The Effects of Seasonal and Annual Differences in Prey and Environmental Conditions on a Colonial Seabird at the Southern Limit of its Breeding Range

by

Kyle James Nestor d'Entremont (BSc. Hons.)

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ABSTRACT

The Northern Gannet (*Morus bassanus*) is the largest seabird breeding in the North Atlantic Ocean. Their breeding colonies stretch across a broad geographical range, and colonies near the southern extent of their breeding range have recently exhibited poor productivity. Gannets are opportunistic, generalist foragers and consume a wide range of prey including Atlantic mackerel (*Scomber scombrus*), capelin (*Mallotus villosus*), Atlantic herring (*Clupea harengus*) and Atlantic saury (*Scomberesox saurus*). The distribution and availability of these pelagic fishes depend on ocean temperature. In this thesis, I fill in critical knowledge gaps on how gannets nesting at their southernmost colony at Cape St. Mary's, NL respond to differences in prey availability and sea surface temperature. In Chapter 2, I examine the effects of prey availability and sea surface temperature during the breeding season on gannet productivity over a multi-decadal timespan. I found that declines in mackerel availability and warming waters in late chick-rearing were associated with depressed productivity. In Chapter 3, I examine the foraging behaviour of gannets and how it differs between and within years. Gannets switched their foraging tactics from preying on capelin in early chick-rearing to larger pelagics in late chick-rearing. Gannets exhibited greater foraging effort during early chick-rearing in 2020 than 2019 which was associated with lowered capelin availability. Overall, gannets were negatively impacted by lowered prey availability and warming sea surface temperatures.

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EPIGRAPH

“…Let me fish off Cape St. Mary’s, Where the hagdowns sail and the foghorns wail…Take me back to that snug green cove, Where the seas roll up their thunder…”

- Otto P. Kelland

CHAPTER 1: PREY AVAILABILITY AND OCEAN CLIMATE INFLUENCES ON FORAGING TACTICS: THEORY, BACKGROUND, AND THESIS OUTLINE

1.1 THEORY

1.1.2 Central Place Foraging Theory

For at least part of their lives, many animals are constrained by having to forage from a central location to which they must return. This behaviour known as central place foraging (CPF) is typically associated with offspring provisioning and is frequently exhibited by colonial animals, such as many social insects (Cresswell et al. 2001; Burd & Howard 2005; Naug & Wenzel 2006), some marine mammals (Baylis et al. 2008), and many species of seabirds during the breeding season (Burke & Montevecchi 2009; Elliott *et al.* 2009). A corollary of CPF theory, optimal foraging theory, suggests that when foraging from a central location, the energetic benefits received from prey/food captured must outweigh the energetic costs associated with travel, search, prey capture and transport (MacArthur & Pianka 1966). Therefore, the expectation is that larger or more energy rich prey would be associated with longer foraging trips to produce sustainable energetic balance.

In the Northwest Atlantic, the energetic value (kJ/g) of forage fishes varies, with large pelagic fish, such as Atlantic mackerel (*Scomber scombrus*, 10.3 kJ/g) and Atlantic herring (*Clupea harengus*, 9.2 kJ/g), being larger and about twice as energy dense as small inshore forage fish such as capelin (*Mallotus villosus*, 4.2 kJ/g; Montevecchi et al. 1984). As Northern Gannets are generalist, opportunistic, and prey-switching foragers, foraging theory predicts that during breeding they should preferentially target different prey types based on energy content, distance of prey from the colony, and the associated effort/gain trade-off (Garthe et al. 2007).

1.1.3 Ashmole's Halo/ Prey Depletion Hypothesis

When considering CPF theory, prey depletion and availability near the colony must also be taken into account in the foraging decisions of parental seabirds. Ashmole (1963; 1971) hypothesized that parental colonial seabirds reduce the quantity of available prey around the colony via their self-sustenance and chick-provisioning activities. This depletion of prey radiating from the colony centre has since been termed Ashmole's or alternatively, Storer-Ashmole's halo (Birt et al. 1987; Elliott et al. 2009). Depletion of prey around seabird colonies inflicts a density-dependent constraint on the per capita growth rate, as well as colony size (Lewis et al. 2001; Ainley et al. 2003). Consistent exploitation of prey by seabirds does not only cause dispersal of fish further away from the colony as the breeding season progresses, but it can also push fish schools to deeper depths to evade capture (Ainley et al. 2003; Elliott et al. 2009). These circumstances compel seabirds to either dive deeper or travel further for their prey (Lewis et al. 2001). Alternatively, prey availability around seabird colonies during the breeding season is altered by the phenology of forage fishes, with abundance of some species within the foraging range of colonies increasing due to inshore movements for their spawning period (e.g. capelin, Carscadden et al. 2013), or post-spawning migration (e.g. mackerel, Moores et al. 1975).

1.2 BACKGROUND INFORMATION

With consistent predation pressure possibly limiting prey abundance and distribution surrounding colonies, we must consider how changes in the environment may also influence prey and the resultant behaviour of marine top predators. Rising global temperatures and associated environmental changes are greatly impacting biodiversity, including the abundance, distribution, behaviour, and interactions of marine and terrestrial animals in diverse ecosystems (Walther et al. 2002; Miller-Rushing et al. 2010). Changes in breeding phenology (the timing of breeding/spawning) of many organisms, especially at higher latitudes, have been heavily linked to these climactic shifts (Thackeray et al. 2010; 2016) and have put many animals at risk (Bradshaw & Holzapfel 2006). Rising ocean temperatures have had adverse effects on the breeding phenology of many marine fish species (Fincham et al. 2013; Macqueen & Marshall 2017) and have been linked to distributional shifts of marine fishes in the North Atlantic, with fish populations moving to higher latitudes and deeper waters (Perry et al. 2005; Dulvy et al. 2008). Increased environmental variability (i.e. sea surface temperature fluctuations) associated with climate change has also had profound impacts on the recruitment and population dynamics of marine prey species (Attrill & Power 2002; Richards et al. 2012) and top predators (Regehr & Montevecchi 1997).

For example, capelin (*Mallotus villosus*), the keystone forage fish species of the Northwest Atlantic (Lavigne 1996; Davoren et al. 2007), experienced an ocean climate forced bottom-up stock collapse in the early 1990s associated with a centennially significant cold-water perturbation (Buren et al. 2014). Since then, they have exhibited little population recovery, along with distributional shifts, delayed and protracted spawning, spawning at younger ages and reduced size (Buren et al. 2019; Montevecchi et al. 2019). These shifts have had varying consequences for seabird top predators of the Northwest Atlantic (Montevecchi & Myers 1996; Davoren & Montevecchi 2003; Davoren et al. 2012). Given that the cold-blooded fish species that seabirds prey upon are initial responders to changes in ocean temperature, predator-prey mismatches in time and space are the expectation, circumstances that make seabirds exceptionally vulnerable to oceanic climate change (Keogan et al. 2018). By studying their diets, foraging tactics, and breeding success, seabirds provide a robust indication of prey availability and distribution, thereby providing inference on the condition of marine food webs (Gaston et al.

2009). As the reproductive and migratory strategies of forage fish species are heavily reliant upon ocean temperature (Perry et al. 2005; Dulvy et al. 2008; Fincham *et al.* 2013; Macqueen & Marshall 2017), ocean climatic anomalies can directly impact the availability of forage fish in proximity to a colony on a 3-dimensional scale (vertical and horizontal displacement). This environmentally dependent availability of prey can have varying consequences for marine birds in the form of dramatic alterations in foraging behaviour and potential implications for reproductive success.

By monitoring their breeding success, foraging tactics, and dietary composition, I will obtain valuable information on how Northern Gannets (*Morus bassanus*) breeding at the southern limit of their breeding range might respond to seasonal and annual shifts in prey availability and distribution associated with varying intra- and inter-annual ocean conditions.

1.3 STUDY SPECIES

The Northern Gannet is a large long-lived seabird of the North Atlantic that nests in dense colonies on coastal islands and cliffs (Mowbray 2020). They are monogamous, tending to mate with the same individual for life. Clutch size is limited to one egg, though an egg may be replaced during the breeding season. Their breeding season in the Northwest Atlantic runs from April through October. Gannets are generalists and feed opportunistically on a wide spectrum of forage fishes including capelin, Atlantic mackerel (*Scomber scombrus*), Atlantic herring (*Clupea harengus*) and Atlantic saury (*Scomberesox saurus;* Montevecchi 2007). They can switch diet composition radically from primarily cold-water species (such as capelin and herring) to migratory warm-water fish species (such as mackerel and saury) as ocean temperature fluctuates (Montevecchi 2007). Gannets plunge dive for pelagic fish and squid, reaching depths of up to 22 metres with durations of up to 38 seconds (Garthe et al. 2000). At times, they exploit scraps and discards from fishing vessels (Votier et al. 2013; Patrick et al. 2015). Parental provisioning alternates between mates, with the male provisioning neonatal chicks at greater rates and females feeding chicks more frequently during later development (Montevecchi & Porter 1980). Breeding adults forage primarily within 60 km of colony (Kirkham *et al.* 1985) but have been known to range as far away from the colony as 138 km with total travelled distances of 452 km in the Northwest Atlantic (Garthe et al. 2007) and as far as 232 km with total distance travelled of 540 km in the North Sea (Hamer et al. 2001). Average foraging trip durations of 14.9 h and 28.0 h have been recorded in the Northwest Atlantic at colonies on Funk Island and Bonaventure Island, respectively (Garthe et al. 2007). Gannets respond to reduced prey availability by increasing foraging effort, often in the form of increased range and duration of foraging trips (Garthe et al. 2011). Dive profiles of gannets can also provide inference on the prey species they are likely feeding on, with rapid vertical V-shaped dives representing capture of a single large pelagic fish near the top of the water column, and longer, deeper U-shaped dives representing the capture of numerous smaller pelagic fishes such as capelin (Garthe et al. 2000).

1.4 STUDY SITE

Research was carried out at the Cape St. Mary’s Ecological Reserve (46.831944 N, -54.165833 W), Newfoundland (Fig. 1) during June through October in 2019 and July through October in 2020.

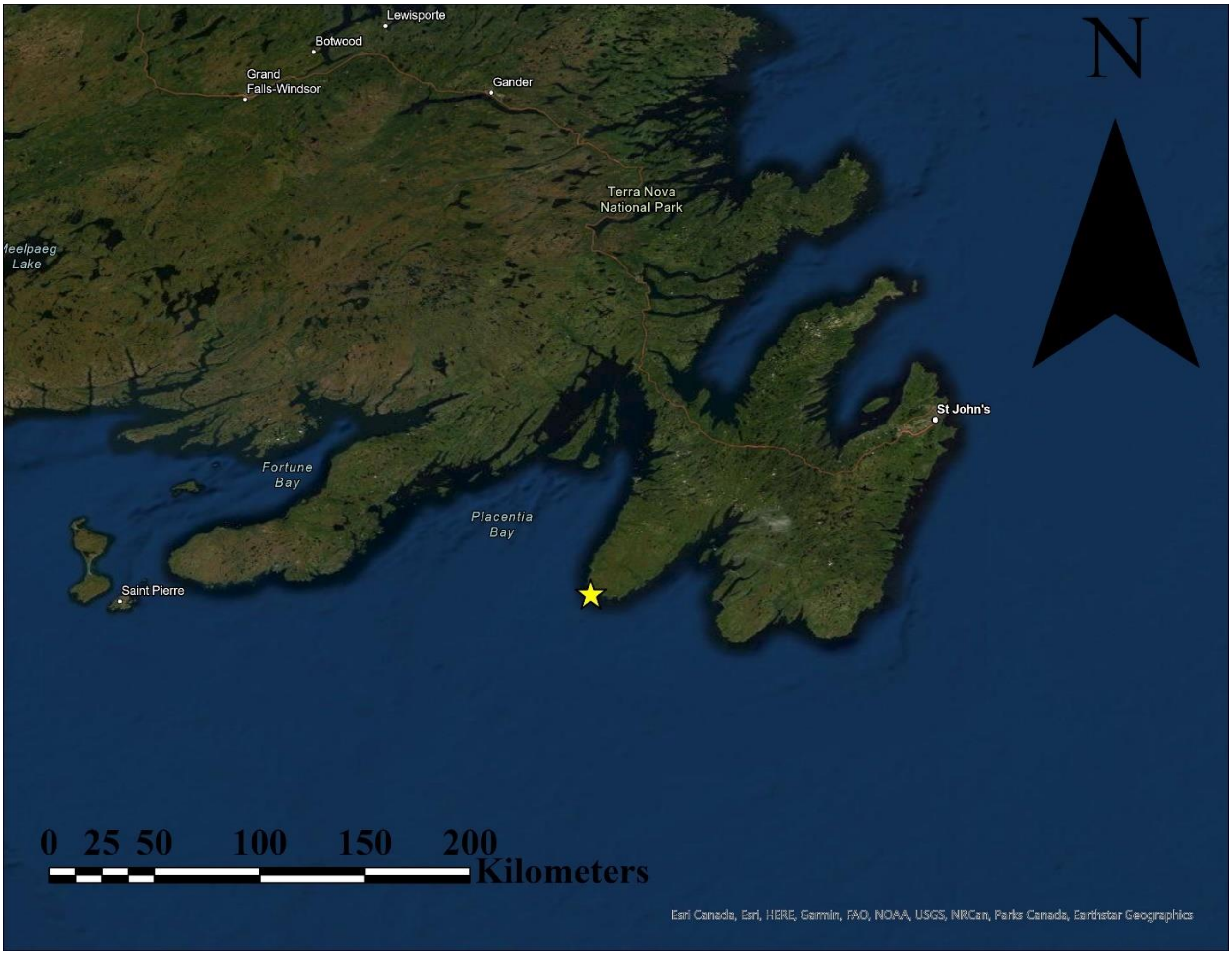

Figure 1.1 Map of the location of Cape St. Mary's Ecological Reserve, Newfoundland and Labrador indicated by the yellow star.

Cape St. Mary's is the site of the Northern Gannets' southernmost colony in the world and before my thesis work, there has been no research conducted on the foraging ecology of these birds at this location. With this colony's geographic location being situated at the southernmost extent of the species' breeding range, it is expected to experience the negative influences of oceanic climate change before colonies at higher latitudes (Montevecchi et al. 2021). In fact, the gannet colony at this location has experienced a prolonged period of poor productivity and plateaued population growth since 2012, when mass colony abandonment and record low breeding success coincided with the 2012 Northwest Atlantic marine heatwave event (Montevecchi et al. 2021, S Wilhelm unpubl. data). Additionally, plateaued population growth and low productivity have also been witnessed at southerly colonies in the Gulf of St. Lawrence (e.g. Bonaventure Island, Great Bird Rock, J-F Rail unpubl. data). Thus, it is critical to disentangle the impacts of warming ocean temperatures and alterations in prey availability and distributions on the reproductive success and foraging ecology of this colony.

1.5 THESIS OUTLINE

The main objective of this study is to further our understanding of how forage fish availability and distribution, as well as ocean temperature, affects the breeding success, foraging behavior and parental diets of Northern Gannets at the southern limit of their breeding range at Cape St. Mary's, Newfoundland and Labrador. I predict that gannet productivity will be negatively influenced by warmer sea surface temperature and lowered prey availability, as the distribution of critical prey species for gannets such as capelin, Atlantic mackerel and Atlantic herring is dependent on ocean temperature. Consistent with Ashmole's Halo hypothesis and optimal foraging theory, I predict that gannet foraging effort (e.g. distance travelled, dives per trip, trip duration) will increase when prey availability is lower and/or when gannets are pursuing more energetically dense prey sources (e.g. the pursuit of mackerel compared to capelin). The thesis is comprised of four chapters, and both Chapters 2 and 3 have been formatted as manuscripts for publication in peer-reviewed journals.

The present chapter, **Chapter 1**, serves as a general introduction of theory and background information. It also outlines the novelty of my tracking data for this location, as well as the importance of my study, as the Northern Gannet colony at Cape St. Mary's may be one of the first to be subjected to the influences of our warming climate owing to its southerly geographic location.

Chapter 2 documents the productivity of gannets nesting at Cape St. Mary's and investigates the influences of biophysical factors such as sea surface temperature (SST) within their foraging range, as well as abundance of key forage fish species such as capelin, Atlantic Herring and Atlantic Mackerel upon their reproductive success.

Chapter 3 investigates the foraging tactics of parental Northern Gannets, and how they change during the chick-rearing period and between years by using GPS telemetry. Specifically, I determine whether there are any temporal differences in foraging range, foraging trip distance and duration, dive characteristics (dive profiles, frequency of dives, etc.), and foraging behavioural states (transit, area-restricted search/foraging, and rest) as the breeding season progresses and between years. By examining foraging trip distance and duration and number of dives, I infer how foraging effort changes over time during chick-rearing. Additionally, examining behavioural states allowed to disentangle the proportion of time gannets engaged in activities of varying energetic costs. Diet samples were also collected to cross-validate prior assumptions of dive profile shapes with specific prey types.

Finally, **Chapter 4** concludes the thesis with a general summary and discussion by amalgamating information from Chapters 2 and 3 with existing literature.

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1.7 CO-AUTHORSHIP STATEMENT

Chapter 2:

Chapter 2 has been published in the ICES Journal of Marine Science (DOI: 10.1093/icesjms/fsab240). The following is a list of co-authors and their contributions to the paper.

Kyle J. N. d’Entremont – Conceptualization, Methodology, Data Collection, Data analysis, Writing

Leanne Guzzwell – Data collection, Methodology

Sabina I. Wilhelm – Data collection, Methodology, Writing (Review and edits)

Vicki L. Friesen – Data collection, Writing (Review and edits)

Gail K. Davoren – Writing (Review and edits)

Carolyn J. Walsh – Writing (Review and edits)

William A. Montevecchi – Conceptualization, Methodology, Writing (Review and edits), Supervision

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Kyle J. N. d’Entremont – Conceptualization, Methodology, Data collection, Data analysis, Writing

Gail K. Davoren – Conceptualization, Writing (Review and edits)

Carolyn J. Walsh – Writing (Review and edits)

Sabina I. Wilhelm – Writing (Review and edits)

William A. Montevecchi – Conceptualization, Methodology, Data collection, Writing (Reviews and edits), Supervision

CHAPTER 2: NORTHERN GANNETS (MORUS BASSANUS) BREEDING AT THEIR SOUTHERN LIMIT STRUGGLE WITH PREY SHORTAGES AS A RESULT OF WARMING WATERS

2.1 ABSTRACT

Northern Gannet (*Morus bassanus*) colonies near the species' southernmost limits are experiencing plateaued or declining population growth and prolonged poor productivity. These trends have been linked to reductions in the availability of the species' key prey, the Atlantic mackerel (*Scomber scombrus*). Declines in mackerel availability have been associated with warming ocean temperatures and over-fishing. Here, we assessed the influence of prey availability, abundance, and sea surface temperature (SST) during the breeding season on Northern Gannet reproductive success over a multi-decadal time span at their southernmost colony at Cape St. Mary's, NL, Canada. We demonstrate that warming SST affects reproductive success differently in early versus late chick-rearing, but that overall, declining mackerel availability (landings and biomass) due to warming SST and over-exploitation has resulted in poor productivity of Northern Gannets at their southernmost limit. Our study is consistent with previous findings in other colonies in Atlantic Canada and France, and contrasts with findings in more northern colonies where mackerel population increases, and range expansion are coinciding with gannet population growth. This implies that warming SST is having opposing influences on Northern Gannets and mackerel at the different extremes of the gannets' breeding range.

2.2 INTRODUCTION

Seabirds exist in a dynamic ocean environment. Their survival and reproductive success depend on their behavioural and physiological capacity to negotiate the biophysical variation that they encounter daily (Botha and Pistorius 2018, Cerveira et al. 2020). Beyond this, seabirds are vulnerable to a myriad of anthropogenic influences. These include mercury contamination (Albert et al. 2020), oil and gas production (Wiese and Robertson 2004), bycatch (Anderson et al. 2011), light pollution (Rodriguez et al. 2012) and changes in prey distribution and abundance associated with fishing and over-fishing (Cury et al. 2011; Montevecchi 2022).

Anthropogenic climate change is the most potent and urgent stressor for seabirds (Dias et al. 2019, Piatt et al. 2020). Rising ocean temperatures have induced shifts in the breeding phenology and distribution of many marine fishes and zooplankton (Perry et al. 2005, Dulvy et al. 2008, Fincham and Engelhard 2013, Macqueen and Marshall 2017, Olafsdottir et al. 2019). Seabirds have however exhibited limited plasticity of their breeding phenology in response to ocean warming (Keogan et al. 2018), creating spatiotemporal mismatches with their cold-blooded prey (Regular et al. 2014). Increased seabird mortality and decreased productivity have been associated with reduced prey availability and quality due to anomalous ocean climate events (Montevecchi and Myers 1997, Buren et al. 2012, 2019, Watanuki and Izzo 2012, von Biela et al. 2019, Piatt et al. 2020, Montevecchi et al. 2021) and to over-exploitation by commercial fisheries (Cury et al. 2011, Montevecchi 2022). Seabird responses to these stressors are expressed in reproductive success and foraging behaviour (Cairns 1988). Warming ocean climate can alter behaviour, survival and reproductive success via indirect impacts on prey availability and quality during the breeding season. Heightened sea surface temperature (SST) during the breeding season has been linked to increased foraging effort (e.g. travelling further distances for food) and reproductive failure by way of decreased primary productivity and diminished forage fish quality and quantity (Jones et al. 2018, Piatt et al. 2020, Osborne et al. 2020).

Northern Gannets (*Morus bassanus*) are the largest breeding seabirds of the North Atlantic Ocean. Their breeding range in 48 known colonies is distributed across almost 30 degrees of latitude (46.81 to 74.35 °N). In Europe, colonies range from Rouzic Island, France in the south (Le Bot et al. 2019, Grémillet et al. 2020) to Bjørnøya, Norway inside the Arctic Circle (Barrett et al. 2017), with other colonies in Iceland, Russia, the Faeroe Islands, the United

Kingdom, and Ireland, Germany, and (Table 1, Mowbray 2020). In North America, six colonies are located in Atlantic Canada (three in Québec; three in Newfoundland), all of which are further south than European colonies, with the exception of Funk Island Newfoundland, Canada (49.7569° N, 53.1811° W) which lies at a higher latitude than the southernmost European colony - Rouzic Island (48.8992° N, 3.4373° W).

Owing to a prolonged breeding season from late spring (April-May) until early fall (September-October), Northern Gannets are subject to wide seasonal variation in environmental conditions and shifts in prey availability through the breeding season. Key prey species include, capelin (*Mallotus villosus*), Atlantic herring (*Clupea harengus*), Atlantic mackerel (*Scomber scombrus*), Atlantic saury (*Scomberesox saurus*), and short-finned squid (*Illex illecebrosus*), as well as several other species of schooling fish during the non-breeding period (Montevecchi et al. 2007, 2009). The distribution and phenology of these species are heavily reliant on ocean temperature (Brunel and Dickey-Collas 2010, Buren et al. 2019, Fisheries and Oceans Canada (DFO) 2019, Olafsdottir et al. 2019). Depending on environmental conditions and prey availability during the breeding season, Northern Gannets switch from cold-water species such as capelin to warm-water species such as Atlantic mackerel and Atlantic saury (Montevecchi 2007, Garthe et al. 2007).

With such a broad dietary spectrum and plasticity, declines in productivity and populations of Northern Gannets would signal concern for ecosystem health and resiliency, indicating that forage fish availability may be waning (Guillemette et al. 2018). This appears to be the case at the southern extent of the species' breeding range, where reproductive success has been relatively low (Le Bot et al. 2019, Grémillet et al. 2020, Montevecchi et al. 2021, Rail et al. unpubl. data), and where three of the four colonies considered declining are located (Table 2.1).

Table 2.1. Latest estimated population size and growth trend of all Northern Gannet colonies.

Colony	Latitude	Longitude	Year Counted	Population Trend	Breeding Pairs	Source
Canada						
Cape St. Mary's	46.81	-54.18	2018	Stable/Plateaued	14789	S. Wilhelm unpubl. data
Great Bird Rock	47.83	-61.15	2017	Stable/Plateaued	25000	Rail et al. unpubl. data
Baccalieu Island	48.12	-52.78	2018	Increasing	2253	S. Wilhelm unpubl. data
Bonaventure Island	48.5	-64.15	2020	Stable/Plateaued	49000	Rail et al. unpubl. data
Anticosti Island	49.15	-61.7	2019	Declining	200	Rail et al. unpubl. data
Funk Island	49.77	-53.18	2018	Increasing	9987	S. Wilhelm unpubl. data
France						
Rouzic Island	48.90	-3.44	2017	Declining	18000	Le Bot et al. 2019
Channel Islands						
Les Etacs	49.70	-2.24	2015	Increasing	5960	Copping et al. 2018
Ortac	49.72	-2.29	2015	Stable/Plateaued	2777	Copping et al. 2018
Wales						
Grassholm Island	51.73	-5.48	2015	Declining	39000	JNCC 2016
Ireland						
Bull Rock	51.59	-10.27	2014	Increasing	6388	Newton et al. 2015
Little Skellig	51.78	-10.51	2014	Increasing	35294	Newton et al. 2015
Great Saltee	52.12	-6.62	2014	Increasing	4722	Newton et al. 2015
Ireland's Eye	53.40	-6.06	2014	Stable/Plateaued	547	Newton et al. 2015
Lambay	53.49	-6.02	2014	Increasing	728	Newton et al. 2015
Clare Island	53.80	-10.00	2014	Increasing	267	Newton et al. 2015
England						
Bempton Cliffs	54.15	-0.17	2017	Increasing	13392	JNCC 2016
Germany						
Heligoland	54.18	7.89	2017	Unknown	656	Dierschke et al. 2018
Scotland						
Scar Rocks	54.67	-4.70	2014	Stable/Plateaued	2375	Murray et al. 2015
Ailsa Craig	55.25	-5.12	2014	Increasing	33226	Murray et al. 2015
Bass Rock	56.08	-2.64	2014	Increasing	75259	Murray et al. 2015
Barra Head	56.78	-7.64	2014	Increasing	7	Murray et al. 2015
Troup Head	57.69	-2.29	2014	Increasing	6456	Murray et al. 2015
St. Kilda	57.81	-8.59	2013	Stable/Plateaued	60290	Murray et al. 2015
Flannan Isles	58.29	-7.59	2013	Increasing	5280	Murray et al. 2015
Sule Stack	59.02	-4.51	2013	Stable/Plateaued	4550	Murray et al. 2015
Sule Skerry	59.08	-4.41	2013	Increasing	1870	Murray et al. 2015
Sula Sgeir	59.10	-6.16	2013	Increasing	11230	Murray et al. 2015
Westray	59.29	-2.98	2014	Increasing	751	Murray et al. 2015
Fair Isle	59.54	-1.63	2014	Increasing	3591	Murray et al. 2015
Foula	60.13	-2.07	2013	Increasing	1226	Murray et al. 2015
Noss	60.14	-1.02	2014	Increasing	11786	Murray et al. 2015
Hermaness	60.81	-0.88	2014	Increasing	25580	Murray et al. 2015
Faeroe Islands						
Mykinesholmur	62.10	-7.68	2004	Unknown	2000	Jensen et al. 2005
Iceland						
Vestmannaeyjar	63.38	-20.35	2014	Increasing	15044	Garðarsson 2008, 2019
Eldey	63.74	-22.96	2013	Stable/Plateaued	14810	Garðarsson 2008, 2019
Skrúður	64.90	-13.62	2014	Increasing	6051	Garðarsson 2008, 2019
Skoruvíkurbjarg	66.38	-14.87	2013	Increasing	656	Garðarsson 2008, 2019
Rauðinúpur	66.51	-16.54	2013	Increasing	655	Garðarsson 2008, 2019
Russia						
Kharlov	68.82	37.33	2016	Stable/Plateaued	241	Barrett et al. 2017
Norway						
Buholemene	67.77	12.75	2015	Increasing	725	Barrett et al. 2017
Oddskjæran	68.33	14.25	2015	Stable/Plateaued	13	Barrett et al. 2017
St. Ulvøyhomen	68.52	14.52	2015	Stable/Plateaued	330	Barrett et al. 2017
Forøya Islands	69.30	15.97	2015	Increasing	187	Barrett et al. 2017
Kvitvær	70.22	18.70	2015	Declining	21	Barrett et al. 2017
Syltefjord	70.60	30.30	2016	Stable/Plateaued	563	Barrett et al. 2017
Storstappen	71.15	25.32	2015	Stable/Plateaued	1450	Barrett et al. 2017
Bjørnøya	74.35	19.12	2016	Increasing	52	Barrett et al. 2017

Northern Gannet populations in the Northwest Atlantic experienced rapid growth since the 1980s (Chardine et al. 2013). In recent years, however, gannet colonies at the southern extent of the species' breeding range have exhibited stagnant and leveling population growth and poor reproductive success (Montevecchi et al. 2021; Rail et al. unpubl. data). These negative trends coincide with warming ocean temperatures within the foraging ranges of breeding colonies and declining standing stock biomass (SSB) of key forage fish species such as Atlantic mackerel, Atlantic herring, and capelin (Guillemette et al. 2018, Buren et al. 2019, Montevecchi et al. 2021). These concerning demographic trends mimic similar population declines and poor productivity at the southern extent of the species' range in the Northeast Atlantic on Rouzic Island (Le Bot et al. 2019, Grémillet et al. 2020), suggesting that colonies near the species' southern limits may be suffering from food scarcity. In contrast, colonies at the northern extent of the Northern Gannets' range in the eastern Atlantic have expanded into the Arctic Circle in Norway and have exhibited population growth and colony proliferation (Barrett et al. 2017). These trends coincide with rapidly warming water that has facilitated mackerel range expansions into Arctic waters (Olafsdottir et al. 2019). Warming ocean climate effects are having opposing impacts at the northern and southern limits of the Northern Gannets' breeding range.

The Northern Gannets' southernmost colony at Cape St. Mary's has plateaued in recent years with breeding pairs rising from 5,515 in 1984 to ~14,598 pairs at present (Chardine et al. 2013, S Wilhelm unpubl. data). Bonaventure and Rouzic Islands show similar trends. Reproductive success at Cape St. Mary's was monitored sporadically in the 1970s and 1980s, and systematically every year since 2009. Success has been poor since 2012 when mass colony abandonment and reproductive failure occurred in conjunction with a marine heatwave (Montevecchi et al. 2021).

Given warming ocean conditions and forecasts of increasing frequency of extreme marine heatwaves (Oliver et al. 2019, Schlegel et al. 2021) and fishery pressures (DFO 2019), as well as the negative population trends in colonies at similar latitudes, it is timely to assess the associations of the Northern Gannet's southernmost colony with environmental change and forage fish availability. We predict that reduced forage fish availability in their foraging range will have the greatest influence on reproductive success as it is a direct biological constraint. Secondarily, we predict that above normal SST departures in their foraging range during the breeding season will have secondary indirect influences on Northern Gannet productivity through alterations in the phenology and distribution of key prey species.

2.3 METHODS

2.3.1 Study Site

At Cape St. Mary's, the gannets nest on an isolated sea-stack known as Bird Rock, and on adjacent mainland cliffs. Their maximum foraging range from Cape St. Mary's is approximately 250km (see Fig. 2.1).

2.3.2 Reproductive Success

Since 2009, collaborations among the Canadian Wildlife Service, Memorial University of Newfoundland (MUN), and Newfoundland and Labrador Parks staff have monitored the reproductive success of Northern Gannets breeding at Cape St. Mary's, Newfoundland, Canada (46.81 ^{o} N, -54.18 ^{o} W). Northern Gannet nests were monitored for reproductive success from

2009 to 2020, (Table 2.2) in four study plots on Bird Rock, each consisting of 30 – 50 monitored nests per year. Two plots were on the plateau of Bird Rock, one on a sheer cliff face protected from the dominant southerly winds and one on a heavily sloped cliff. Reproductive success data were also collected in 1977 and from 1983 to 1986 in the two plots on the plateau.

Reproductive success for 1977, 1983, and 2009 through 2020 was determined by whether pairs had successfully brooded a pre-fledging chick by early to mid-September. Reproductive success values from 1984 to 1986 were calculated from nest checks conducted in late September. Nests that were monitored during 1977 and 1983-1986 were located within study plots that were monitored annually from 2009 to 2020. Annual reproductive success was estimated by calculating the average proportion of apparently occupied nests (AON, nest sites which had either an adult(s) or chick present) within the study plots during a one-day count of nests that had a near-fledgling chick present on or as near as possible to 1 September (Guzzwell et al. unpubl. data).

2.3.3 Fisheries Landings and SSB as Proxies for Prey Availability

Total landings (tonnes) of three key forage fish species (mackerel, herring, capelin) within the 3K, 3L, 3Pn, 3Ps and 3O Northwest Atlantic Fisheries Organization (NAFO) fishing designations (Fig. 2.1) from 1977, 1983 to 1986, and from 2009 to 2020 were used as proxies for prey availability (see Pauly et al. 2013). These zones were chosen as they encompass the entire known foraging range of Northern Gannets breeding at Cape St. Mary’s (Fig. 2.1) and provide the best available estimates for mackerel, herring and capelin abundance in the region.

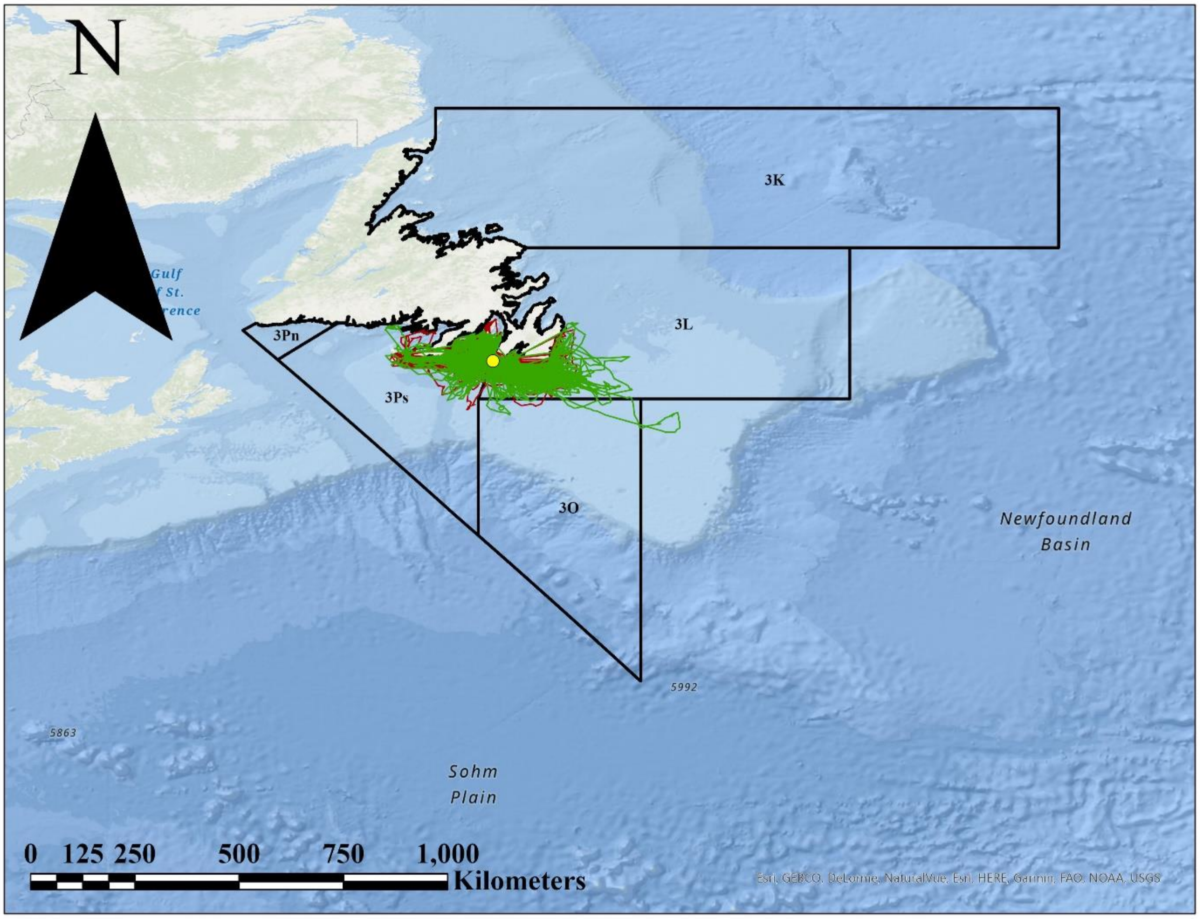

Figure 2.1. Location of 3K, 3L, 3O, 3Pn and 3Ps NAFO divisions (NAFO 2021) relative to Cape St. Mary's, Newfoundland, Canada (yellow dot) and parental Northern Gannet foraging tracks during the breeding season (July to October) from 2019 (green) and 2020 (red).

Landings data were used for initial analysis as SSB was unavailable for Atlantic herring and capelin. Fisheries landings data were extracted from the STATLANT 21A NAFO database (https://www.nafo.int/Data/STATLANT). As SSB data were available for mackerel, a separate model was constructed with SSB replacing landings to further explore the relationship between mackerel availability and Northern Gannet reproductive success. Mackerel SSB data from 1968 to 2018 for the northern stock complex that spawns in the Gulf of St. Lawrence were retrieved from Smith et al. (2020).

2.3.4 Sea Surface Temperature (SST)

To assess possible influences of SST on reproductive success, mean SST trends during early (June-July) and late chick-rearing (August to September) within a grid (45.87° to 47.55° N, -56.87° to -51.30° W, resolution 2.5 ° x 2.5 °) that encompassed the entire foraging range of Northern Gannets from Cape St. Mary's (see Fig. 2.1) were assessed for 1948 to 2020. SST data were retrieved from the National Center for Environmental Prediction (NCEP) and the National Center for Atmospheric Research (NCAR, https://psl.noaa.gov/cgi-bin/data/timeseries/timeseries1.pl, Kalnay et al. 1996).

2.3.5 Statistical Analysis and Model Selection

To assess the associations of biophysical factors on Northern Gannet reproductive success (0 or 1), several General Linear Mixed Models (GLMMs) were constructed using the "lme4" (Bates et al. 2015) package in the statistical software "R" (R Core Team 2020). To assess influences on reproductive success, we used the "glmer" function to construct GLMMs with a logit link and a binomial error distribution. To detect any multi-collinearity issues, variance inflation factors (VIFs) were calculated for final models using the "vif" function in the "car" package. To verify that the assumptions of each model were met, overdispersion was assessed using the "overdisp_fun" function. Values for SST, landings and SSB were normalized to avoid model convergence.

To assess which models were most predictive of reproductive success, we evaluated sample size corrected Akaike's information criteria (AICc). The number of apparently occupied nests was used as our sample size for AICc calculation. Variables included in analyses were divided into two sub-categories (prey species landings, SST within foraging range). We conducted initial screening in each variable category to determine which variable had the greatest influence upon Northern Gannet reproductive success. To determine which variable in each category was most predictive of reproductive success, the variable with the greatest cumulative rank (i.e. explaining the most variation) was selected for further analysis. Following Burnham et al. (2002), all models within a difference in AICc (ΔAICc) of 2.0 were considered plausible, while any models above a ΔAICc of 4.0 were not considered to be reasonable models for predicting reproductive success. Akaike weights (w) were also calculated to rank models.

A null model was constructed that could reasonably account for any variation in reproductive success not accounting for environmental factors. The NULL model included Plot_ID as a fixed effect and Year as a categorical random effect. Other possible variables that could contribute to reproductive success such as pair bond length and breeding experience were not included because these variables could not be ascertained, as very few individual gannets at this location have been banded.

GLMMs with combinations of the following biophysical factors were assessed: mackerel landings (Mack), herring landings (Herr), capelin landings (Cap), and mean SST within foraging range during early and late chick-rearing (SST_F). The model with the lowest AICc score was then selected as the model most predictive of reproductive success for gannets nesting at Cape St. Mary’s. If ΔAICc in the final competing models was <2.0, cumulative model weights were used to determine the variable/model most predictive of reproductive success. As mackerel SSB was available for the region, we constructed a model with solely mackerel SSB to compare with the mackerel landings model. Generalized additive models (GAMs) using the “gam” function in the package “mgcv” were used to visualize multi-decadal trends in variables included in the top models.

2.4 RESULTS

Reproductive success ranged from a low of 0.39 fledglings/AON in 2017 to a high of 0.94 fledglings/AON in 1983 (Table 2.2). The grand mean across all monitored years was 0.63 fledglings/AON (CI 0.54-0.72). Average reproductive success from 1977 and 1983 to 1986 was 0.77 fledglings/AON (CI 0.56-0.97), while average reproductive success from 2009 to 2020 was 0.57 fledglings/AON (CI 0.48-0.67).

Table 2.2. Reproductive success (95 % CI) of Northern Gannets at Cape St. Mary’s, Newfoundland from 2009 to 2020. Reproductive success values were calculated by dividing the number of chicks present on ~1 September by the number of monitored nests.

Year	# of Nests	Reproductive success (95% CI, fledglings per nest)
1977*	17	0.882 (0.711 - 1.000)
1983	33	0.939 (0.852 - 1.000)
1984*	100	0.710 (0.620 - 0.800)
1985*	101	0.574 (0.476 - 0.672)
1986*	50	0.720 (0.591 - 0.849)
2009	122	0.803 (0.732 - 0.875)
2010	48	0.813 (0.698 - 0.927)
2011	135	0.689 (0.610 - 0.768)
2012	133	0.414 (0.329 - 0.498)
2013	141	0.596 (0.514 - 0.678)
2014	141	0.475 (0.392 - 0.559)
2015	133	0.481 (0.395 - 0.567)
2016	142	0.493 (0.410 - 0.576)
2017	154	0.390 (0.312 - 0.467)
2018	161	0.491 (0.413 - 0.569)
2019	156	0.628 (0.552 - 0.705)
2020	145	0.586 (0.505 - 0.667)

*Values in 1977, 1984, 1985 and 1986 were determined from nest checks in late September.

There was no evidence of over-dispersion in any of the candidate models (over-dispersion ratio ≤ 1.00). All VIFs in the two best models were below 1.41, suggesting minimal collinearity between variables (O'Brien 2007).

The best model for the prey species category contained mackerel, herring and capelin. However, models containing mackerel accounted for 0.970 of the cumulative model weights and all models containing mackerel (except for herring and mackerel) had a ΔAICc value within ~ 4.0 (Table 2.3). Therefore, we selected mackerel as the best indicator for reproductive success out of the forage fish indices. Compared to mackerel landings (AICc= 2497.708), mackerel SSB (AICc= 2081.903) was significantly more predictive of reproductive success and therefore, was selected for the final analyses.

Table 2.3. Reproductive success models with variations on key forage fish indices. Mack=mackerel landings, Cap=capelin landings and Herr=herring landings.

Model	#Pars	AICc	dAICc	W
MackHerrCap	5	2493.681	0.000	0.397
MackHerr	4	2493.681	0.000	0.397
MackCap	4	2496.019	2.338	0.123
Mack	3	2497.708	4.027	0.053
Cap	3	2501.539	5.520	0.025
HerrCap	4	2503.542	9.861	0.003
Herr	3	2504.681	11.000	0.002

The best model for influence of foraging range SST during chick-rearing on reproductive success contained both the early and late chick-rearing periods, and the model containing both periods accounted for 0.878 of cumulative model weights (Table 2.4). Thus, the model containing foraging range SST during both early and late chick-rearing was selected and used in further analyses.

Table 2.4. Reproductive success models with different variations of mean foraging range SST during early and late chick-rearing.

Model	#Pars	AICc	dAICc	w
EarlyLate	4	2495.721	0	0.878
Late	3	2500.273	4.552	0.090
Early	3	2502.320	6.599	0.032

The overall best model for predicting reproductive success contained mackerel SSB within Newfoundland waters, and foraging range SST (Table 2.5), however, the model containing only mackerel SSB was within 2 ΔAICc and models containing mackerel SSB accounted for ~1.00 of cumulative model weights, suggesting that mackerel SSB was the best predictor of Northern Gannet reproductive success.

Table 2.5. Reproductive success models with different variations of the best forage fish and climate index models. SSTf=foraging range SST in both early and late chick-rearing and Mack=mackerel SSB.

Model	#Pars	AICc	dAICc	w
MackSSTf	4	2080.517	0	0.667
Mack	3	2081.903	1.386	0.333
SSTf	3	2495.721	415.204	0.000
Null Model	2	2502.83	422.313	0.000

Model averaged estimates for each of the three most important variables for predicting reproductive success from the top models (Table 2.6, Fig. 2.2) revealed a positive effect of increased mackerel SSB and increased foraging range SST in early chick-rearing and a negative effect of increased foraging range SST in late chick-rearing (Table 2.6).

Table 2.6. Model averaged parameter estimates from all models included in final analyses (Table 5), Mack=mackerel SSB, SSTe=foraging range SST in early chick-rearing, and SSTl=foraging range SST in late chick-rearing.

	Mack	SSTe	SSTl
Mean	0.95	1.20	-0.91
SE	0.5	0.5	0.6

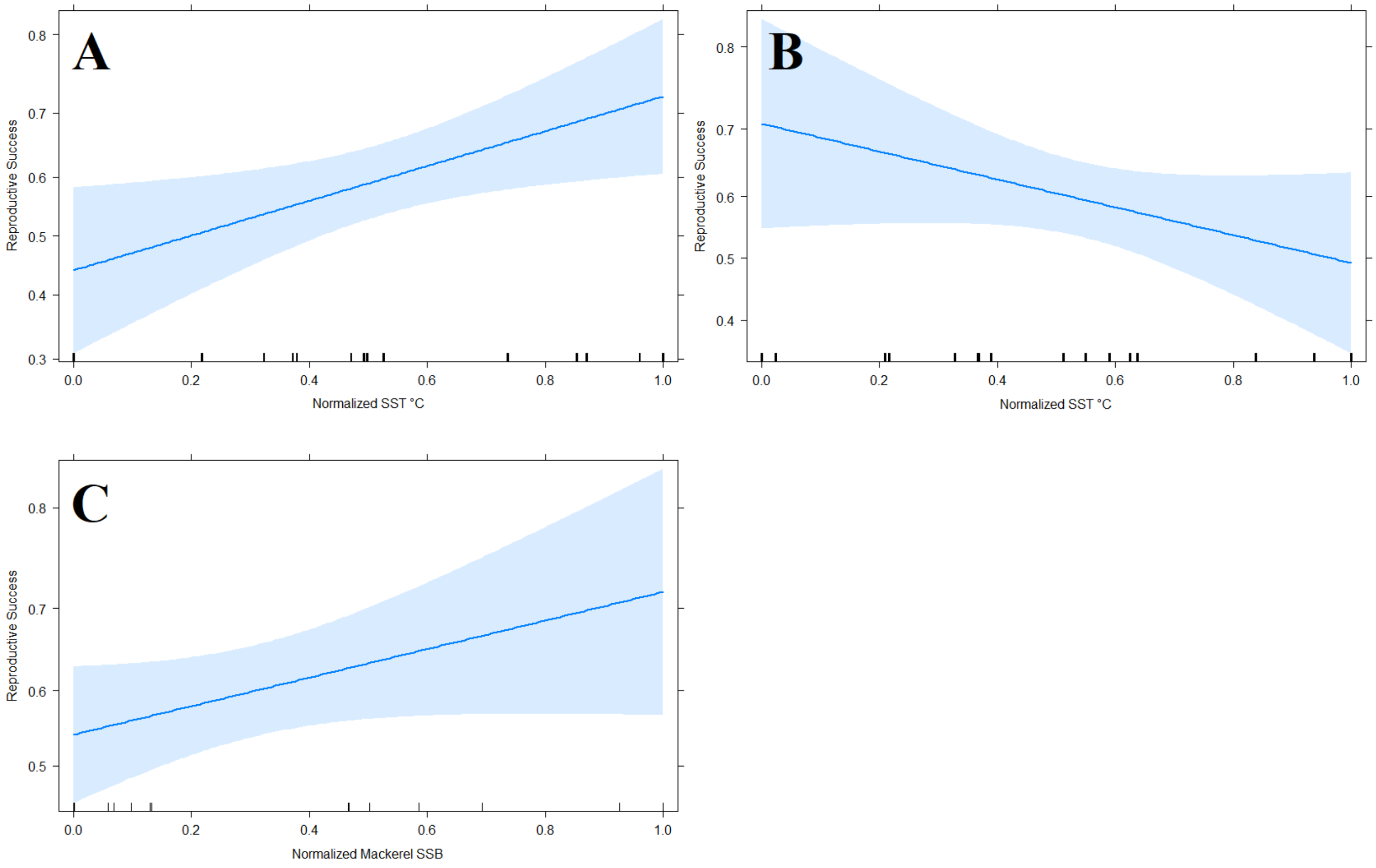

Figure 2.2. The association of a) normalized SST in early chick-rearing, b) normalized SST in late chick-rearing, and c) normalized mackerel SSB on the reproductive success of Northern Gannets at Cape St. Mary’s, Newfoundland, Canada.

Multi-decadal trends in mackerel landings and SSB show that landings increased prior to a decline in Northern Gannet productivity in the early 2010s, while SSB has declined steadily since the 1990s to record lows in 2020 (Fig. 2.3).

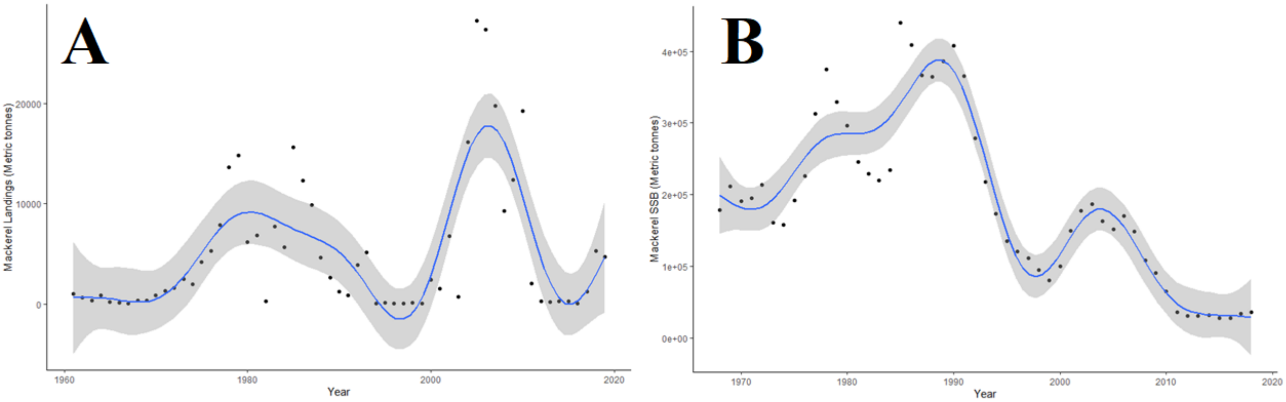

Figure 2.3. Multi-decadal trends of a) Atlantic mackerel landings within NAFO zones (3K, 3L, 3O and 3P) adjacent to Newfoundland, Canada from 1960-2019 and b) Atlantic mackerel northern stock complex SSB from 1968 to 2018.

Multi-decadal trends in foraging range SST have varied, with minimal long-term change in average SST in early chick-rearing, and a steady increase during late chick-rearing since the 1970s (Fig. 2.4).

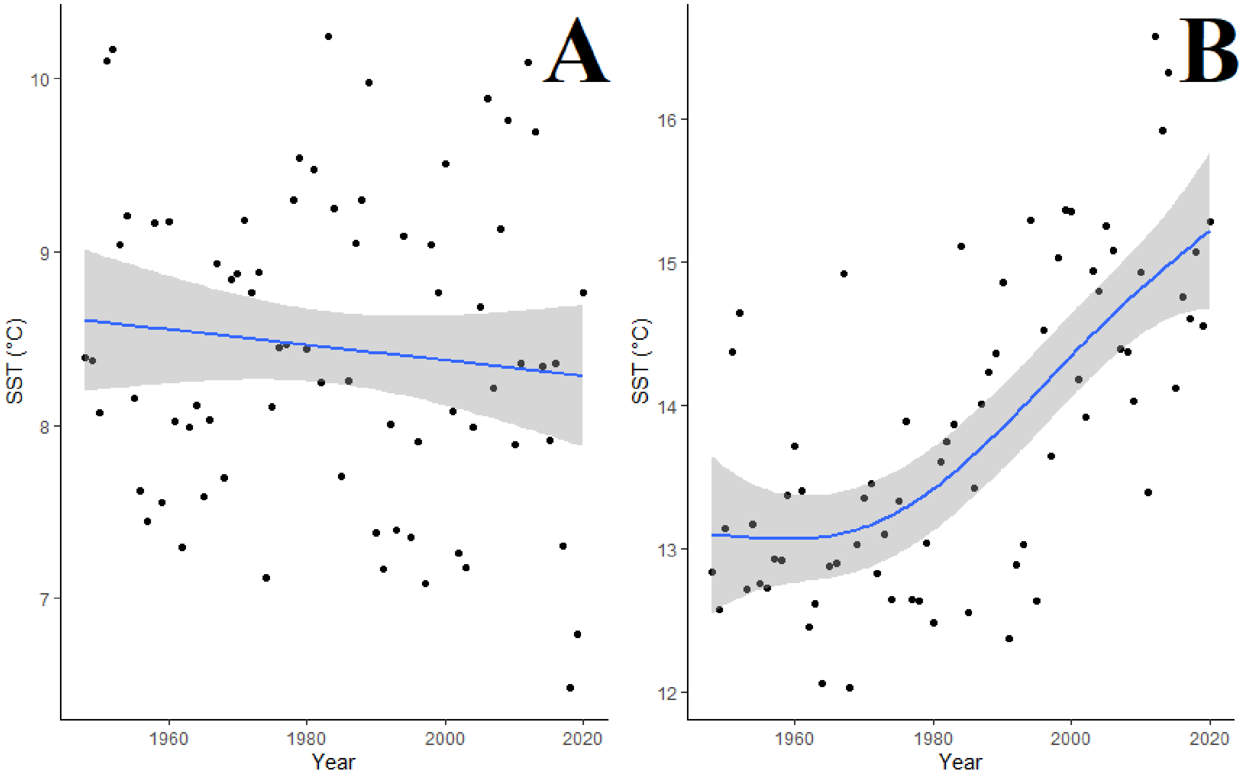

Figure 2.4. Multi-decadal mean SST trends during early (A; June-July) and late (B; August-September) chick-rearing within the foraging range of gannets nesting at Cape St. Mary’s.

2.5 DISCUSSION

Northern Gannet colonies near their southern limits are experiencing decreased productivity in recent years (J-F Rail unpubl. data., Le Bot et al. 2019, Grémillet et al. 2020, Montevecchi et al. 2021). Hence, it is critical to assess potential drivers of these declines. In the present study, we assessed the influence of prey availability and foraging range SST given their influence of these variables on population trends in other Northern Gannet colonies near the species’ southern limit (Guillemette et al. 2018, Le Bot et al. 2019). We found that reproductive success at the Northern Gannets’ southernmost colony at Cape St. Mary’s, Newfoundland was significantly negatively influenced by lower availability (landings and SSB) of a key prey species (Atlantic mackerel) over a multi-decadal timespan. Increased SST within their foraging range during late chick-rearing also negatively influenced reproductive success, while increased SST in early chick-rearing had a positive influence.

2.5.1 Influence of Prey Availability on Reproductive Success

The ability of seabirds to successfully rear offspring depends heavily on available food supplies near the colony (Cairns 1988). Of the three key prey species for Northern Gannets examined in this study, Atlantic mackerel abundance had the greatest influence on reproductive success. Atlantic mackerel is a critical prey species for Northern Gannets during the breeding season, as it is a lipid-saturated calorically dense food that plays a key role during late chick-rearing (Montevecchi et al. 1984). The availability (landings) and abundance (SSB) of this key prey influenced Northern Gannets' ability to successfully rear chicks at Cape St. Mary's. Similar findings at neighboring Northern Gannet colonies in the Northwest Atlantic, including the largest North American colony at Bonaventure Island, Québec, Canada have shown that prey reductions (particularly mackerel), above all other factors, have been influential in recent decreases in reproductive success (Guillemette et al. 2018). Mackerel landings attained an all-time high in Newfoundland waters in the early 2000s, coinciding with a decline in mackerel SSB (Fig. 2.3) just prior to the decline in Northern Gannet reproductive success. Atlantic mackerel spawning stock biomass in the Northwest Atlantic is classified in the Critical Zone (point at which there is high probability that fishing mortality will directly impact the population) of Canada's Precautionary Approach (DFO 2019). Continued fishing pressure could inhibit population recovery which would not bode well for Northern Gannet productivity.

Similarly, population declines and decreased reproductive success have also been observed in Europe's southernmost Northern Gannet colony on Rouzic Island, France (where mackerel is also becoming scarce (Le Bot et al. 2019; Grémillet et al. 2020). Contrasting opposing trends are ongoing at the northern limit of the Northern Gannets' range in the Northeast Atlantic Ocean. Northern Gannet range expansions into the Arctic Circle, population increases, colony establishment and high productivity (Murray et al. 2015, Anker-Nilssen et al. 2017, Barrett et al. 2017) in the Northeast Atlantic have spatiotemporally coincided with increased stock sizes and the movement of mackerel into higher latitudes (Olafsdottir et al. 2019). Thus, the availability and distribution of Atlantic mackerel appears to be a key determinant of Northern Gannet reproductive success and population dynamics throughout the species' breeding range. Warming ocean conditions are associated with mackerel production and range expansion at the northern extent of the Northern Gannets' breeding range but paradoxically not at the southern extent. This difference may be due to the Atlantic mackerel's preferred temperature range between 9 °C and 13 °C and their occurrence in temperatures between 5 °C and 15 °C (Olafsdottir et al. 2019). Atlantic mackerel tend to avoid temperature of > 15 °C – conditions that are ongoing in the Northwest, but not in the Northeast Atlantic (see Montevecchi et al. 2021).

Herring availability was not a significant predictor of Northern Gannet reproductive success. Herring spawning stocks have declined in the Northwest Atlantic during a similar timescale as mackerel (DFO 2020a, 2020b). Herring spawning in Newfoundland typically occurs in spring (e.g. before June, Melvin et al. 2009), and herring are more prevalent in coastal regions during the gannets' pre-laying and incubation than during chick-rearing. Herring has a thermal preference of 5-9^o C for juveniles and 8-12^o C for adults (Brennan et al. 2016); a thermal range which is rarely exceeded in early summer within the Northern Gannets' foraging range at Cape

St. Mary's (Fig. 4). Though herring stocks in the Northwest Atlantic have declined, access to this prey source may not have been greatly altered, as SST during the spawning period in southern Newfoundland has yet to exceed the Atlantic herring's thermal preference (Fig. 2.4). Long term dietary data from the Northern Gannet colony on nearby Funk Island, Newfoundland, indicate that herring have comprised a small, but consistent portion of Northern Gannet diets since the late 1970s (W Montevecchi unpubl. data), suggesting that herring are a minor dietary supplement for gannets in the Northwest Atlantic.

Capelin landings were also not a significant predictor of Northern Gannet reproductive success. The commercial fishery for capelin is not as extensive as the herring and mackerel fisheries, and likely does not provide a representative estimate of availability in the region. Further, timing and location of capelin spawning likely plays a larger role for exploitation by seabirds than does general availability (Davoren et al. 2012). A centennially significant cold-water perturbation in the Northwest Atlantic induced a bottom-up population collapse of capelin in the early 1990s, causing a 30-fold decrease in capelin biomass, and the species has exhibited delayed spawning in subsequent years (Buren et al. 2014, 2019). The reduced abundance and delayed spawning may influence Northern Gannet productivity and warrants long-term monitoring and further investigation.

Important non-commercial species for Northern Gannets such as Atlantic saury have minimal data on availability, abundance or SSB, besides what can be inferred from avian predators. Saury consistently make up a major component of Northern Gannet diets in the Northwest Atlantic (Montevecchi 2007) and of Cape Gannets in the South Atlantic (Green et al. 2015). Saury occur at higher rates in Northern Gannet diets when water temperatures are warm, and mackerel are also present (Montevecchi 2007). However, since 2010, saury has become the dominant warm-water prey species at the Northwest Atlantic's northernmost gannet colony on Funk Island (W Montevecchi unpubl. data), suggesting gannets are exploiting prey species based on availability.

2.5.2 Influence of Climate on Reproductive Success

Ocean climate change is influencing the reproductive success of marine birds, with long-term multi-decadal warming trends (Mauck et al. 2018) and acute marine heatwaves (Piatt et al. 2020, Montevecchi et al. 2021). Both have ocean-basin effects on food webs in the long- and immediate term. Mean SST in the gannets' foraging range during breeding at Cape St. Mary's has held steady in early chick-rearing since the late 1940s, while it has trended upwards during late chick-rearing. Increased SST in late chick-rearing had a significant negative association with productivity, suggesting that later seasonal warming compromises prey availability. Rising SST can alter the pelagic fish distribution on both vertical and horizontal dimensions, as well as temporal scales (Perry et al. 2005; Dulvy et al. 2008; Fincham et al. 2013; Macqueen & Marshall 2017). Seabirds have limited phenological plasticity in adjusting to climate-induced distributional shifts, which sometimes results in spatiotemporal mismatches with prey availability (Regular et al. 2014; Keogan et al. 2018). With rapid warming occurring in their foraging range during late summer (August/September), predator-prey mismatches may be occurring during late chick-rearing and contributing to reduced reproductive success. Conversely, increased SST in early chick-rearing associated with increased reproductive success suggests that high SST during early summer (June-July) may augment available prey.

2.5.3 Other Influences on Reproductive Success

It is possible that the colony at Cape St. Mary's has reached carrying capacity after years of suppressed numbers due to anthropogenic disturbance (Montevecchi and Wells 1984). The colony attained its highest population on record in 2009 and has remained relatively constant since (Chardine et al. 2013, S Wilhelm unpubl. data), suggesting that the population may be levelling off due to density dependent prey depletion or interference (Lewis et al. 2001, Ainley et al. 2003, Gaston et al. 2007). More frequent assessments of population size would allow for a more robust examination of their effects on the productivity of this colony. Alternatively, the mainland portion of the colony at Cape St. Mary's may be suppressed from further growth due to predation pressure from coyotes (Montevecchi et al. 2019).

2.5.4 Conclusions

This study demonstrates that decreased mackerel availability was associated with declining reproductive success in Northern Gannet reproductive success at their southernmost colony over a multi-decadal period. This finding aligns with other colonies near the southern edge of the species' range, where reduced mackerel availability is associated with decreased productivity and populations that are either leveling or declining (J-F Rail unpubl. data, Le Bot et al. 2019, Grémillet et al. 2020). Contrastingly, ocean warming appears to be enhancing Northern Gannet population growth at their northern range-limits in the Northeast Atlantic (see Table 2.1) where mackerel abundance and availability are increasing (Olafsdottir et al. 2019). These opposing trends imply that critical biological temperature thresholds for mackerel are being exceeded near southern gannet colonies, while conditions are becoming more favourable for mackerel near northern colonies.

At Cape St. Mary’s, increased foraging range SST during late chick-rearing was associated with a decline in reproductive success and likely represented climate-driven reductions in mackerel availability. Conversely, increased foraging range SST during early chick-rearing was associated with increased breeding success, which suggests that warming waters in early chick-rearing may be enhancing the availability of prey species during this time period. Thus, variation in the impacts of warming SST within the breeding season should be considered in studies examining the influence of SST on marine birds and their prey.

Long-term monitoring of reproductive success at gannet colonies should be continued to further investigate climate, fisheries, prey and predator interactions and their influences on population demographics. On a broader scale, it is also of high importance to monitor the impacts of our warming oceans on species at the extremes of their range.

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CHAPTER 3: INTRA- AND INTER-ANNUAL SHIFTS IN FORAGING TACTICS BY PARENTAL NORTHERN GANNETS (*MORUS BASSANUS*) IN RESPONSE TO CHANGING PREY FIELDS

3.1 ABSTRACT

Seabirds are constrained by central-place foraging during breeding, when energy content obtained from prey must outweigh the expenses 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 species' southernmost colony 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-dives in early chick-rearing to primarily V-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 2019. Kernel Density 50% utilization distributions were larger and expanded further from the colony during early chick-rearing in 2020 (7297 +/- 1419 km^2) than 2019 (2382 +/- 797 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.

3.2 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 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 provide 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*) is a large, generalist seabird of the North Atlantic that 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 (*Ilex 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) and capelin being the smallest and least energetically dense (4.2 kJ/g, Montevecchi et al. 1984). Saury and herring fall between these two values, with energetic content of 6.8 kJ/g and 4.3 kJ/g, 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 would 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 size, burst swimming speed, and distribution in the water column of prey species, gannets must employ different dive behaviours when in pursuit of different prey species (Garthe et al. 2000). For example, mackerel are larger fish capable of explosive burst speeds of 18 body lengths per second (Wardle & He 1988). Therefore, gannets need to 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 (~1.5-1.7 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 plateaued, and reproductive success has been poor since the early 2010s at the southern limit of the species' breeding range (d'Entremont et al. 2021). These population trends first manifested in 2012, when a marine heatwave coincided with mass colony abandonments and record low reproductive success at three 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, S Wilhelm et al. unpubl. data) have been associated with declining forage fish stocks due to fisheries pressure and warming ocean climate (Guillemette et al. 2018, d'Entremont et al. 2021). As these observed declines in reproductive success and plateaued 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, prey availability, and foraging behaviour to determine whether these observed declines in gannet productivity are a product of alterations in foraging effort due to decreased availability of prey.

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. 3.1). Owing to 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 d’Entremont et al. 2021, Montevecchi et al. 2021).

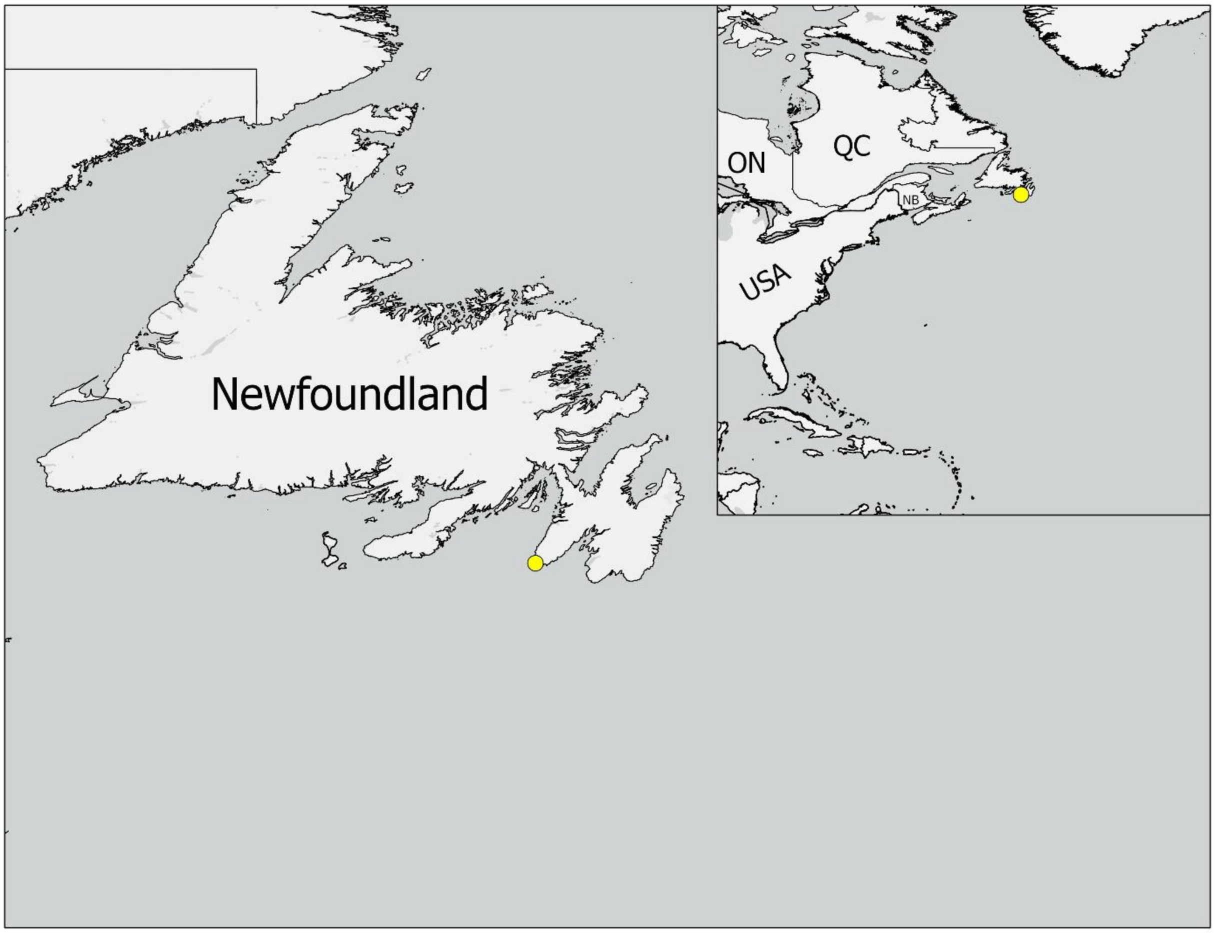

Figure 3.1. Location of Newfoundland and Cape St. Mary's (yellow dot) relative to eastern North America.

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 gannets 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.

3.3 METHODS

3.3.1 Study Site

Cape St. Mary's is home to 14,598 breeding pairs at last estimate in 2018 (S Wilhelm unpubl. data). 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.

3.3.2 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: 36x22x12.5 mm) and were attached to the 4 innermost rectrices just below 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 aluminum bands on their right legs. Birds were bled for sex determination in 2019 and foraging effort (e.g. maximum and total trip distance, number of dives, etc.) was compared between the sexes, where no significant differences were found and therefore sex was omitted from subsequent analysis. Mean mass of tagged gannets in our study was 3652 g +/- 423 (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 (3 solar-powered, 2 battery-powered) were deployed on both July 18, 2019 and August 21, 2019 (2 solar-powered, 3 battery-powered). Seven devices were deployed on July 18, 2020 (5 solar-powered, 2 battery-powered). We were able to recapture and redeploy devices on three individuals in 2020 that were fitted with GPS devices in 2019, allowing for inter-annual comparisons for the same individuals. An Ecotone base station with a directional antenna was deployed in the colony area ~25m 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 ~2-4 weeks old when devices were deployed.

3.3.3 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 August 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 likely still provide an accurate representation of prey fields being exploited by parental gannets during the same period (Kirkham et al. 1985). Diet samples were unable to 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 regurgitates were identified to species and counted. Opportunistic regurgitates were also assessed for prey species composition during the tagging process in 2019 and 2020.

3.3.4 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” (Freitas 2012). 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 (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 (e.g. location determined by positional fixing) which occurred within 30 mins before a recorded dive.

3.3.5 Dive analysis

Dive depth and duration from foraging trips of tagged gannets were determined using the package ‘diveMove’ (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 $\geq$ 3 s, and/or total duration > 10 s and depth > 8 m were classified as “U” dives and all dives with a bottom time < 3 s and/or total duration < 10 s and depth < 8 m were classified as “V” dives (Garthe et al. 2000). All dives less than 1 m in depth were removed from analysis, as these could have been associated with bouts of bathing and were unlikely to be foraging dives. In both 2019 and 2020, a shift from predominantly 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 (consisting of predominantly U-shaped dives), and 2) the late chick-rearing period from August 16 onwards (consisting of primarily V-shaped dives). This division of the chick-rearing period is also consistent with the age of chicks at this time, as most chicks were ~7-8 weeks old on August 15, and the total chick-rearing period for the species is typically 13 weeks (Mowbray 2020).

3.3.6 Identifying core foraging areas and ranges

Locations associated with dives across all foraging trips for each individual were presented as 50% utilization density Kernel Density distribution maps using the ‘adehabitatHR’ package (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.

3.3.7 Behavioural States Analysis

Behavioural states analysis was conducted to assess differences in the proportion of time spent in different behavioural states during foraging trips during the breeding season and across years. Previous work on gannets has concluded that they exhibit three different behavioural states during foraging trips: transit, rest, and area-restricted search (ARS; Bodey et al. 2014, Bennison et al. 2017). There are a variety of methods utilized for determining 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 an ~80% rate of dives being associated with ARS defined GPS fixes (Bennison et al. 2017).

We used the package “momentuHMM” (McClintock and 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 location data collected 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 mins and < 60 mins 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.

3.3.8 Statistical Analyses

Generalized Linear Mixed Models (GLMMs) constructed using the package “glmmTMB” (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 (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” (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.

3.3.9 Sea Surface Temperature

Sea surface temperature (SST) data (0.1 by 0.1° resolution) for the region was obtained from the Environmental Research Division Data Access Program (ERDDAP) database (Simons 2020). SST values were averaged over the two chick-rearing periods (early and late) for both 2019 and 2020. Interval contours of 2 °C were created to visualize any intra- and inter-annual differences in SST.

3.3.10 Capelin Spawning Sites

To assess capelin availability to parental gannets ranging from Cape St. Mary’s, the timing and location of used spawning sites in both 2019 and 2020 was obtained within foraging ranges of gannets from Cape St. Mary’s from eCapelin.ca (CON 2021). 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 nearby 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 and Davoren 2019), the timing of spawning indicates when capelin become available for 2-4 weeks during the breeding season of seabirds (Davoren et al. 2012).

3.4 RESULTS

We obtained locational data from all 10 birds that were tracked in 2019 and all 7 birds that were tracked in 2020 (Table 3.1). Birds were tracked for 17-76 d (341-2,547 GPS fixes) and we identified a total of 506 individual foraging trips with 11 - 66 trips per tagged individual (Table 3.1, Fig. S1).

Table 3.1. 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 color-coded.

Year	Individual	# Foraging Trips	Days Tracked	# Days Tracked	Maximum Distance from Colony (km)	Mean Dives per Trip (±SE)	Mean Total Distance (km) ±SE	Mean Maximum Distance (km) ± SE	Mean Directness (±SE)	Mean Duration (mins) ±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	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	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

3.4.1 Dive Profiles

The proportion of U- and V-shaped dives varied throughout the breeding season in both 2019 and 2020, with capelin-associated U-dives being more prevalent in July to ~August 15 before becoming primarily larger pelagics-associated V-dives (Fig. 3.2).

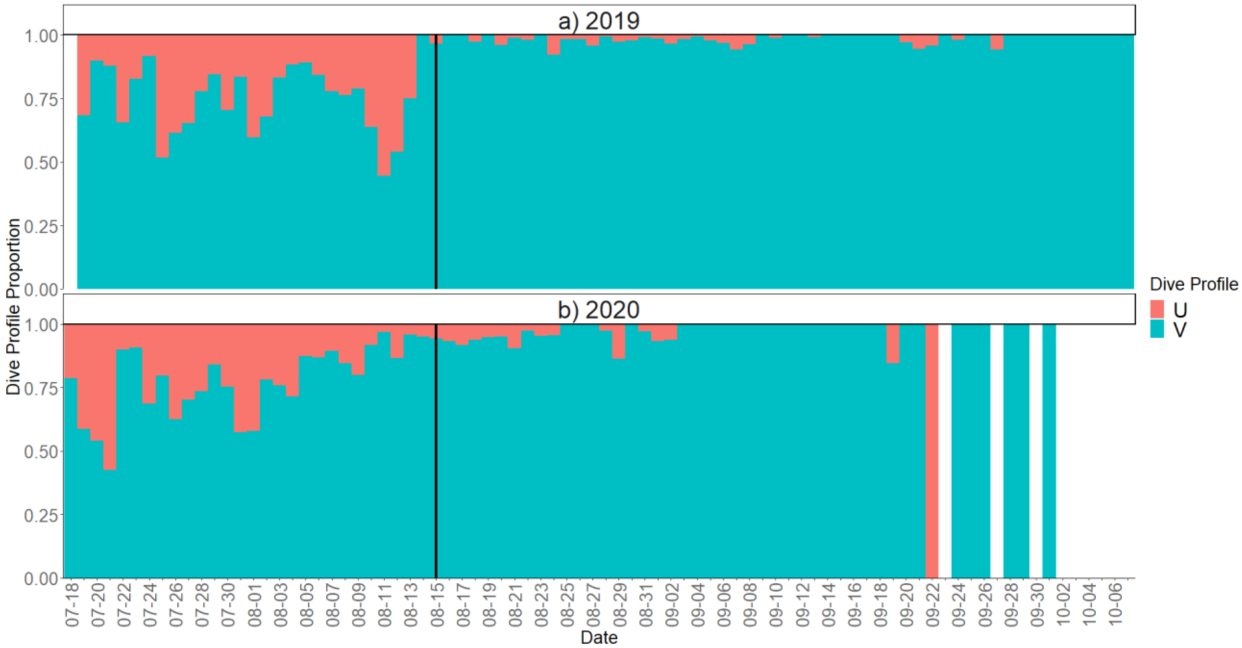

Figure 3.2. Dive profile proportions of all tracked parental Northern Gannets combined per day in 2019 (top, n=10) and 2020 (bottom, n=7). White bars correspond to days which no birds with active GPS devices embarked on a foraging trip. The black line denotes the split between early and late chick-rearing.

These same trends were observed within individuals in both years, with each demonstrating a shift from U-dives to V-dives as the breeding season progressed (Fig. 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).

3.4.2 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 3.2).

Table 3.2. 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

3.4.3 Foraging Trip Characteristic Comparisons Within and Between Years

Average trip directness was significantly greater during late relative to early chick-rearing in both 2019 and 2020 (Table 3.3). The number of dives per trip was significantly greater during early relative to late chick-rearing in both 2019 and 2020 (Table 3.3). Average total and maximum trip distance was significantly greater in late relative to early chick-rearing in 2019, while there was no significant difference between periods in 2020 (Table 3.3). Average trip duration was significantly greater during early relative to late chick-rearing in 2020, with no difference between periods in 2019 (Table 3.3). There was no significant difference in time spent resting during foraging 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 3.3).

Table 3.3. Summary of mean (±SE) foraging trip characteristics and behavioural states 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 in bold.

	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**					**Early**				
					0.321	0.104	500	3.079	**0.002**	-0.462	0.115	500	-4.001	**<0.001**
					2020					**Late**				
					-0.197	0.108	500	-1.828	0.068	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**					**Early**				
					0.445	0.097	500	4.593	**<0.001**	-0.441	0.109	500	-4.067	**<0.001**
					2020					**Late**				
					-0.028	0.1	500	-0.281	0.779	0.032	0.121	500	0.266	0.79
Duration (mins)	784.7 ± 53.1	907.3 ± 50.6	964.7 ± 64.5	642.0 ± 61.1	**2019**					**Early**				
					0.117	0.107	500	1.09	0.276	-0.326	0.12	500	-2.72	**0.007**
					2020					**Late**				
					-0.351	0.11	500	-3.181	**0.002**	0.142	0.141	500	1.01	0.313
Directness	0.41 ± 0.02	0.51 ± 0.02	0.41 ± 0.01	0.52 ± 0.03	**2019**					**Early**				
					0.217	0.054	500	4.046	**<0.001**	-0.011	0.06	500	-0.189	0.85
					2020					**Late**				
					0.205	0.055	500	3.697	**<0.001**	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**					**Early**				
					-0.276	0.108	495	-2.558	**0.011**	-0.126	0.116	495	-1.086	0.278
					2020					**Late**				
					-0.685	0.111	495	-6.19	**<0.001**	0.283	0.138	495	2.06	**0.04**
Behavioural States Proportions														
ARS	0.47 ± 0.03	0.43 ± 0.03	0.49 ± 0.03	0.50 ± 0.03	**2019**					**Early**				
					-0.44	0.183	142	-2.398	**0.018**	0.206	0.209	142	0.988	0.325
					2020					**Late**				
					0.004	0.341	142	0.011	0.991	-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**					**Early**				
					0.748	0.163	142	4.586	**<0.001**	-0.203	0.189	142	-1.074	0.285
					2020					**Late**				
					0.564	0.288	142	1.959	0.052	-0.019	0.271	142	-0.069	0.945
Rest	0.32 ± 0.03	0.19 ± 0.03	0.27 ± 0.03	0.41 ± 0.05	**2019**					**Early**				
					-0.178	0.177	142	-1.005	0.317	0.198	0.187	142	1.054	0.294
					2020					**Late**				
					-0.49	0.411	142	-1.193	0.235	0.509	0.406	142	1.253	0.212

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 3.3). Trip directness did not differ significantly between years during either chick-rearing period (Table 3.3). The number of dives per trip was significantly greater during late relative to early chick-rearing in 2019 but did not differ between years during late chick-rearing (Table 3.3). 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).

3.4.4 Spatial Analysis

Average core foraging range sizes (50% utilization distributions) of parental gannets were significantly greater in late (8558 +/- SE 1693 km^2) relative to early chick-rearing (2382 +/- SE 797 km^2) during 2019 (p=0.009, t= 3.300, df=9), but did not differ between chick-rearing periods in 2020 (p=0.720, t=0.395, df=3, Fig. 3.3).

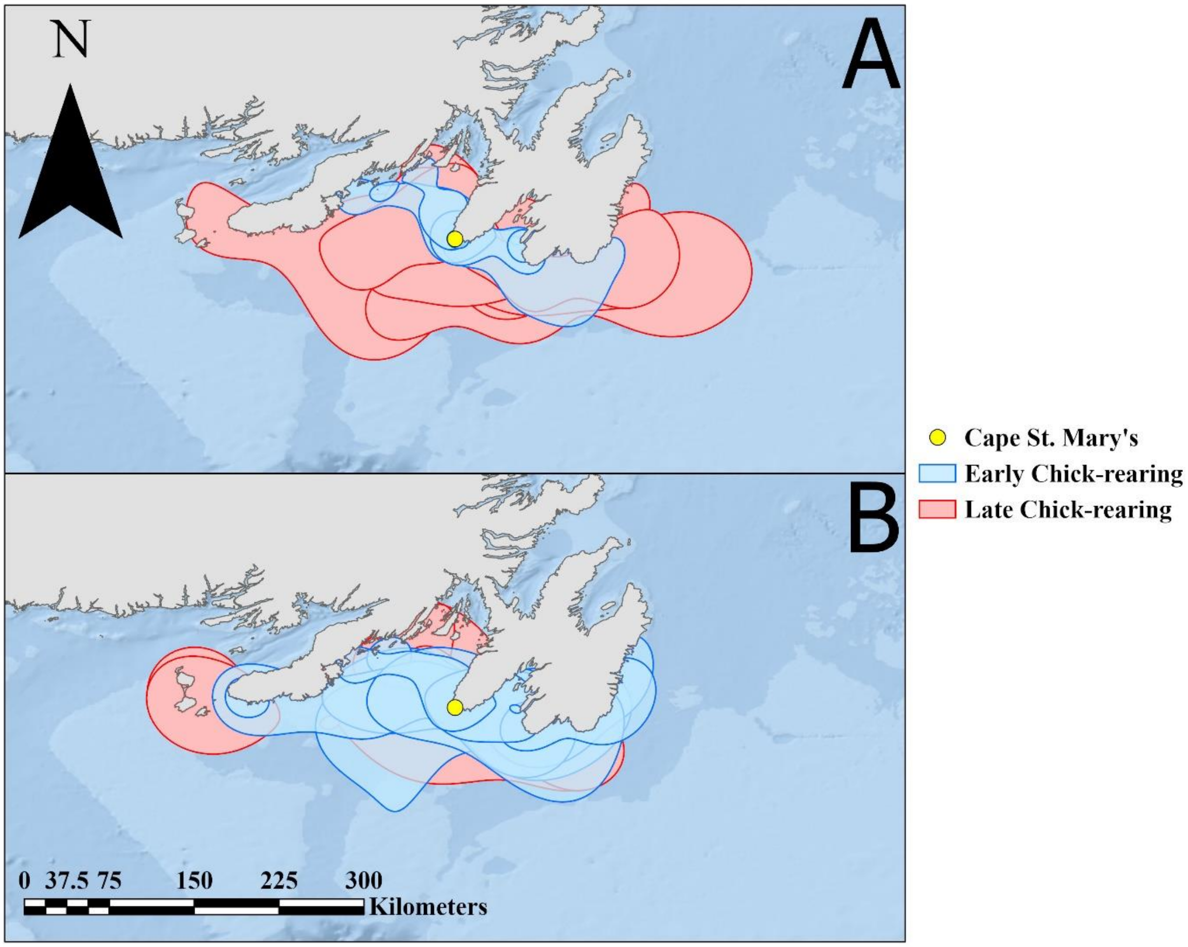

Figure 3.3. Intra- and inter-annual 50% Kernel Density utilization distributions of tagged parental gannets ranging from Cape St. Mary's, Newfoundland, Canada in a) 2019 and b) 2020 across both chick-rearing periods.

Average core foraging area size was significantly greater (p=0.0145, t=3.02, df=9) during early chick-rearing in 2020 (7297 ± SE 1420 km^2) compared to 2019 (2382 ± SE 797 km^2). No significant difference (p=0.945, t=0.070, df=10) in core foraging area sizes were found in late chick-rearing between 2019 (8558 ± SE 1693 km ^{2}) and 2020 (8798 ± SE 3531 km^2).

3.4.5 Sea Surface Temperature

Average sea surface temperature during early chick-rearing differed between years, with the cooler 12-14 °C isotherm enveloping Cape St. Mary's and much of the observed foraging range of tagged birds in 2019, and a northward shift of the 14-16 °C isotherm observed in early chick-rearing in 2020 (Fig. 3.4). A similar trend was observed for the late chick-rearing period, with the 12-14° C isotherm persisting around the Southern Avalon and Burin Peninsulas in 2019, and the 14-16° C isotherm covering much of the gannet's foraging range in 2020. Further, the 16-18° C isotherm permeated further north in 2020, overlapping partially with the foraging ranges of Cape St. Mary's birds during late chick-rearing (Fig. 3.4).

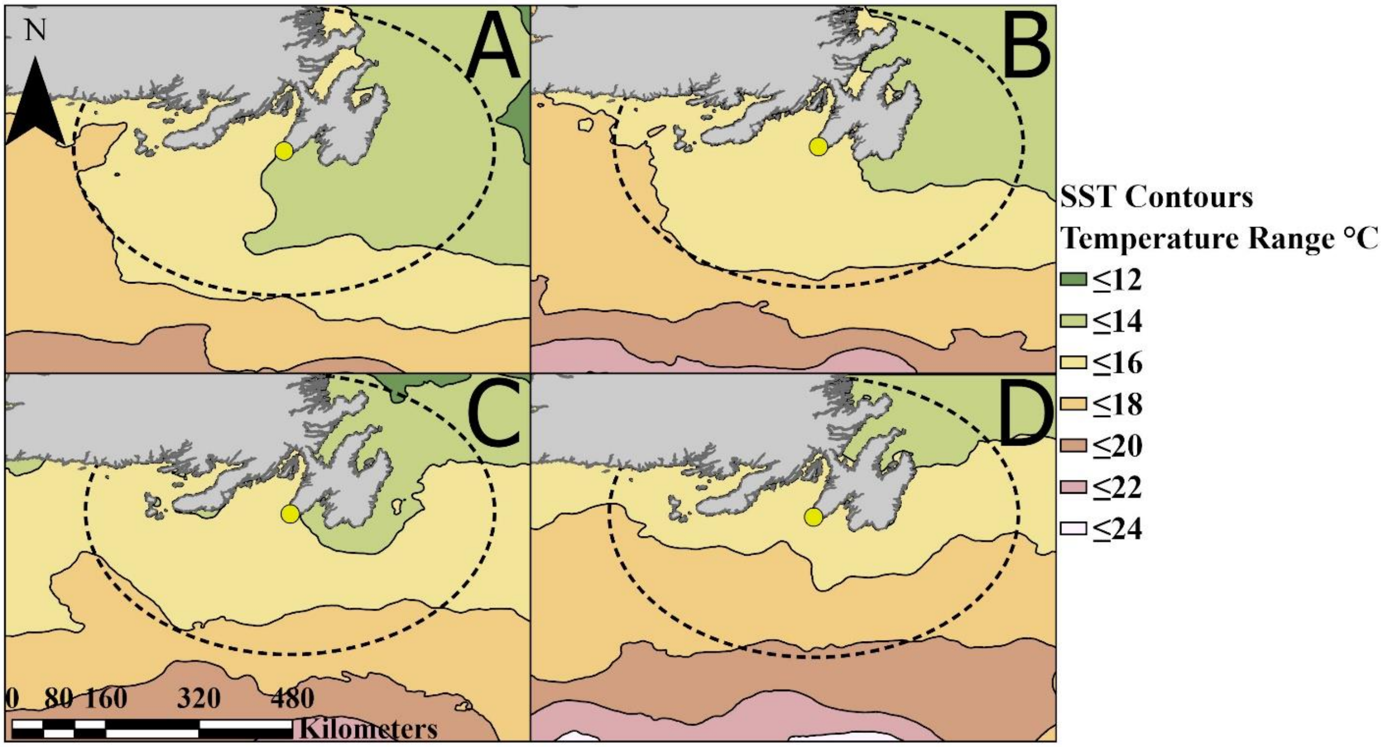

Figure 3.4. Mean sea surface temperature contours in southeast Newfoundland from a) early chick-rearing in 2019, b) early chick-rearing in 2020, c) late chick-rearing in 2019, and d) late chick-rearing in 2020.

3.4.6 Capelin Spawning Sites

There were fewer reported used beach spawning sites of capelin during early chick-rearing within the foraging range of Cape St. Mary's gannets in 2020 (n=19) compared to 2019 (n=26; Fig. 3.5, CON 2021). 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 days, n=19) than in 2019 (July 9 ± 5.9 days, n=26).

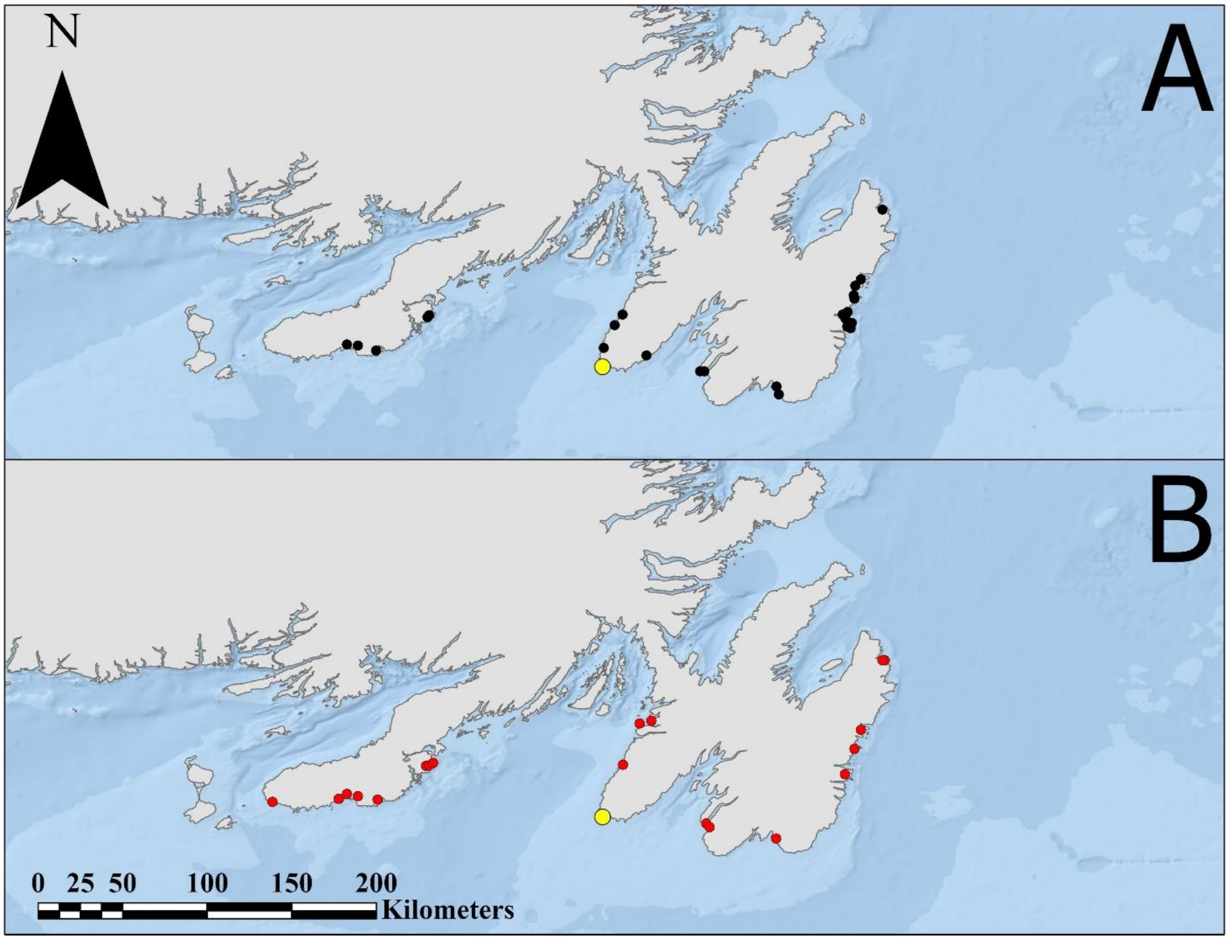

Figure 3.5. Reported capelin spawning sites within the foraging range of gannets from Cape St. Mary’s, Newfoundland from a) 2019 and b) 2020 (CON 2021).

3.5 DISCUSSION

Due to central-place foraging constraints, parental gannets must direct their foraging effort on the most energetically profitable food source. Available prey fields often change dramatically within and between years based on environmental conditions and biological constraints (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).

Similar to previous findings for Cape Gannets (*Morus capensis*; Botha & Pistorius 2018), we demonstrate that gannet foraging tactics can 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 availability waned following their spawning period (Carscadden et al. 2013). This was shown by consistent shifts in dive profiles from U-shaped to V-shaped 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, maximum and total distance was 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 ocean climate-driven annual differences in prey distribution and availability in the region.

3.5.1 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 (Fig. 2, Figs. S2 and S3). Capelin-associated U-dives were prevalent during early chick-rearing before shifting to almost exclusively larger pelagics (mackerel, saury) associated V-dives in late chick-rearing. Previous research on dive strategies of Australasian Gannets (*Morus serrator*) suggested that dive profiles were driven by prey depth (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 the early chick-rearing stage, Northern Gannet diet samples collected in our study, as well as previous work demonstrating the link between dive profiles of Northern Gannets and prey types (Garthe et al. 2000, 2011, 2014), support an intra-annual shift in the exploitation of different prey types.

It has been demonstrated previously that 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 in early chick-rearing, to mackerel and saury in late-chick-rearing during mid-August. 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). Similar findings have been reported for Cape Gannets, as parental diets shifted 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 timing of data collection during the breeding season. Inter-colony dietary or foraging behaviour comparisons (e.g., Garthe et al. 2007) must consider oceanographic differences in the timing of migration/spawning of prey species as this will influence dietary composition and foraging tactics.

Consistent with central place foraging (MacArthur & Pianka 1966, Burke & Montevecchi 2009) predictions, foraging trip maximum and total distance were significantly greater during late chick-rearing in 2019 when exploiting more energy dense mackerel and saury that were captured farther from the colony than were capelin. The smaller less energy dense capelin are typically inshore near intertidal or subtidal spawning locations during the early chick-rearing period (Nakashima & Wheeler 2002). Meanwhile, the more energetically dense mackerel and saury that migrate through the region during late chick-rearing are less constrained for 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 and 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 proportion of time in ARS was significantly greater in early chick-rearing, although 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 as such, 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). Proportion of time spent foraging per day in juvenile European Shags (*Phalacrocorax aristotelis*) has been found to be 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 young in adulthood. Further, to survive and successfully rear young, 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).

3.5.2 Inter-Annual Variation in Foraging Tactics

Foraging effort in the form of trip duration and maximum and total distance was significantly greater during early chick-rearing in 2020 compared to 2019 (Table 2, Fig. 3). This increased effort may 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, as well as more variation in timing of spawning in comparison to 2019 (Fig. 5, CON 2021). Reduced occupation of spawning sites may be explained by warmer waters (>14°C) along the southeast Newfoundland coast during early chick-rearing in 2020 (Fig. 4), as capelin typically spawn at sites < 12°C (Davoren 2013, Crook et al. 2017).

Increased foraging effort among seabirds was not limited to gannets breeding in coastal Newfoundland during 2019 compared 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 foraging 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 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 foraging effort 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 sea surface temperature threshold of ~15-16 °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 sea surface temperature within the foraging range of parental gannets ranging 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 declines in reproductive success (Guillemette et al. 2018, d'Entremont et al. 2021).

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 deterioration of gannet nutritional condition was observed during this marine heatwave event in 2012 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 may also be impacting mackerel distributions and recruitment through bottom-up effects upon their planktonic prey (Castonguay et al. 2008, Pacariz et al. 2016). This could induce increased foraging effort and lowered reproductive success in gannets. Alternatively, recent modelling has shown that warming waters may 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 may be flexible to shifts in fish assemblages and distribution associated with warming climate by shifting their effort towards exploiting other key prey species such as Atlantic Saury or Shortfin Squid *Illex illecebrosus* which have higher temperature tolerances (Dudley et al. 1985, Montevecchi 2007). 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 Montevecchi unpubl. data).

3.5.3 Conclusions/Future Directions

This study demonstrates that gannets shift their foraging effort across species from the least energetically dense (capelin) to the most energetically dense prey species (mackerel, saury) as the breeding season progresses and prey fields move in and out of the region. Further, 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 foraging range, where their tolerances to changing climate and prey availability is expected to be most fragile (Barrett et al. 2017, Montevecchi et al. 2021, d'Entremont et al. 2021).

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CHAPTER 4: GENERAL DISCUSSION AND SUMMARY

Globally, many marine bird populations are declining at an alarming rate (Paleczny et al. 2015). These declines have been associated with many anthropogenic risks, including oiling (Wiese & Robertson 2004), bycatch (Anderson et al. 2011), mercury burdens (Albert et al. 2020), and reductions in prey availability and quality associated with over-exploitation by fisheries (Cury et al. 2011, Montevecchi 2022) and climate change (Piatt et al. 2020; Orgeret et al. 2021). Though all these stressors pose concern and work in tandem to impose negative effects on marine birds, the most pervasive and urgent is the effect of climate change (Keogan et al. 2018). The impacts of climate change are visible in seabirds via increased foraging effort, declines in productivity, and population declines (Jones et al. 2018, Osborne et al. 2020, Piatt et al. 2020, Fromant et al. 2021, Montevecchi et al. 2021).

Northern Gannets (*Morus bassanus*) have generally exhibited increased population growth and general stability across much of their range in recent decades (see Chapter 2). However, colonies near the species' southern limits in the Gulf of St. Lawrence, Newfoundland and France have experienced prolonged poor productivity and their population growth has plateaued in association with ocean warming and declines in available prey (Guillemette et al. 2018, Le Bot et al. 2019, Montevecchi et al. 2021). The purpose of this thesis was to assess the influence of sea surface temperature (SST) and prey availability on the productivity and foraging behaviour of Northern Gannets breeding at their southernmost colony for the first time.

In Chapter 2, I demonstrate that Northern Gannet productivity at their southernmost colony is linked to SST and the availability of Atlantic mackerel (*Scomber scombrus*). Increased SST in late chick-rearing and declines in mackerel landings and standing stock biomass (SSB) had negative associations with gannet productivity, while increased SST in early chick-rearing had a positive influence. This suggests that gannet productivity is most negatively impacted by environmental and prey conditions in late chick-rearing. Mackerel, the most energetically dense prey species for gannets, is a critical prey species during late chick-rearing as the energetic demands of growing chicks increases (Montevecchi et al. 1984). As mackerel has thermal preferences of 5-15° C (Olafsdottir et al. 2019), it is not unexpected that SST values trending above this threshold have been linked to declines in gannet productivity. With mackerel availability depressed due to over-fishing (DFO 2019), warming waters could further inhibit gannets from accessing this key prey species through vertical and horizontal distributional shifts (Montevecchi et al. 2021). Poor productivity could continue at Cape St. Mary's if gannets are unable to adjust to shifts in mackerel availability and if stocks do not rebound. Alternatively, as generalist predators, gannets might increasingly exploit other warm-water prey, such as Atlantic saury (*Scomberesox saurus*) as ocean temperatures increase. As Atlantic saury is not exploited by the commercial fishery, a northward range shift by this species may provide a more plentiful prey source for gannets in late chick-rearing and could potentially lead to increased productivity in the years ahead.

In Chapter 3, I show that gannet foraging tactics shifted both within and between years. In both 2019 and 2020, gannets shifted their attention from capelin in early chick-rearing, to larger prey such as mackerel during late chick-rearing. This was demonstrated by changes in the frequency of U- and V- shaped dive profiles, which are targeted at small (e.g. capelin) and large pelagic fishes (e.g. mackerel), respectively (Garthe et al. 2000). These shifts occurred abruptly in early August in both 2019 and 2020, suggesting a critical threshold during the breeding season where gannets must switch from the less energetically dense capelin to larger pelagics. A switch in foraging tactics also likely reflected changes in availability of prey types, as capelin migrate offshore following inshore spawning (Carscadden et al. 2013), and mackerel begin to move into Newfoundland waters in greater numbers in July (Moores et al. 1975). This shift likely occurred due to Central Place Foraging Theory constraints, by which the cost associated with capture of one prey species must not outweigh the nutritional benefits (MacArthur and Pianka 1966). It is also possible that this shift away from capelin occurred due to consistent exploitation of capelin by gannets causing dispersal away from the colony and to deeper waters, thus rendering the effort required for acquiring capelin greater than the energy gained (Lewis et al. 2001). As chick growth requirements increased in late chick-rearing (Montevecchi et al. 1984) and prey distributions shifted (e.g. capelin spawning ceased, mackerel and saury moved into the region), parental gannets switched their foraging tactics to optimize offspring provisioning and energy efficiency.

Parental gannet foraging effort also differed between years. Foraging effort was greater during early chick-rearing in 2020 than in 2019. This suggests that prey availability during early chick-rearing in 2020 was lower than in 2019, as gannets worked harder to provide food for their young. Indeed, capelin availability was lower in 2020 as indicated by fewer reported capelin spawning sites in Placentia Bay and the Southeast Newfoundland coast (see Chapter 3). This increased workload in search of prey during early chick-rearing in 2020 might have been reflected in productivity, as breeding success was marginally lower in 2020 (0.586 chicks fledged/apparently occupied nest) compared to 2019 (0.628 chicks fledged/apparently occupied nest). Foraging effort in late chick-rearing was not significantly different between years, which suggests that prey availability in late chick-rearing was similar between years. As mackerel availability was found to be a significant determinant of gannet reproductive success in Chapter

2, it might be expected that increased foraging effort associated with lowered mackerel availability in late chick-rearing could lead to more dramatic differences in productivity.

To fully disentangle the effects of prey availability on the productivity of Northern Gannets, further attempts should be made to create more precise estimates of SSB for critical forage species for which data are deficient, such as capelin (*Mallotus villosus*), Atlantic herring (*Clupea harengus*) and Atlantic saury. Long-term tracking studies at this highly accessible colony should also be considered to examine how differences in foraging effort associated with different prey types affects productivity. Inter-annual comparisons of gannet foraging effort over a multi-year timescale would allow for further examination of the influence of ocean temperature on availability and distribution of prey bases and behavioural responses by the gannets at this colony. Future studies should consider monitoring foraging effort during the incubation period to determine which prey species are of greatest importance during this period and whether there are any significant differences in space use between incubation and chick-rearing periods. Tracking during the incubation period would also likely allow for further inference on the location of capelin and their spawning sites, as capelin spawning peaks from June to early August (Carscadden et al. 2013), which also coincides with the incubation period (Mowbray 2020). As gannets exhibit dramatically different dive behaviour in pursuit of capelin (e.g. U-dives) compared to other prey species, habitat suitability models employing the use of GPS locations associated with U-dives could also provide inference on critical capelin habitat, and therefore, regions of multi-species conservation concern. Finally, long-term monitoring of gannet reproductive success at Cape St. Mary’s and at other colonies should be continued indefinitely so more concrete influences of prey availability and climate change can be evaluated.

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4.2 SUPPLEMENTARY MATERIAL

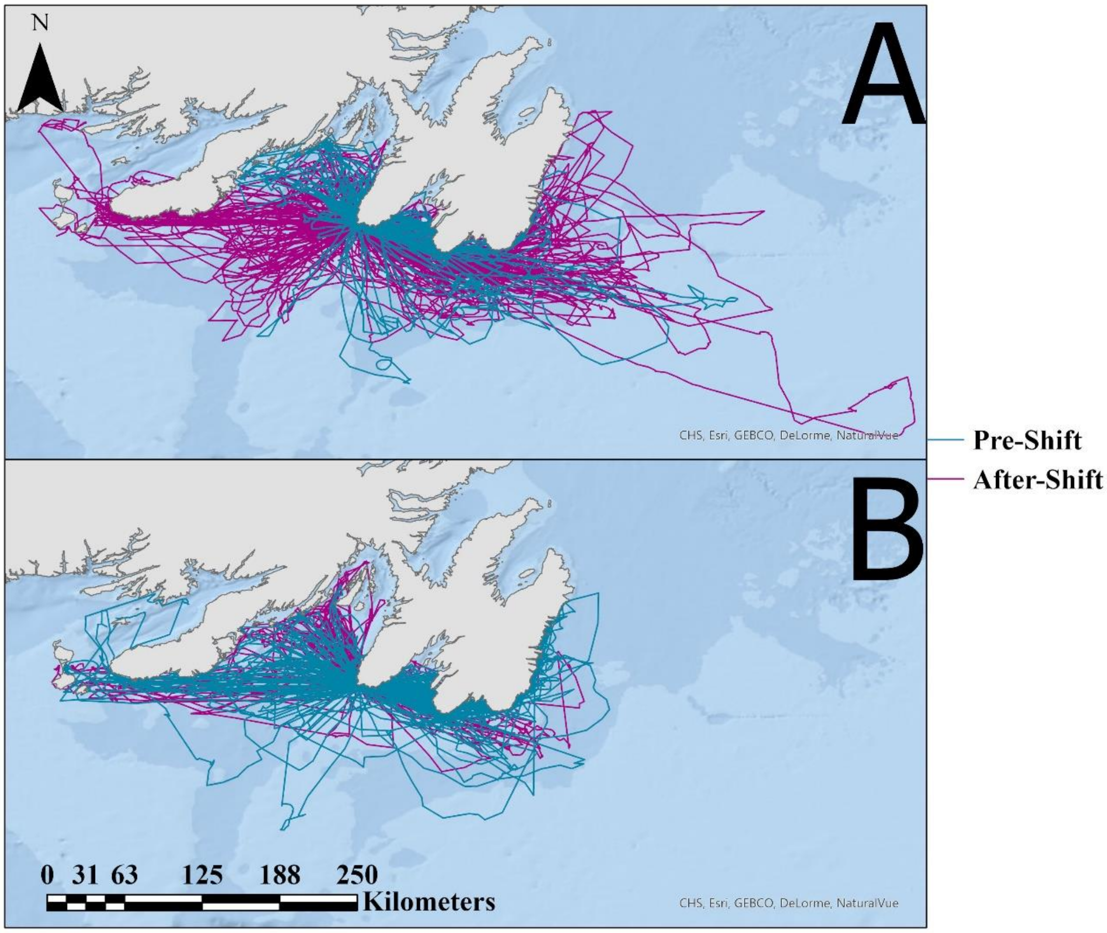

Figure S1. Tracks from early chick-rearing (blue) and late chick-rearing (purple) from both 2019 (A) and 2020 (B).

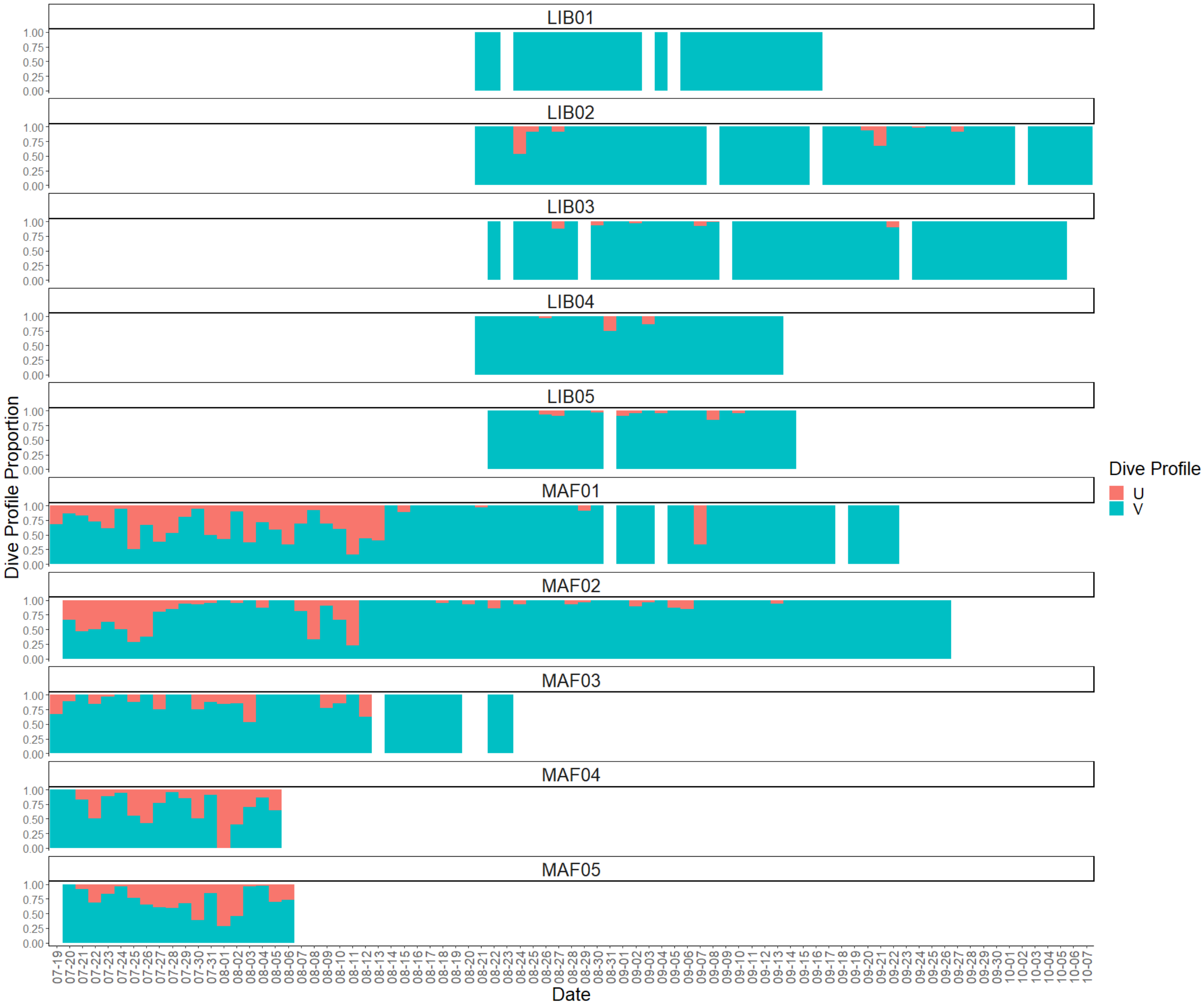

Figure S2. Individual daily dive profile proportions from all 10 parental Northern gannets tagged at Cape St. Mary’s, Newfoundland in 2019.

Figure S3. Individual daily dive profile proportions from all 10 parental Northern gannets tagged at Cape St. Mary's, Newfoundland in 2020.

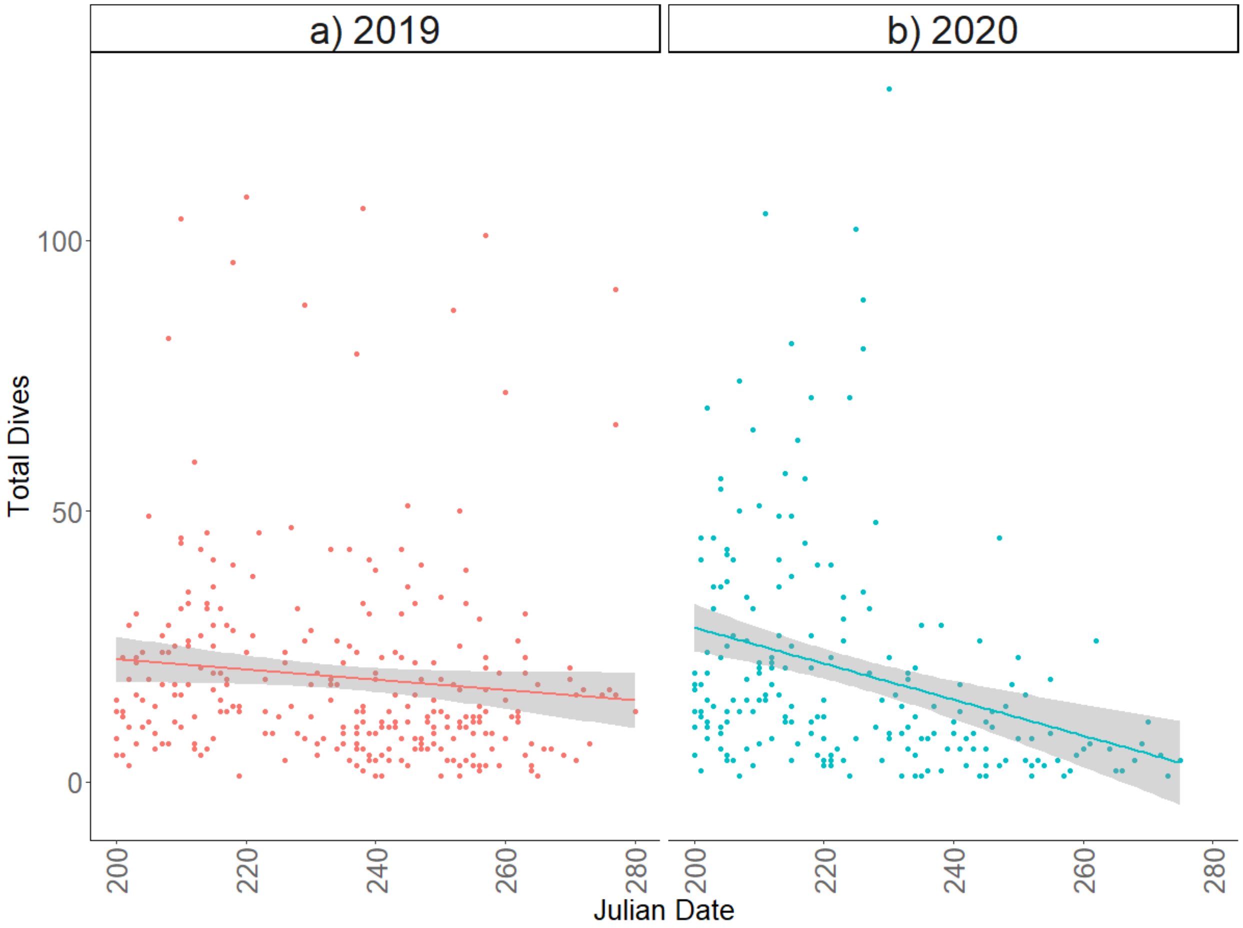

Figure S4. Daily dives per trip from all tagged parental Northern gannets in a) 2019 and b) 2020.