.2 (McClintock & Michelot 2018) to determine the step lengths and turning angles between each successive GPS point for all tagged individual gannets,

and to fit a 3-state model including transit, rest and ARS. *K*-means clustering was used to determine initial step length and angle parameters. We used a gamma distribution to describe the step lengths, the von Mises distribution to describe turning angles and the Viterbi algorithm to estimate the most likely behavioural state per observation (Zucchini et al. 2016). As is the case for most behavioural state modelling methods, HMM requires the collected location data to have a uniform sampling interval to create biologically meaningful outputs. Though our GPS data were collected at 15 min intervals, there were variable temporal gaps in the dataset due to periodic inability of GPS devices to communicate with satellites (e.g. thick fog, dense cloud cover, physical obstruction). To correct for missing data points, track segments were interpolated where gaps of >15 and <60 min occurred within individual tracks before assigning behavioural classifications. Tracks which had large temporal gaps >60 min were not included in this analysis as they produced large segments of linear interpolated locations which altered behavioural classifications.

2.8. Statistical analyses

Generalized linear mixed models (GLMMs) constructed using the package 'glmmTMB' Version 1.0.2.1 (Brooks et al. 2017) were used to assess intra- and inter-annual variation in foraging trip and dive characteristics. For each model, 'Year' and 'Period' were fixed effects with 'Bird ID' as a random effect, and the interaction between 'Year' and 'Period' was assessed. All models were assessed for dispersion, goodness of fit, homogeneity of variance and within group variation from uniformity using the 'DHARMA' package Version 0.3.4 (Hartig 2021). Gamma regression models with a 'log' link were used to assess intra- and inter-annual differences in trip duration, maximum and total distance, and directness, as these variables were continuous with non-negative values. A generalized Poisson regression model with a 'log' link was used to assess intra- and inter-annual differences in number of dives per trip, as this variable was over-dispersed, non-zero count data. Finally, beta regression models with a 'logit' link were used to assess intra- and inter-annual differences in the proportion of time spent in each behavioural state (rest, transit, ARS), as these were proportional data bounded between 0 and 1. Zero-inflated beta models were used for both 'rest' and 'transit'. Post-hoc analyses for the interaction between Year and Period

were assessed using the 'lsmeans' function from the package 'emmeans' Version 1.5.4 (Lenth et al. 2021). All trips with behavioural state proportions of 0 or 1 were removed from further behavioural states GLMMs. A Welch's unpaired *t*-test was used to assess differences in core foraging range size between chick-rearing periods and years.

2.9. Sea surface temperature

Sea surface temperature (SST) data (Multi-scale Ultra-high Resolution (MUR) SST Analysis fv04.1, global, 0.01°, 2002–present, daily) for the region were obtained from the Environmental Research Division Data Access Program (ERDDAP) database (Simons 2020). SST values were averaged over the early and late chick-rearing periods for both 2019 and 2020. Interval contours of 2°C were created to visualize any intra- and inter-annual differences in SST.

2.10. Capelin spawning sites

To assess capelin availability within the foraging ranges of parental gannets breeding at Cape St. Mary's, the timing and location of spawning sites

used in both 2019 and 2020 were obtained from eCapelin (<https://ecapelin.ca/>). Distances of each capelin spawning site from the colony were calculated for both 2019 and 2020. Average spawning date across sites was calculated for each year. These factors were used as a proxy for capelin availability during early chick-rearing, as gannets have been shown to exclusively forage for capelin at and near coastal spawning sites (Garthe et al. 2007). Additionally, as capelin undergo long-distance inshore migrations from offshore during the summer to spawn, resulting in a doubling of the inshore prey biomass (Gulka & Davoren 2019), the timing of spawning indicates when capelin become available for 2 to 4 wk during the breeding season of seabirds (Davoren et al. 2012).

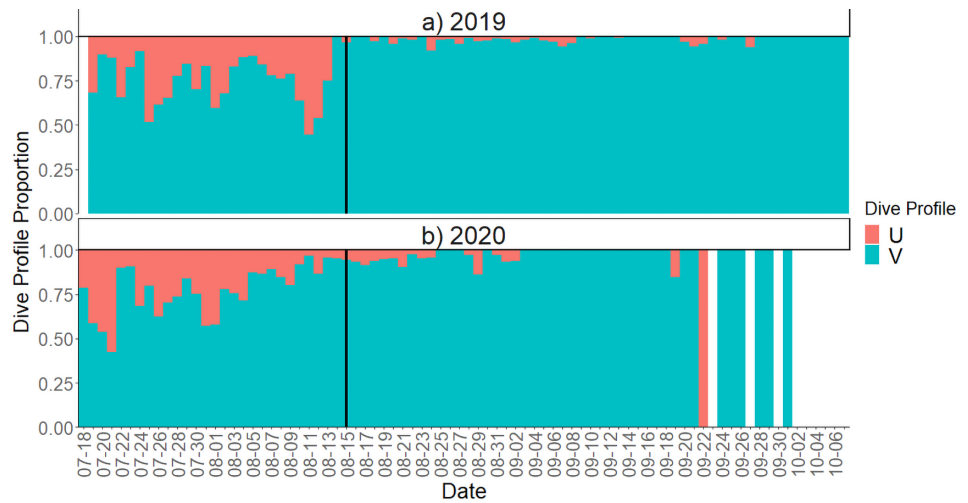
3. RESULTS

We obtained locational data from all 10 birds that were tracked in 2019 and all 7 birds that were tracked in 2020 (Table 1). Birds were tracked for 17 to 76 d (341 to 2547 GPS fixes per bird) and we identified a total of 506 individual foraging trips with 11 to 66 trips per tagged individual (Table 1, Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m698p155_supp.pdf).

Table 1. Summary of foraging trip characteristics of parental northern gannets from Cape St. Mary's, Newfoundland, Canada during 2019 and 2020. Individuals that were tracked in both 2019 and 2020 are colour-coded

Individual	No. foraging trips	Days tracked	No. days tracked	Maximum distance from colony (km)	Dives per trip (mean ± SE)	Total distance (km) (mean ± SE)	Maximum distance (km) (mean ± SE)	Directness (mean ± SE)	Duration (min) (mean ± SE)
2019									
MAF01/BRU02	55	19 Jul to 22 Sep	65	195.5	16.2 ± 2.6	158.4 ± 17.5	63.6 ± 6.5	0.42 ± 0.02	706.5 ± 73.0
MAF02	45	19 Jul to 26 Sep	69	239.2	25.9 ± 2.9	251.6 ± 24.5	99.8 ± 8.0	0.44 ± 0.02	1256.2 ± 115.1
MAF03	34	19 Jul to 28 Aug	40	146.3	17.2 ± 3.3	130.4 ± 16.4	52.5 ± 6.0	0.46 ± 0.03	694.1 ± 81.0
MAF04/LIB06	17	19 Jul to 05 Aug	17	91.8	17.2 ± 2.6	101.6 ± 18.0	44.5 ± 6.6	0.50 ± 0.08	561.6 ± 98.4
MAF05	22	19 Jul to 15 Aug	27	125.7	23.8 ± 2.4	108.8 ± 18.8	46.7 ± 7.8	0.43 ± 0.04	833.8 ± 90.6
LIB01	20	21 Aug to 17 Sep	27	157.7	14.5 ± 5.0	114.8 ± 24.7	46.1 ± 7.7	0.51 ± 0.04	622.3 ± 146.9
LIB02	36	21 Aug to 10 Oct	50	348.5	13.1 ± 2.2	193.2 ± 26.6	85.4 ± 11.0	0.49 ± 0.03	880.9 ± 142.6
LIB03/BRU01	31	21 Aug to 06 Oct	46	192.3	20.0 ± 4.3	184.3 ± 17.5	74.0 ± 9.4	0.41 ± 0.03	813.5 ± 95.1
LIB04	16	21 Aug to 13 Sep	23	165.1	21.9 ± 4.2	182.9 ± 22.8	110.6 ± 9.3	0.85 ± 0.19	1305.4 ± 159.9
LIB05	19	21 Aug to 14 Sep	24	151.0	25.8 ± 4.4	166.2 ± 18.8	74.2 ± 8.1	0.50 ± 0.05	909.4 ± 93.9
2020									
MAF04/LIB06	16	18 Jul to 07 Aug	20	126.8	22.6 ± 4.2	124.6 ± 24.5	47.3 ± 7.6	0.44 ± 0.04	871.4 ± 156.2
LIB07	15	18 Jul to 08 Aug	21	150.6	22.1 ± 4.8	250.0 ± 33.3	96.1 ± 10.7	0.42 ± 0.03	1152.5 ± 289.9
LIB03/BRU01	11	18 Jul to 09 Aug	22	163.0	31.5 ± 5.7	229.8 ± 32.1	82.0 ± 12.6	0.36 ± 0.03	1000.9 ± 173.5
MAF01/BRU02	29	18 Jul to 03 Sep	47	169.2	22.9 ± 4.7	212.7 ± 21.5	87.8 ± 8.3	0.43 ± 0.02	973.5 ± 133.1
BRU03	46	18 Jul to 12 Sep	56	147.9	28.8 ± 3.5	210.5 ± 16.9	77.7 ± 5.0	0.41 ± 0.02	1061.0 ± 82.2
BRU04	66	18 Jul to 02 Oct	76	159.9	10.5 ± 1.6	150.6 ± 12.5	66.3 ± 4.0	0.49 ± 0.03	519.8 ± 54.0
BRU05	28	18 Jul to 25 Aug	38	165.3	19.9 ± 4.0	181.9 ± 25.4	65.2 ± 7.7	0.40 ± 0.02	862.0 ± 164.9

Fig. 2. Dive profile proportions of all tracked parental northern gannets combined per day in (A) 2019 ($n = 10$) and (B) 2020 ($n = 7$). White bars: days on which no birds with active GPS devices embarked on a foraging trip; black line: split between early and late chick-rearing. Dates are given as mm-dd



3.1. Dive profiles

The proportion of U- and V-shaped dives varied throughout the breeding season in both 2019 and 2020. V-shaped dives were typically more common (>50% of daily dive proportions), with capelin-associated U-shaped dives occurring more regularly in July to approximately August 15, becoming rare thereafter (Fig. 2). These same trends were observed within individuals in both years, with each demonstrating a shift from U- to V-shaped dives as the breeding season progressed (Figs. S2 & S3). The average number of dives per day trended downward from early to late chick-rearing in both years, peaking at 66 dives on August 8 in 2019, and 68 dives on August 14 in 2020 (Fig. S4).

3.2. Diet samples

Diet samples collected from roosting gannets further corroborated the difference in prey types being exploited in the different dive behaviour periods, with the majority of regurgitates from August 4, 2019 during early chick-rearing containing almost solely capelin, while prey proportions of regurgitates collected on August 28, 2019 in late chick-rearing consisted of mackerel and saury (Table 2). One opportunistic regurgitate consisting of capelin was observed during the GPS tagging process on July 19, 2019. One herring and 1 capelin regurgitate were observed during the GPS tagging process on August 21, 2019. Five opportunistic regurgitates were examined during the GPS tagging process on July 18, 2020: 4 contained capelin and 1 contained mackerel.

3.3. Foraging trip characteristic comparisons within and between years

Average trip directness was significantly lower during early relative to late chick-rearing in both 2019 and 2020 (Table 3). The number of dives per trip was significantly greater during early relative to late chick-rearing in both 2019 and 2020 (Table 3). Average total and maximum trip distance was significantly lower in early relative to late chick-rearing in 2019, while there was no significant difference between periods in 2020 (Table 3). Average trip duration was significantly greater during early relative to late chick-rearing in 2020, with no difference between periods in 2019 (Table 3). There was no significant difference in time spent resting during forag-

Table 2. Diet sample contents from gannets roosting on the mainland at Cape St. Mary's in August 2019

Date	Sample number	Sample contents
04 Aug	1	5 capelin
	2	2 herring
	3	4 capelin
	4	12 capelin
	5	9 capelin
	6	9 capelin
	7	9 capelin
28 Aug	8	5 mackerel, 1 saury
	9	3 mackerel, 1 saury
	10	3 mackerel, 1 saury
	11	1 mackerel
	12	2 mackerel, 3 saury
	13	3 mackerel, 1 saury
	14	1 saury
	15	2 saury

Table 3. Summary of mean \pm SE foraging trip characteristics and behavioural state proportions and post-hoc results for pairwise comparisons of parental northern gannets from Cape St. Mary's, Newfoundland across chick-rearing periods and years. p-values of <0.05 significance are given in **bold**. ARS: area-restricted search

	— 2019 —		— 2020 —		— Period —					— Year —				
	Early	Late	Early	Late	Estimate	SE	df	t	p	Estimate	SE	df	t	p
Individuals	5	8	7	4										
Total trips	108	187	131	80										
Foraging trip characteristics														
Total distance (km)	133.3 ± 11.7	188.5 ± 9.7	199.1 ± 10.9	159.5 ± 11.3	2019 0.321 0.104		500	3.079	0.002	Early -0.462 0.115		500	-4.001	<0.001
					2020 -0.197 0.108		500	-1.828	0.068	Late 0.056 0.128		500	0.441	0.659
Maximum distance (km)	51.8 ± 4.3	82.5 ± 3.7	74.4 ± 3.4	71.0 ± 4.2	2019 0.445 0.097		500	4.593	<0.001	Early -0.441 0.109		500	-4.067	<0.001
					2020 -0.028 0.1		500	-0.281	0.779	Late 0.032 0.121		500	0.266	0.790
Duration (min)	784.7 ± 53.1	907.3 ± 50.6	964.7 ± 64.5	642.0 ± 61.1	2019 0.117 0.107		500	1.090	0.276	Early -0.326 0.12		500	-2.720	0.007
					2020 -0.351 0.11		500	-3.181	0.002	Late 0.142 0.141		500	1.010	0.313
Directness	0.41 ± 0.02	0.51 ± 0.02	0.41 ± 0.01	0.52 ± 0.03	2019 0.217 0.054		500	4.046	<0.001	Early -0.011 0.06		500	-0.189	0.850
					2020 0.205 0.055		500	3.697	<0.001	Late 0.001 0.071		500	0.014	0.989
Dives per trip	22.8 ± 1.8	17.1 ± 1.4	25.6 ± 1.9	11.1 ± 1.8	2019 -0.276 0.108		495	-2.558	0.011	Early -0.126 0.116		495	-1.086	0.278
					2020 -0.685 0.111		495	-6.19	<0.001	Late 0.283 0.138		495	2.060	0.040
Behavioural state proportions														
ARS	0.47 ± 0.03	0.43 ± 0.03	0.49 ± 0.03	0.50 ± 0.03	2019 -0.440 0.183		142	-2.398	0.018	Early 0.206 0.209		142	0.988	0.325
					2020 0.004 0.341		142	0.011	0.991	Late -0.237 0.326		142	-0.727	0.469
Transit	0.21 ± 0.02	0.39 ± 0.04	0.27 ± 0.03	0.41 ± 0.05	2019 0.748 0.163		142	4.586	<0.001	Early -0.203 0.189		142	-1.074	0.285
					2020 0.564 0.288		142	1.959	0.052	Late -0.019 0.271		142	-0.069	0.945
Rest	0.32 ± 0.03	0.19 ± 0.0	0.27 ± 0.03	0.41 ± 0.05	2019 -0.178 0.177		142	-1.005	0.317	Early 0.198 0.187		142	1.054	0.294
					2020 -0.49 0.411		142	-1.193	0.235	Late 0.509 0.406		142	1.253	0.212

ing trips throughout chick-rearing. However, proportion of time in ARS was significantly greater and proportion of time transiting was significantly lower during early chick-rearing in 2019 (Table 3).

Average total and maximum trip distance, and average trip duration were significantly greater in 2020 during early chick-rearing than in 2019, with no significant differences between years during late chick-rearing (Table 3). Trip directness did not differ significantly between years during either chick-rearing period (Table 3). The number of dives per trip was significantly lower during early relative to late

chick-rearing in 2019, but did not differ between years during late chick-rearing (Table 3). There were no significant differences in the proportion of time spent resting, transiting or in ARS between years during early or late chick-rearing (Table 3).

3.4. Spatial analysis

Average core foraging range sizes (50% utilization distributions) of parental gannets were significantly lower in early (2382 ± 797 km²; mean \pm SE) relative to

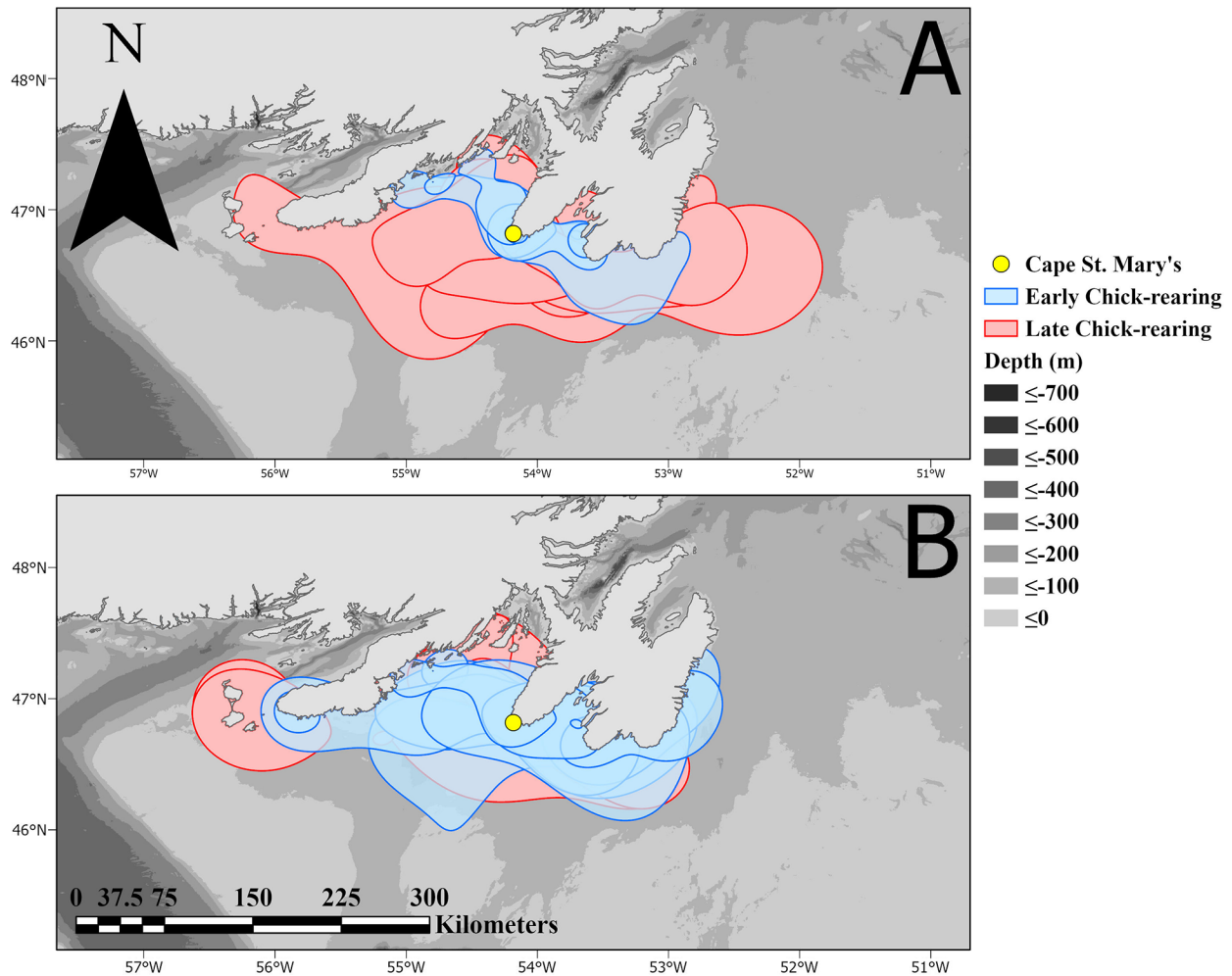


Fig. 3. Intra- and inter-annual 50% kernel density utilization distributions of tagged parental gannets from Cape St. Mary's, Newfoundland, Canada in (A) 2019 and (B) 2020 across both chick-rearing periods

late chick-rearing ($8558 \pm 1693 \text{ km}^2$) during 2019 ($t = 3.300$, $df = 9$, $p = 0.009$), but did not differ between chick-rearing periods in 2020 ($t = 0.395$, $df = 3$, $p = 0.720$; Fig. 3) Average core foraging area size was significantly greater ($t = 3.02$, $df = 9$, $p = 0.0145$) during early chick-rearing in 2020 ($7297 \pm 1420 \text{ km}^2$) compared to 2019 ($2382 \pm 797 \text{ km}^2$). No significant differences ($t = 0.070$, $df = 10$, $p = 0.945$) in core foraging area sizes were found in late chick-rearing between 2019 ($8558 \pm 1693 \text{ km}^2$) and 2020 ($8798 \pm 3531 \text{ km}^2$).

3.5. SST

Average SST during early chick-rearing differed between years, with the cooler 12 to 14°C isotherm enveloping Cape St. Mary's and much of the

observed foraging range of tagged birds in 2019 (Fig. 4A), and a northward shift of the 14 to 16°C isotherm observed in early chick-rearing in 2020 (Fig. 4B). A similar trend was observed for the late chick-rearing period, with the 12 to 14°C isotherm persisting around the Southern Avalon and Burin Peninsulas in 2019 (Fig. 4C), and the 14 to 16°C isotherm covering much of the gannet foraging range in 2020 (Fig. 4D). Further, the 16 to 18°C isotherm permeated further north in 2020, overlapping partially with the foraging ranges of Cape St. Mary's birds during late chick-rearing (Fig. 4D).

3.6. Capelin spawning sites

There were fewer reported used capelin beach spawning sites during early chick-rearing within the

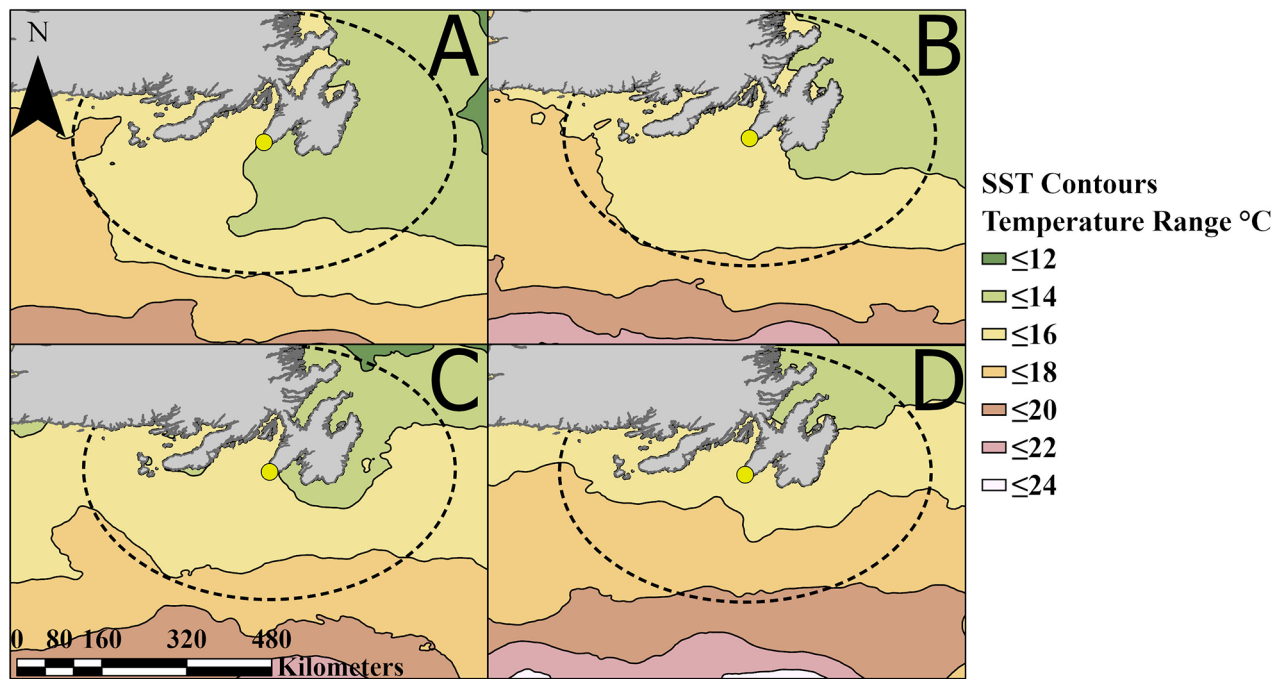


Fig. 4. Mean sea surface temperature (SST) contours in southeast Newfoundland from (A) early chick-rearing in 2019, (B) early chick-rearing in 2020, (C) late chick-rearing in 2019 and (D) late chick-rearing in 2020. (yellow dot) Location of the gannet colony at Cape St. Mary's

foraging range of Cape St. Mary's gannets in 2020 ($n = 19$) compared to 2019 ($n = 26$; Fig. 5, <https://ecapelin.ca/>). The nearest spawning site to the colony in 2020 was 34.3 km away compared to 13.2 km in 2019. Site-specific capelin spawning dates were slightly earlier on average and more variable in 2020 (July 3 ± 12.6 d, $n = 19$) than in 2019 (July 9 ± 5.9 d, $n = 26$).

4. DISCUSSION

Due to central-place foraging constraints, parental gannets must direct their foraging effort on the most energetically profitable prey. Available prey fields often change dramatically within and between years based on environmental and biological conditions (Montevecchi 2007, Garthe et al. 2011, Botha & Pistorius 2018). Intra-annual changes in foraging tactics and effort can also be modified by prey depletion around the colony (Lewis et al. 2001, Elliott et al. 2009).

As has been found among Cape gannets *Morus capensis* (Botha & Pistorius 2018), we demonstrate that northern gannet foraging tactics shift dramatically within the breeding season. Parental northern gannets exhibited prey switching, as they shifted away from capelin in early chick-rearing to solely

warm-water migratory pelagic fishes (mackerel, saury) in late chick-rearing, as capelin migrated out of coastal waters following their spawning period in June/July (Carscadden et al. 2013). This was shown by consistent changes in dive profiles, with U-shaped dives practically disappearing in favour of V-shaped dives in late chick-rearing during the breeding season in both 2019 and 2020, along with corroborative diet samples collected in 2019. Foraging effort in the form of increased foraging trip duration, and maximum and total distance were significantly higher during early chick-rearing in 2020 compared to 2019, while the number of dives per trip was significantly greater during late chick-rearing in 2020. These differences may have been associated with annual ocean climate-driven differences in prey distribution and availability in the region.

4.1. Intra-annual variation in foraging tactics

Daily dive profiles of parental northern gannets in 2019 and 2020 indicated changes in foraging tactics presumably linked to changes in prey choices during the breeding season based on the availability and distribution of different prey species and increasing energetic requirements of chicks (Figs. 2, S2 & S3; see also Montevecchi et al. 1984). Capelin-associated

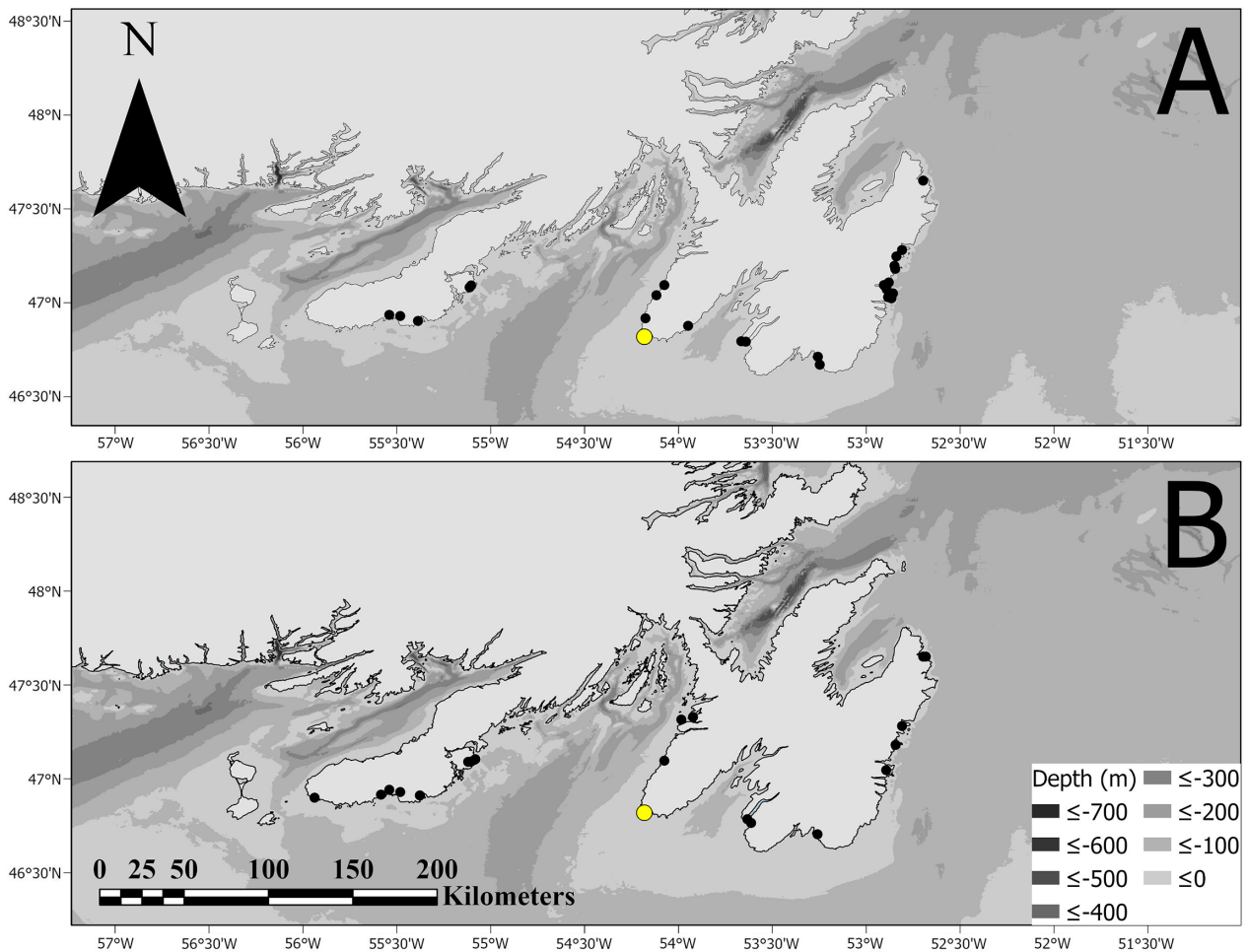


Fig. 5. Reported capelin spawning sites (black dots) within the foraging range of gannets from Cape St. Mary's, Newfoundland from (A) 2019 and (B) 2020 (<https://ecapelin.ca/>). (yellow dot) Location of the gannet colony at Cape St. Mary's

U-shaped dives occurred regularly during early chick-rearing before shifting to almost exclusively V-shaped dives in late chick-rearing. Previous research on dive strategies of Australasian gannets *M. serrator* suggested that dive profiles were driven by prey depth (Machovsky Capuska et al. 2011). Though dive profiles may differ due to prey depth, which likely accounts for some of the variation in dive profiles during early chick-rearing, our diet samples and previous work demonstrating the link between dive profiles of northern gannets and physiological and phenological constraints for capture of different prey (Garthe et al. 2000, 2011, 2014) support an intra-annual shift in the exploitation of different prey types. However, as U- and V-shaped dives both occur frequently in early chick-rearing, V-shaped dives at this time may be associated with herring or early arriving mackerel or saury, low density aggregations of capelin, fisheries discards and/or failed prey cap-

ture attempts. Further collection of diet samples concurrent with GPS tracking would help to ascertain these associations with dive profiles and prey types.

Northern gannets in the Northwest Atlantic are capable of prey switching between years based on environmental conditions and associated prey availability (Montevecchi 2007, Montevecchi et al. 2009, Garthe et al. 2011). Here we demonstrate that these same prey-switching patterns occur consistently intra-annually, as gannets demonstrated foraging flexibility in the form of behavioural shifts from exploiting capelin consistently in early chick-rearing, to mainly mackerel and saury in late-chick-rearing. These shifts are likely due to a combination of changing prey fields during the breeding season, with capelin moving off-shore following spawning and mackerel moving into Newfoundland waters in greater numbers from July onwards (Moores et al. 1975, Carscadden et al. 2013), as well as increasing

energetic demands of the chick (Montevecchi et al. 1984). The parental diets of Cape gannets also shift from primarily smaller, less calorically dense anchovy *Engraulis encrasicolus* in the guard stage of chick-rearing to larger, more energetically profitable saury in the post-guard stage (Botha & Pistorius 2018). Thus, comparative dietary studies of gannets, both within and across colonies, need to account for the timing of data collection during the breeding season. Inter-colony dietary or foraging behaviour comparisons (e.g. Garthe et al. 2007) need to integrate oceanographic differences in the timing of prey migration/spawning as this will influence foraging tactics and dietary composition.

Consistent with predictions from central-place foraging (MacArthur & Pianka 1966, Burke & Montevecchi 2009), foraging trip maximum and total distance were significantly greater during late chick-rearing in 2019 when parents were mainly exploiting more energetically dense mackerel and saury that were captured farther from the colony than capelin. The smaller less energetically dense capelin are typically inshore near intertidal or subtidal spawning locations during early chick-rearing (Nakashima & Wheeler 2002). Meanwhile, the more energetically dense mackerel and saury that migrate through the region during late chick-rearing are less constrained by coastal proximity, as mackerel spawning in Atlantic Canada is typically restricted to the Gulf of St. Lawrence (Sette 1943, Arai et al. 2021) and saury do not spawn regionally (Leim & Scott 1966). Contrastingly, in 2020, there were no significant differences in maximum or total foraging trip distance across chick-rearing periods, and average foraging trip duration was significantly higher in early chick-rearing. This was likely due to the lower abundance of capelin, as indicated by fewer occupied capelin spawning sites, along with the more variable timing of capelin spawning in the region in 2020, which may have necessitated higher search effort for high-density aggregations of spawning capelin, and/or an earlier switch to different prey sources. Trip directness was significantly greater during late chick-rearing than in early chick-rearing in both 2019 and 2020. This is likely because gannet diets consisted mainly of larger, more energetically dense pelagic prey in late chick-rearing, and thus, birds were likely to return to the colony after fewer foraging bouts. This is further reflected by dives per trip, as there were significantly fewer dives per trip in late chick-rearing in both years.

Proportion of time spent actively foraging during trips did not significantly differ between years,

suggesting that parental northern gannets did not alter their activity budgets during foraging trips in response to differing prey types and availability associated with annual differences in environmental conditions. However, in 2019, transiting times were higher in early relative to late chick-rearing and the proportion of time in ARS was significantly greater in early chick-rearing, though this was likely an artifact of higher proportions of time transiting in late chick-rearing. To clarify, the proportion of time spent foraging per individual trip remains relatively constant, and likely is not the best metric for comparing changes in foraging effort of parental northern gannets. Previous work has found differences in proportion of time spent in behavioural states between juvenile and adult seabirds. Juvenile wandering albatrosses *Diomedea exulans* have been found to spend more time resting on the water at sea than adults (Riotte-Lambert & Weimerskirch 2013). In addition, the proportion of time spent foraging per day by juvenile European shags *Phalacrocorax aristotelis* is less than that of adults, and increased juvenile mortality has been associated with lower foraging efficiency (e.g. more time spent actively foraging; Daunt et al. 2007). Thus, activity budgets of time spent foraging during foraging trips is likely a learned skill critical for survival that juvenile seabirds must acquire to provide for themselves, and ultimately for their offspring in adulthood. Further, to survive and successfully rear young, the proportion of time spent actively foraging by parental gannets is likely bounded by energetic constraints, as plunge/pursuit diving is the most arduous and energetically costly behaviour during foraging trips (Green et al. 2009).

4.2. Inter-annual variation in foraging tactics

Foraging effort in the form of trip duration and maximum and total distance were significantly greater during early chick-rearing in 2020 compared to 2019 (Table 3, Fig. 3). This increased effort could indicate that prey availability/quality close to the colony was lower during this period in 2020, as parental gannets needed to work harder to acquire resources. Occupied capelin spawning sites reported in 2020 in southeastern Newfoundland corroborate this idea, as there were far fewer capelin spawning sites in proximity to Cape St. Mary's, and more variation in timing of spawning compared to 2019 (Fig. 5, <https://ecapelin.ca/>). Reduced occupation of spawning sites might be due to warmer waters (>14°C)

along the southeast Newfoundland coast during early chick-rearing in 2020 (Fig. 4); capelin typically spawn at sites $<12^{\circ}\text{C}$ (Davoren 2013, Crook et al. 2017).

Increased foraging effort among seabirds was not limited to gannets breeding in coastal Newfoundland from 2019 to 2020. Striking similarities were also seen in the foraging behaviour of razorbills *Alca torda* along the northeast coast of Newfoundland, where foraging trip distance and duration were much greater in 2020 compared to previous years (Lescure 2021). This increased effort was also linked to reduced capelin availability, as 2020 had the lowest peak capelin biomass on the northeast coast as assessed from yearly hydroacoustic surveys since 2009 (G. K. Davoren unpubl. data). Though capelin appeared to be scarce in Newfoundland waters in 2020, it is also possible that mackerel and/or saury arrived earlier, and gannets shifted their attention towards the more energetically profitable prey sooner.

In contrast to the observed increase in foraging effort during early chick-rearing and possible associations with capelin availability and distribution, there were no significant differences in trip duration and distance in late chick-rearing between years, suggesting that prey availability (e.g. mackerel, saury) did not differ significantly between years. This lack of difference in foraging effort during late chick-rearing could be explained by the fact that a critical SST threshold of approximately 15 to 16°C for mackerel (Olafsdottir et al. 2019) was not surpassed in much of the foraging range of Cape St. Mary's gannets in either year (Fig. 4). However, multidecadal trends in average SST within the foraging range of parental gannets from Cape St. Mary's suggest that this temperature threshold will likely be surpassed in the future, which could result in lowered availability of mackerel and resultant increases in foraging effort and low reproductive success (Guillemette et al. 2018, d'Entremont et al. 2022).

Declining mackerel availability has been linked to lower gannet reproductive success on nearby Bonaventure Island in the Gulf of St. Lawrence (Guillemette et al. 2018), where warming ocean temperatures are likely further compounding ill effects on the stock associated with fisheries pressure (Plourde et al. 2015). For example, a marine heatwave event in the Northwest Atlantic in 2012, where the 16°C isotherm permeated across the region, resulted in mass colony abandonment and reproductive failure of gannets across several colonies in Atlantic Canada (Montevecchi et al. 2021). Additionally, a rapid onset deterioration of gannet nutritional

condition was observed during this marine heatwave event on Bonaventure Island (Franci et al. 2015), suggesting acute, climate-driven prey scarcity had dramatic effects on these populations. Thus, rapid ocean warming during late chick-rearing may alter the availability and distribution of critical prey species such as mackerel (Olafsdottir et al. 2019). The effects of changing climate could also impact mackerel distributions and recruitment through bottom-up effects on their planktonic prey (Castonguay et al. 2008, Pacariz et al. 2016). These influences could induce increased foraging effort and low reproductive success in gannets. Alternatively, recent modelling has shown that warming waters might increase spawning habitat suitability of mackerel in southern Newfoundland towards the latter half of this century (Mbaye et al. 2020), which could improve gannet foraging conditions and reproductive success.

Even so, as generalist foragers, gannets appear flexible to shifts in fish assemblages and distribution associated with changing climate by exploiting other key prey species such as Atlantic saury, which have higher temperature tolerances (Dudley et al. 1985). Indeed, a shift towards saury as the preferred warm-water prey may already be occurring, as it now appears to be the main warm-water prey species in gannet diets on nearby Funk Island (W. A. Montevecchi unpubl. data).

4.3. Conclusions/future directions

This study suggests that gannets in the Northwest Atlantic shift their foraging effort as the breeding season progresses and different prey fields move in and out of the region. Differences in foraging effort between and within years are associated with varying prey availability which is influenced in part by ocean climate. Monitoring of foraging behaviour and reproductive success should be continued to further assess the interactions between changing climate, prey availability and top-predator responses. Key colony sites would include those at the extremes of their breeding range, where their tolerance to changing climate and prey availability is expected to be most vulnerable (Barrett et al. 2017, Montevecchi et al. 2021, d'Entremont et al. 2022).

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