

# **SEABIRDS IN A CHANGING OCEAN: AN OVERVIEW OF 20 YEARS OF RESEARCH AND MONITORING ON MACHIAS SEAL ISLAND, BAY OF FUNDY, CANADA**

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## **ABSTRACT**

This paper reviews some of the more obvious changes in the populations and diets of seabirds breeding on Machias Seal Island, at the junction of the Bay of Fundy and the Gulf of Maine, from 1995 through 2015. This is the largest seabird colony in this oceanic ecosystem, hosting colonies of cold-water species at the southern edge of their distribution. My lab's research over 20 years has been focused in two directions – exploring how several closely-related species persist in co-existence here, and interpreting changes in the birds' biology in terms of responses to environmental changes. Diet played a major role in ecological isolation, but has changed considerably in response to virtual disappearance of juvenile herring since the late 1990s and the recent appearance of juvenile haddock. Ocean warming since 2000 has accelerated, especially after a sudden decrease in water temperature and salinity around 2005, which had as much deleterious effect as the subsequent warming. A major finding has been that the three most abundant breeders – Atlantic Puffin, Razorbill, and Arctic Tern – exchange individuals with other colonies in the Gulf of Maine and so each constitutes a true meta-population. This study, with similar collaborative work on those colonies, provides a unique spatial perspective on marine seabird population dynamics in a rapidly-changing ecosystem. Two species (Razorbills and Common Murres) show wholly unexpected increases in numbers, despite declines in several demographic measures that bode ill for the long-term sustainability of this colony.

## **INTRODUCTION**

Recognition of the value of using responses of organisms to environmental change is increasing, as examples of extreme changes in

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wildlife are interpreted in terms of what they tell us about our shared environments (Wagner *et al.* 2021). One of the fastest-changing ecosystems in eastern Canada is the Bay of Fundy, the north-eastern extension of the Gulf of Maine Large Marine Ecosystem where ocean temperature is increasing faster than 99% of the world's oceans (Pershing *et al.* 2015). The small rocky island of Machias Seal (MSI) at the junction between the Bay and the larger Gulf, between Canada and the USA, supports the most diverse seabird colony in the Canadian Maritimes and largest in the broader Gulf of Maine (GOM) ecosystem.

In 1995, my lab at the University of New Brunswick (UNB) set up a long-term research and monitoring program to record and investigate changes in the seabirds breeding on MSI, focusing on how such changes might reflect or reveal changes in the marine ecosystem on which they depend (Diamond and Devlin 2003). The current paper summarises some of the major changes recorded over the next twenty years, focusing on changes in the environment, population size, and diet.

### **Theoretical framework**

Our research addresses two fundamental ecological concepts. The first is competitive exclusion, an ecological principle reaching back at least to the 1930s (Gause 1934) and arguing that species with identical ecology cannot co-exist because one species will inevitably out-compete the other (see also Hardin 1960). Seabird colonies are classic examples of multiple species feeding on similar prey within reach of the colony to which they must return during the breeding season (Lack 1967). On MSI, two species of tern (Sternidae) and three of auks (Alcidae) live in the same colony and feed principally on small forage fish in the surrounding ocean. The ecological interest, particularly for the two terns and three auks, is in how they keep separate but sympatric breeding populations. Since bird populations are generally limited by food supply (Newton 1998, 2013), studies of diet are particularly germane to this issue.

The second is the concept of seabirds as indicators, principally of marine food supplies (Cairns 1987) but also of environmental change more broadly (Einoder 2009). Seabird breeding colony sizes are commonly considered to be limited by the availability of food within foraging range of the colony, even depleting that supply over the course of a breeding season (Ashmole 1963,

Diamond 1978, Furness and Birkhead 1984, Birt *et al.* 1987), so colony size should reflect food abundance. However, the relation between food supply and colony size is an ‘ultimate’ effect, in the sense that it is the end-point of a chain of more immediate or ‘proximate’ effects on short-term seabird responses including phenology (date of laying), clutch size (in species laying more than 1 egg per season – on MSI, only the terns), hatch success, chick growth rate and fledging condition, and fledging and breeding success. Fledging refers to maturation of the chick to the point where it leaves the nest, and fledge success is the number of chicks fledged per chick hatched; breeding success (or productivity) is therefore the product of hatch success and fledge success (chicks fledged per egg laid). Food availability likely affects each seabird response (hatch success, fledge success) over different time-scales and to different degrees (Cairns 1987), so each of the demographic parameters reflects both timing and extent of changes in food availability, thus serving as indicators of changes in the food-web supporting the prey species (Scopel *et al.* 2018, 2019). Seabirds can live for many decades, so negative impacts of climate (or any other) change will show up sooner in such measures as low clutch size, poor breeding success etc., than in number of breeders, acting as early warning signs of difficulties long before they become obvious in terms of population size.

Demographic changes and their relation to regional oceanographic and climate changes are described more fully in Scopel *et al.* (2019) and Major *et al.* (in press) for auks, and Scopel (2021) for terns. Here I focus on environmental changes measured on the island: changes in population size (and thus biodiversity); breeding success (reflecting conditions over a whole breeding season); chick growth (indicating conditions when energy demand is greatest); survival, which has most effect on population trajectory; and diet, through which environmental conditions are translated into seabird outcomes.

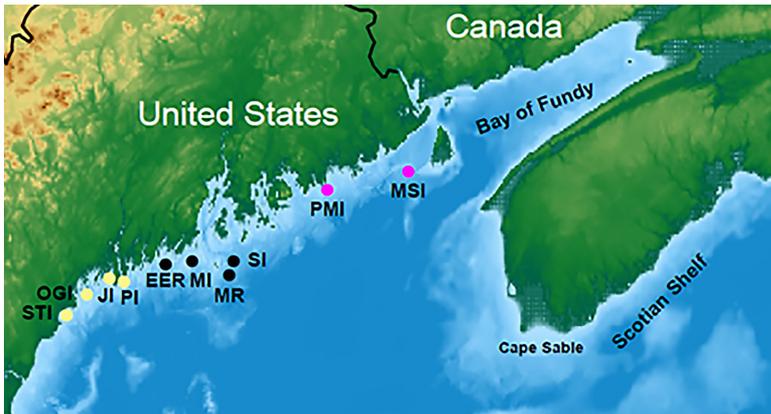
## STUDY AREA AND METHODS

The island, its habitat types, and our study methods are described in detail in Diamond and Devlin (2003). Briefly, MSI is a small (9.5ha) treeless granite outcrop, equidistant (19 km) from Grand Manan Island and the coast of Maine. It is owned by the Government of Canada, which keeps a manned lighthouse through

the Department of Fisheries and Oceans (DFO) and manages the Migratory Bird Sanctuary through the Canadian Wildlife Service (CWS) of Environment and Climate Change Canada. The lighthouse is manned because of a jurisdictional dispute with the USA (Burnett 1990, Gray 1994, Anon 2007), related to its position in the outer Bay of Fundy bordering on the Gulf of Maine (Fig 1).

A rocky foreshore is most exposed on the south and west of the coast, where most Razorbills (*Alca torda* Linnaeus, 1758) and Common Murres (*Uria aalge* Brisson, 1760) (hereafter Murres) nest, and the vegetated interior provides peaty soil in which Atlantic Puffins (*Fratercula arctica* Pennant, 1768) (hereafter Puffins) and Leach's Storm-Petrels (*Oceanodroma leucorhoa*) dig nesting burrows and on which Arctic and Common Terns (*Sterna paradisaea* Pontopiddan, 1763, and *S. hirundo* Linnaeus, 1758) and Common Eiders (*Somateria mollissima* Linnaeus, 1758) nest.

A research crew of two to four from UNB, usually led by a graduate student, occupies a bungalow loaned by CWS from mid-May through mid-August each summer. CWS hires a caretaker/observer to check tourist numbers for June and July; in recent years, this role has been contracted to UNB and forms part of the research crew.



**Fig 1** Map of seabird colonies in the Outer Bay of Fundy and Gulf of Maine. MSI = Machias Seal Island; PMI = Petit Manan Island; SI = Seal Island National Wildlife Refuge; MR = Matinicus Rock; MI = Metinic Island; EER = Eastern Egg Rock; PI = Pond Island; JI = Jenny Island; OGI = Outer Green Island; STI = Stratton Island. Colours show grouping of colonies (eastern, central, western) based on oceanographic characteristics. Seabird colonies on these islands are connected to various degrees by dispersal.

Transport is provided by a boat bringing tourists from either Cutler, ME, or Grand Manan, NB. Up to 30 tourists are allowed ashore each day and are guided by boat or lighthouse staff to blinds for close observation of nesting birds. Tourists are not allowed in the northern half of the island and researchers can work there without interference.

Our broad approach was for monitoring (which I prefer to think of as long-term research) to continue side-by-side with more focused graduate-student projects; a typical crew might consist of a mid- or late-thesis graduate student as supervisor, a beginning graduate student, and one or two field technicians hired just for the summer. Graduate students are part of the monitoring crew, and technicians help with graduate research projects as well as monitoring. Crew sizes have ranged from two in some of the early years, to three or four in recent years; numbers are limited by the accommodation and provincial regulations, as well as by funding.

Simple weather measurements (rainfall, wind direction and speed, air temperature, sea surface temperature) are taken daily; details of these and research protocols are in Diamond (2014). Timing and success of breeding of Puffins and Razorbills are measured by visiting around 100 permanently-marked burrows or nest sites of each species on fixed schedules and recording nest contents each time. Tern nests in specific areas are marked when they first appear, and checked daily until eggs hatch and frequently until chicks fledge. Field procedures always represent a balance between precision of data and disturbance to the birds, the latter being minimised wherever possible.

Following training with pictures from previous years and collaborators in the USA, diet is measured by fixed watches of selected areas from blinds, recording prey carried in the bill by adults feeding chicks, and estimating the length of each item by comparison with the length of the bird's bill (see also Scopel *et al.* 2018, 2019). We also collect prey dropped in the colony; by measuring and weighing these, we can convert length to weight (Table S3 in Scopel *et al.* 2018).

Chick growth typically follows a curve, low at first, followed by a rapid linear increase before levelling off to an asymptote before departure from the island (except in Razorbills and Murres where linear growth in wing length continues until departure). For mathematical simplicity, we calculate growth rates by measuring

weight and wing-chord two or three times during the linear period of growth, as defined in the literature.

We share research protocols and collaborate closely with colleagues in the USA who manage other seabird colonies in the GOM; the USA Fish and Wildlife Service manage these islands as part of the Maine Coastal Islands National Wildlife Refuge, and contracts much of this work to the Seabird Restoration Project of the National Audubon Society. All seabird researchers and managers, including the UNB team, collaborate in the Gulf of Maine Seabird Working Group. By doing so, we can explore a property of seabirds that is rarely possible to investigate, i.e. the exchange of birds among colonies on different islands. Seabirds have long been considered exclusively philopatric, i.e. breeding only in the colony where they were raised, but this is partly because most long-term studies have been on single islands where it is impossible to measure such movement. We were eager to take the opportunity of multiple colonies within 200 km of each other to assess the possible importance of dispersal among colonies, an important parameter rarely assessed in seabird studies. This collaboration also enables us all to explore the spatial scale of changes in the marine ecosystem, and of seabird responses to those changes. The spatial and temporal extent of this collaboration is unique in seabird studies in the northern hemisphere.

On MSI we focus on three species for intensive study of demography and diet: Puffin, Razorbill, and Arctic Tern. Common Terns were already the focus of a long-term study in Massachusetts (Arnold *et al.* 2004), eiders were the subject of research elsewhere in eastern Canada, and Leach's Storm-Petrels take so long to raise young that we could not measure breeding success before leaving the island in late summer (and are the subject of intensive long-term research on nearby Kent Island). Murres colonised in 2003 and are difficult to incorporate into routine monitoring because they nest under boulders; for the first years after their arrival, we avoided their nesting areas for fear of causing abandonment, but now we band small numbers of chicks and adults, and study their diet the same way as in other species.

Populations are made up of different sexes and age-classes which might respond differently to changes in the environment, so it is important to estimate the proportions of each of these.

This is one of the most challenging tasks in any population study, and requires sustained, systematic recording of individually-marked birds over a period matching the lifespan of the study species – 40 years or more in the case of many seabirds. This we do by banding as many birds as we can without causing undue disturbance, ideally several hundred a year. Standard government bird-bands carry unique nine-digit numbers and are hard to read in the field (i.e., without recapturing the bird), so for Puffins and Arctic terns we order custom-made bands with a four-digit alphanumeric code (e.g., AA 01) from a specialist company in the U.K. These, and the government bands, are made of alloys resistant to the wear which is inevitable in birds which spend the summer on and around granite boulders (Breton *et al.* 2006a).

In the focal species we band more chicks than adults, so that an increasing proportion of the population consists of birds of known age. Banding totals are in Table 1.

Banding a bird is of little value unless that band is then read at another time or place. Thus we spend many more hours looking for banded birds and recording their numbers, than we do banding them in the first place. These band-reading sessions are stints of two to three hours spent with a spotting scope, often in a blind, searching for banded birds and reading their band numbers, from fixed locations around the island (often the same places where we look for birds bringing in prey). Band-numbers read are entered into a database shared with collaborators on other colonies in the GOM. This enables us to measure changes in survival and dispersal to neighbouring colonies in the GOM.

In the focal species the sexes look the same. An important methodological tool that we needed to develop was to allow us to distinguish the sexes in adults, using morphological measurements;

**Table 1** Banding totals of seabirds on Machias Seal Island, 1995-2015

Species	Adults	Chicks	Total
Atlantic Puffin	2,710	6,256	8,966
Razorbill	677	1,212	1,889
Common Murre	69	144	213
Arctic Tern	1,011	2,524	3,535
Common Tern	203	1,283	1,486
Leach's Storm-petrel	220	268	488
Totals	4,890	11,687	16,577

this was achieved as honours or within master's projects for all three focal species (Arctic Terns – Devlin *et al.* 2004; Puffins – Friars and Diamond 2011; Razorbills – Grecian *et al.* 2003). These allow reliable determination of the sex of 70-80% of adults of these species, using discriminant function analysis (DFA) of two or three standard measurements of head and bill. Individuals falling outside the confidence limits of the DFA were sexed genetically using a few of the feathers we collect routinely.

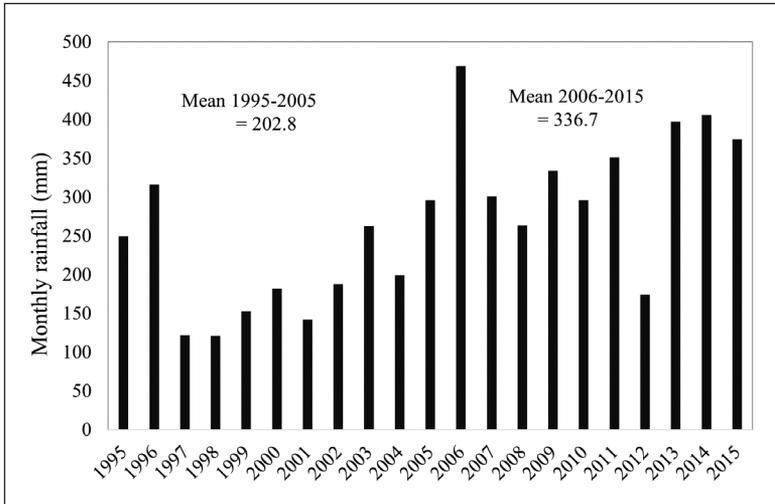
## RESULTS AND DISCUSSION

### Environmental changes

Rainfall on MSI has increased by 66%, on average, since 2005 (Fig 2). The significance of higher rainfall lies in its effects on downy seabird chicks before they have grown feathers to protect them from both wetting and hypothermia. Down provides insulation but not waterproofing, so wet downy chicks are susceptible to chilling unless they are tightly brooded by a parent. A parent must choose between using its own body heat to keep a chick warm and dry, or leaving the chick exposed while the parent goes to sea to find food to fuel its own metabolism and the chick's. This conflict is particularly evident with terns because they nest on the ground, often near thick vegetation which itself can become wet enough to continue being a threat to a downy chick long after rain has ceased to fall.

Terns also may have more than one chick to protect and feed, making them more susceptible to increased rainfall and decreased food supply. Auks have only one chick and are less susceptible to heavy rain and predation because they nest underground (Puffins) or under cover of rocks (Razorbills, Murres), though they can still be affected (Scopel *et al.* 2019).

The sea surface temperature (SST) around MSI has followed a distinctly cyclic trajectory with an apparent overall upward trend of over half a degree Celsius between 1995 and 2015 (Fig 3). This trend hovers around significance in July ( $p = 0.052$ ) and is significant in August ( $p = .034$ ) but not in May or June ( $p > 0.05$  in both cases); inter-annual variation exceeds the temporal trend. Increasing SSTs are potentially most problematic for terns because they feed within the first few centimetres of the surface, while auks dive deep below to cooler water. Seabirds' sensitivity to surface temperature



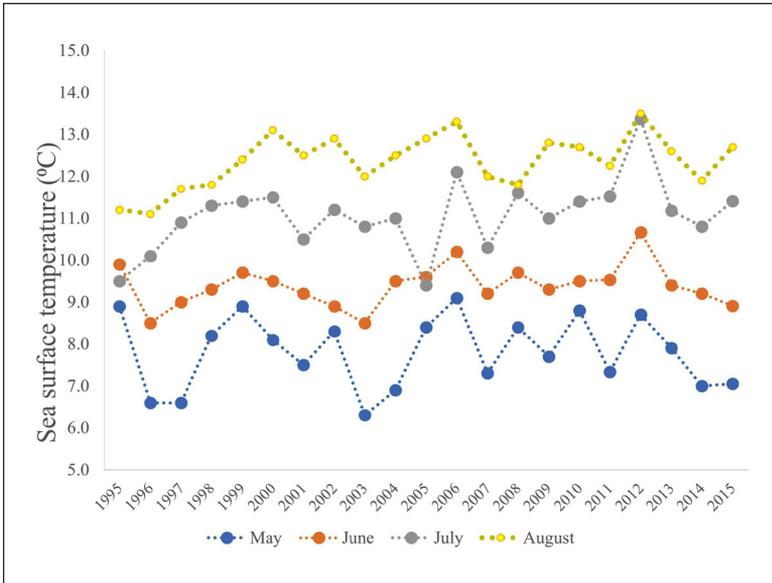
**Fig 2** Trends in summer rainfall (May-August) at Machias Seal Island. Rainfall varied interannually, but averaged 66% higher after 2005; six of the last ten years had higher rainfall than in any year of the previous decade.

operates through the temperature sensitivity of prey; most forage fish and macroplankton have preferred water temperatures and if those are exceeded, they can move to cooler water below. Auks can follow them there, but terns cannot. SST increases during the summer, especially in late summer; terns, Razorbills, and Murres have mostly left the island by late July, leaving Puffins and Storm-petrels to endure the increasing heat of late summer.

SST can fall as well as rise, as is evident in 2005 when July temperatures were below those in June. The changes involved in this sudden oceanographic change were more consistent across measures and species than effects of the marine heatwave year of 2012.

### **Breeding species and colony size**

**Regular breeders.** In 1995 two species of auk (Alcidae) and two of terns (Sternidae) bred, with smaller numbers of eiders and storm-petrels. There had been regular nest counts of terns every two years, carried out by CWS staff until 2004 when UNB took over that task. The numbers of Puffins had been “estimated” by unspecified methods at irregular intervals between 1883 (60 birds) and 1984 (900-1000 birds) (MacKinnon and Smith 1985). Numbers during this study are compared with the most recent earlier numbers in Table 2.



**Fig 3** Trends in monthly summer Sea Surface Temperature measured at Machias Seal Island. SST has varied considerably between years; July and August show an apparent increasing trend to 2000 and especially high temperatures in 2006 and the “heatwave” year of 2012, but with anomalously cool temperatures in July 2005 and 2007. Note that May and August are represented only by the last and first two weeks, respectively, when crews are on the island. No data are available for August, 2005.

Puffins breed in burrows dug in the soil, or in cavities among boulders. Counts of nest sites of Puffins were first made in 2000, counting occupied burrows or nest cavities in 4 m<sup>2</sup> (2 m x 2 m) quadrats on E-W grid lines every 50 m throughout nesting habitat (identified by presence of burrows). Later censuses have been at irregular time intervals. Since 2000, estimates of numbers of breeding Puffins have ranged between about 6,000 and 8,000 pairs.

Razorbills are larger (mean mass 700 g vs. 430 g in Puffins) and lay mostly in larger cavities in piles of boulders. The first census was a complete count of about 600 pairs (Grecian 2005). Numbers then increased so rapidly that a complete count became impracticable, so in later years they have been sampled in the same way as Puffins, reaching about 2500 pairs in 2015 (Fig 4).

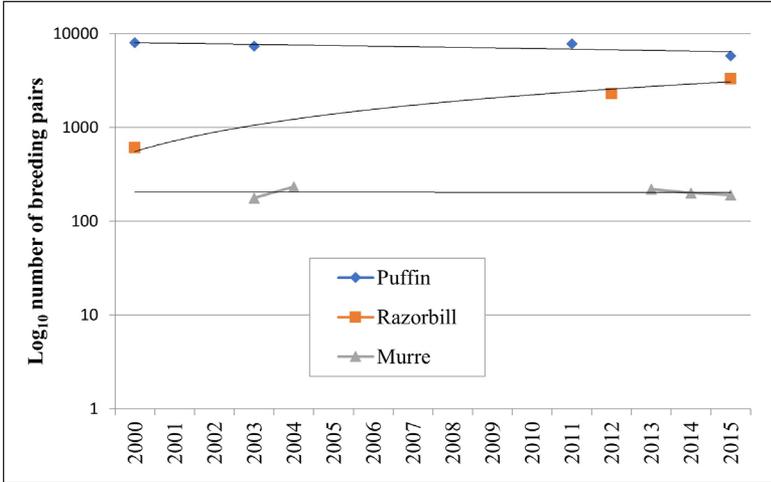
Prior to 2003, considerable numbers of Murres were seen loafing on land and around the island, increasing from 50 in 1999 to over 500 in 2002. A single egg was found in 1994 but there was

**Table 2** Comparison of number of breeding pairs of seabirds on Machias Seal Island, 1995 and 2015. ~ = approximate number.

Species	Number of pairs			Comments
	Nearest previous count or estimate (year)	1995 (or nearest following year)	2015	
Atlantic Puffin	~800 (1982)	~8,000 (1999-2000)	6,400	No census until 1999-2000
Razorbill	75 (1983)	600 (2000)	2,550	No census until 1999-2000
Common Murre	Not nesting	Not nesting	~200	Nesting began 2003
Arctic Tern	2,419 (1994)	1,637 (1996)	141	Colony collapsed in 2006
Common Tern	368 (1994)	608 (1996)	9	Colony collapsed in 2006
Leach's Storm-petrel	82 (1958)	150 (1999)	60 (2017)	
Common Eider	31 (1994)	41 (1996)	32	

no further sign of breeding until 2003, when 47 eggs were counted (Bond and Diamond 2006) but many more could not be counted (AWD, pers. obs.). Breeding has continued ever since; at first, many eggs were laid in the open on the bare rock in the southwest part of the island, seaward of Razorbills and Puffins, but Herring Gulls (*Larus argentatus* Pontopiddan, 1763) and Great Black-backed Gulls (*L. marinus* Linnaeus, 1758) rapidly took those eggs and murrens now lay entirely in “caves” roofed by large boulders balanced on other large boulders. We estimate the numbers of eggs and chicks in each “cave” when most chicks are old enough to be banded (about 12 days); this method produces an under-estimate by the amount of egg loss and early chick mortality. Numbers have remained constant at around 200 pairs since 2004 (Fig 4).

Terns nest on the surface throughout the island, and nests are counted by teams of people moving slowly across the island. The colony contained about 2000 pairs of Arctic Terns and 1,000 pairs of Common Terns in 1995, but in 2006 suffered extremely high egg predation by Herring Gulls and it was abandoned. Possible causes of this extreme event included increased egg predation by gulls, bad weather, and poor food supply. Their relative contributions were not sorted out until Lauren Scopel's analysis (Scopel and

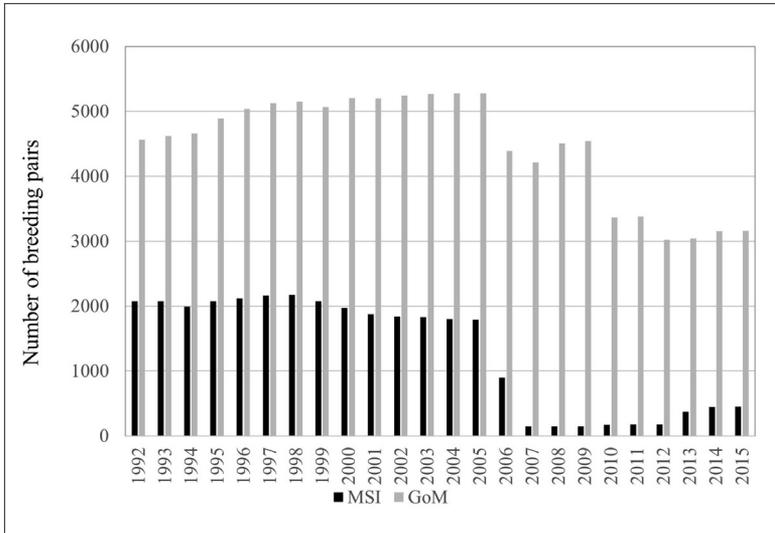


**Fig 4** Changes in numbers of auks breeding on Machias Seal Island, 2000-2015. Puffin numbers remained fairly stable, with a possible slight recent decrease, while Razorbill numbers increased rapidly after 2000 and Murre numbers increased quickly after colonisation but changed little thereafter.

Diamond 2018), which attributed the collapse of the colony primarily to high egg predation by gulls, caused by the cessation in 2000 of lethal control of problem gulls (Pyne 2018). From 2006 until 2014, when a very restricted form of lethal control was restored, no Arctic Tern chicks fledged and numbers fluctuated in the low hundreds or fewer, the terns abandoning the colony each year as eggs were depredated in increasing numbers (Fig 5).

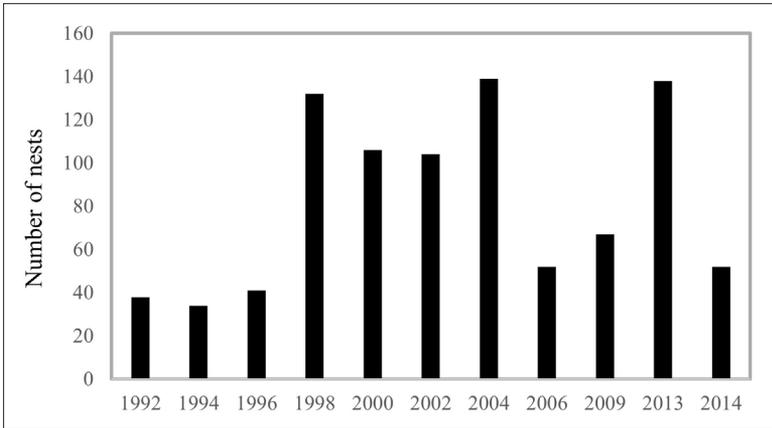
The return of limited lethal deterrence of predatory gulls in 2013 was followed by the fledging of tern chicks in 2014 for the first time since 2005, confirming that the colony failure was due to excessive gull predation (Scopel and Diamond 2018). The significance of the loss of the tern colony is that it was the largest Arctic Tern colony in North America and had been in existence since at least the 1880s, during which time it had failed only in two years in the 1940s (MacKinnon and Smith 1985), and that it supplied many recruits to the other colonies in the GOM (see below).

Common Eiders usually nest in clumps of thick vegetation. Counts of nests and eggs are made during censuses of tern nests. Numbers have fluctuated considerably over 20 years with no consistent trend (Fig 6).



**Fig 5** Number of pairs of Arctic Terns nesting on Machias Seal Island, and in the entire Gulf of Maine (GoM) metapopulation. The broader metapopulation declined by about the same number of pairs as formerly nested on MSI. Data compiled by Lauren Scopel from island-wide censuses.

Nesting underground and not visible during daylight – so unremarked by the many tourists who visit the island in summer – is Leach’s Storm-Petrel which lays its single egg in narrow burrows in the turf. Burrow entrances are only a few centimetres across and can be extremely hard to find; the lack of grazing animals on MSI means that vegetation can be very tall by the time the petrels lay eggs in mid to late June. Ornithologists visiting MSI in the 1930s and 1950s estimated numbers at about 2000 pairs or burrows; a 1966 estimate was between 200 and 500 pairs; by the 1970s, several estimates by CWS wardens ranged between 50 and 200 pairs; in the early 1980s, 60 and 58 burrows were found by two CWS wardens in successive years. Dorothy (McFarlane) Diamond has made complete counts by intense ground searching coupled with sniffing for the distinctive musky scent of petrels in 1999, 2006, and 2017. Over this period, numbers dropped from about 150 to 77 and then 60 pairs. This clear decline is consistent with population trends at several other eastern Canadian colonies in recent years (Wilhelm *et al.* 2020, d’Entremont *et al.* 2020) and with its Canadian status as Threatened (Species at Risk public registry 2021).



**Fig 6** Counts of Common Eider nests found during tern censuses on Machias Seal Island.

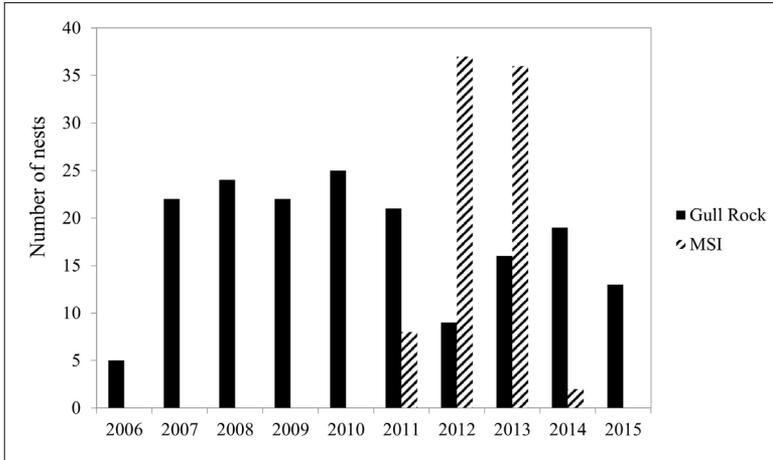
Herring Gulls and Great Black-backed Gulls nest mostly on Gull Rock, a bare island located a few hundred metres north-east of the northern tip of MSI. Gull nests on MSI itself are destroyed (under permit from CWS) to deter gulls from nesting, as part of the strategy to minimise gull predation on tern eggs (Scopel and Diamond 2017, 2018). Gull nests on Gull Rock are counted and eggs destroyed when opportunity allows, by vigorous shaking followed by pricking the shell; gulls whose eggs are so treated usually do not notice the damage and continue incubation beyond the time when they could re-lay. The numbers of gull nests found and destroyed on MSI and Gull Rock are shown in Fig 7.

***Sporadic breeders.*** Five other seabird species have bred on MSI between 1995 and 2015.

A pair of Roseate Terns (*Sterna dougalli* Montagu, 1813) hatched an egg in 2001, and probably fledged the chick, and a pair laid but failed the next year. Social attraction using sound recordings and decoys, attempted in the following three years, was unsuccessful.

Two pairs of Black Terns (*Chlidonias niger* (Linnaeus, 1758)), typically a freshwater species, laid each year from 2002 through 2005, without success.

A single pair of Laughing Gulls (*Leucophaeus atricilla* (Linnaeus, 1758)) nested in 2001, and two pairs in 2003 and 2005, the former probably fledging chicks but the latter not.



**Fig 7** Number of nests of gulls (mostly Herring Gulls) on Gull Rock and Machias Seal Island. Nest counts on Gull Rock were started in 2006. High numbers on MSI in 2012 and 2013 were in response to Bald Eagle (*Haliaeetus leucocephalus*) presence on Gull Rock.

Black Guillemots (*Cephus grille* (Linnaeus, 1758)) are seen in the bay on the east side of the island in many years, and one pair nested among the boulders there in 2008 and hatched a chick; Northern Gannets (*Morus bassanus* (Linnaeus, 1758)) present in 2010 laid an egg in 2011 which was quickly lost, probably to Great Black-backed Gulls which roosted nearby. This, like the Black Guillemot, Black Terns, and Laughing Gulls, was a first nesting record for the island.

**Diversity.** In terms of species richness – simply the number of species breeding regularly – diversity has increased since 1995, from six species in 1995 to seven in 2015, the difference being the addition of Murres. Although the tern colony has been greatly reduced, both Arctic and Common Terns still try to breed so are still included as regular breeders.

Of greater interest, though, is a measure of the relative abundance of species within the breeding community, measured as the “evenness” of population size. A community dominated by one abundant species with others being much less abundant, has low evenness, while a community with the same number of species but of more equal abundance has higher evenness and therefore higher diversity. Shannon’s Diversity Index ( $H'$ ) incorporates both species number and relative abundances, and ranges between 0 and 1. A community

**Table 3** Change in Biodiversity of Seabird Community over 20 years on Machias Seal Island.  $P$  = proportion of total pairs; Shannon Diversity Index  $H' = -\sum_{i=1}^R p_i \log p_i$ ; where  $R$  is the number of species.

Species	1995 (or nearest following year)			2015 (or nearest following year)		
	Number of nesting pairs	$P$	$H'$	Number of nesting pairs	$P$	$H'$
Atlantic Puffin	8,000	0.7249		6,400	0.6814	
Razorbill	600	0.0543		2,550	0.2715	
Common Murre				200	0.0213	
Arctic Tern	1,637	0.1483		141	0.0150	
Common Tern	608	0.0550		9	0.0009	
Leach's Storm-petrel	150	0.0135		60	0.0064	
Common Eider	41	0.0037		32	0.0034	
	<b>11,036</b>		<b>0.397</b>	<b>9,393</b>		<b>0.356</b>

of  $n$  species in which one species is much more numerous than the others would have a lower value than one in which all  $n$  species had similar numbers. Calculations of  $H'$  (Table 3) show that this measure of diversity has decreased slightly from 0.397 in 1995 to 0.356 in 2015, a decline of about 10%. The number of species has increased over this period, but although evenness is raised by the increase in Razorbill numbers, the effect of that increase on  $H'$  is balanced by the reduction in numbers of terns, and the added breeding species (Murre) is not sufficiently numerous to raise the overall evenness of the community.

### Metapopulation status

Two of the focal species – Puffin and Arctic Tern – were the subject of capture-mark-recapture (CMR) models by Ph.D. students at UNB, making use of the data provided by resightings and recaptures of birds banded at MSI and the other colonies of these species in the Gulf of Maine (Breton *et al.* 2006b, Devlin *et al.* 2008). In both species, MSI was revealed as the “mothership” of the Gulf of Maine population, supplying recruits (birds fledged on MSI) to the other breeding colonies (“natal dispersal”). Adult Puffins remained faithful once they had decided where to breed (Breton

*et al.* 2006b, Whidden 2016), but adult Arctic Terns did sometimes change colonies (“breeding dispersal”).

Razorbills were also the subject of a CMR model, by a Ph.D. student from Memorial University of Newfoundland whose own study area was the Gannet Islands in Labrador but who visited MSI and used the data that we had compiled over the previous ten years (Lavers *et al.* 2007, 2008a, 2008b). Lavers (2007) found movement not only among colonies in the Gulf of Maine/Bay of Fundy, but also between those colonies and the Gannet Islands (about 1300 km). One adult on the Gannet Islands had even been banded as a chick in Scotland, suggesting contact throughout the North Atlantic (to which this species, like Puffins, is restricted).

In all three species, our work showed that individual colonies function not as closed populations, but as components of a “metapopulation”, exchanging individuals in ways that wildlife management needs to consider. We have clearly demonstrated that conservation of seabird colonies needs to encompass other colonies linked by dispersal, in this case, between the Gulf of Maine and Bay of Fundy.

### **Breeding success**

Successive parts of a breeding cycle reflect environmental conditions in successive months, allowing each measure to indicate conditions as the season advances (Scopel *et al.* 2019, Scopel 2021): clutch size in terns, and occupancy in auks, depend on food available to the female for building eggs (May-early June); hatch success (the proportion of eggs that hatch) echoes conditions during incubation (mid to late June); fledge success (proportion of chicks that reach independence) and chick growth rate reflect both feeding conditions for the parents, and weather mainly in July (prolonged heavy rain can chill exposed chicks and interfere with the adults’ ability to find food) (Scopel *et al.* 2019). These breeding stages can therefore track environmental changes on a fine time scale, and elucidate the separate effects of varying conditions on the components of breeding which finally contribute most to the dynamics of a population, *i.e.*, the number of chicks produced per breeding pair (productivity). This approach was pursued by Scopel *et al.* (2019) for alcids, and Scopel (2021) for terns. In theory, this approach allows for both lagged effects and carry-over effects from one season to another, of which the clearest example yet is the effect of food (percent by mass of herring in chick diet) during the breeding season of Puffins

on adult survival over the following winter (Breton and Diamond 2014); in this study, over-winter survival of Puffins was positively correlated with both herring landings and the proportion of herring in chick diet in the preceding nesting season, suggesting a carry-over effect between feeding conditions in summer and survival the following winter (see also Scopel *et al.* 2019).

**Arctic Tern.** Demographic research on the Arctic Tern colony has been severely compromised by the inadequate measures available to control the effects of predatory gulls on the nesting terns since 1999. Since then, because routine season-long lethal control has not been available whenever necessary, the major factor affecting productivity of the terns has been egg predation by gulls. Scopel & Diamond (2017) showed that throughout the Gulf of Maine seabird colonies, there is a threshold (25%) of egg predation by gulls, above which terns abandon that year's breeding attempts. Accordingly, in the absence of appropriate management of gull predation, tern breeding success cannot be used as an indicator of food supply or other environmental change, and the decline in numbers reflects egg predation by gulls.

Temporal patterns of components of breeding success show that Arctic Tern clutch size was steady at around 1.7-1.8 eggs per nest until 2000, when it dropped to around 1.5 until 2006, the year that the colony collapsed (Fig 8a). From 2007 through 2013, the few pairs that tried to breed laid fewer eggs on average (1.24) than in either previous period, due in part to continuing egg predation by gulls taking place before eggs were counted, and no eggs hatched. The restoration of lethal control of predatory gulls in 2014 was accompanied not only by more birds nesting, and chicks actually hatching (the first since 2005), but by a return to clutch sizes similar to the best values of the late 1990s. Hatch success followed a similar pattern, except that values after restoration returned to those immediately prior to the colony collapse, rather than pre-2000. The number of chicks fledged per nest was extremely variable between 1995 and 2003, and then was extremely low in the two years immediately before the colony collapsed, but increased to equal the highest on record in only the second year after colony restoration.

In Common Terns (Fig 8b) clutch size, by contrast, remained constant until the collapse of the colony, but as in Arctic Terns, hatch success declined as soon as lethal gull control ceased in 2000, and

productivity in the three years before the collapse was extremely low. Very few Common Terns have recolonized, so too few data have been collected on this species' behaviour since the collapse.

**Atlantic Puffins.** This species lays a single egg, so there is no variation in clutch size. There is variation, though, in the proportion of adults that choose to breed in a particular year; we term this "occupancy" and variation in this parameter could be considered as equivalent to variation in clutch size since it is determined at the same (first) stage of the breeding cycle. Occupancy is measured as the proportion of burrows in which an egg is laid, and varies quite widely throughout the time series (Fig 9a) but most values of 0.8 and over were before 2010, and three of the four before 2005. In both hatch success and productivity, the lowest values all occur after 2005, and mean values after this represent declines of 16% in both cases. Occupancy, hatch success, and productivity declined since 2005 by 4.9, 17, and 18.5%, respectively.

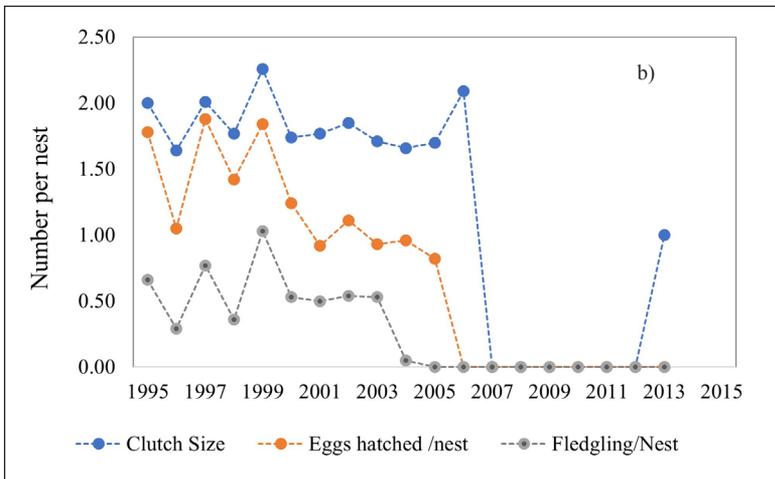
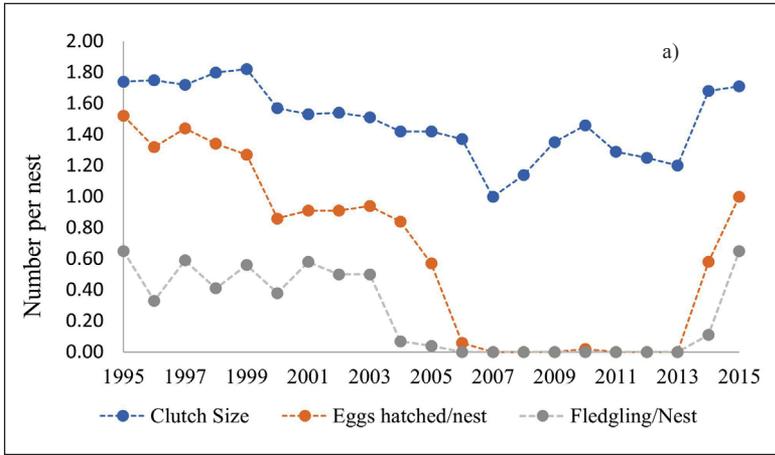
**Razorbills.** Razorbills also lay a single egg. Trends are similar to those in Puffins (Fig 9b), with a break point evident around 2005, but a sharper decline in occupancy; mean values after this year declined by 11.4% in occupancy, 17.9% in hatch success, and 18.3% in productivity.

**Common Murres.** Murres also lay a single egg, but the nest sites they use on MSI (see above) make it impossible to measure their productivity without causing undue disturbance.

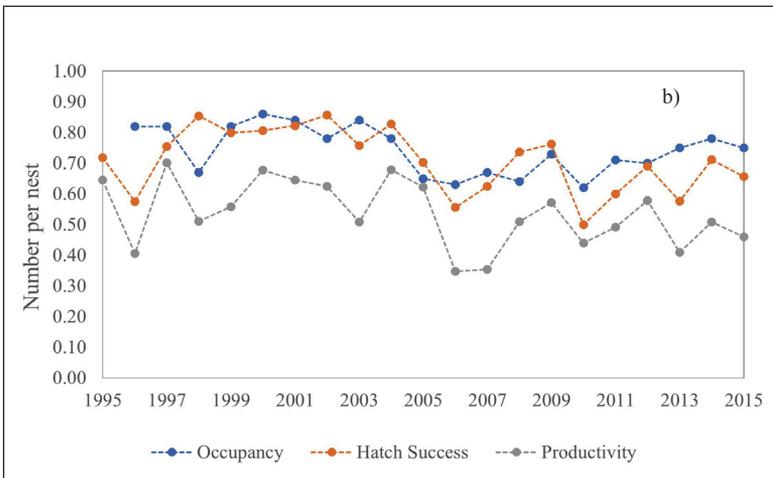
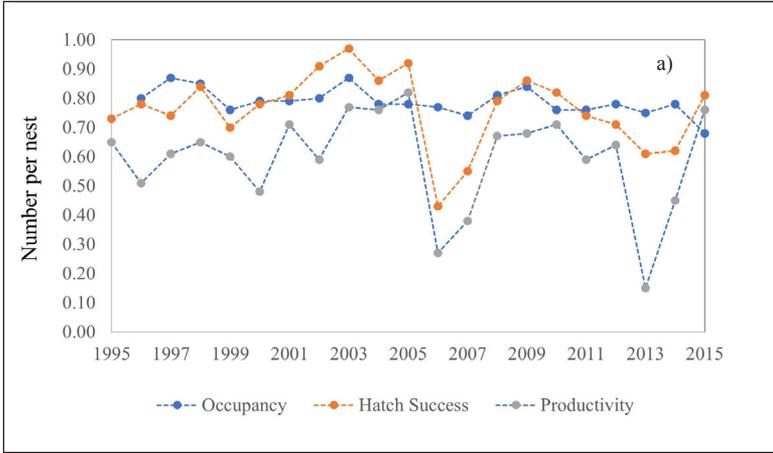
### Chick growth

Measuring the growth rate of chicks gives a fine-grained picture of the impact of short-term changes in the environment as they cascade through the food-web to the tertiary consumers that are seabirds. Chick growth rates reflect food supply over the chick-rearing period (Cairns 1987), in this case between 2-3 weeks (Razorbills), 3-4 weeks (terns, Murres) and 6 weeks (Puffins).

**Arctic and Common Terns** (Fig 10). Mass and wing growth rates were consistent from year to year though less so in Common Terns, probably because they had more chicks on average and chicks from eggs laid later tend to be smaller and grow more slowly, especially when food is short, increasing variation in the annual mean.



**Fig 8** Components of nest success of a) Arctic and b) Common Terns. Too few Common Terns nested in 2014 and 2015 to measure productivity. The tern colony failed every year from 2006 through 2012. Clutch size (number of eggs per nest) in Arctic Terns rebounded to pre-2000 levels following restoration of lethal gull control in 2013. Clutch size in Common Terns was constant before 2006, whereas Arctic Tern clutch sizes declined after 1999.



**Fig 9** Components of productivity (nest success) of a) Puffins and b) Razorbills on Machias Seal Island, 1995–2015. Occupancy declined after 2005, more so in Razorbills than Puffins. In both species, productivity largely tracked hatch success, suggesting that breeding success was determined early in the season. The first unusually warm year in the time series, 2006, is reflected in reduced productivity in both species, which did not recover fully until two years later. The effects of the first “heatwave” year, 2012, were delayed to 2013 and were more evident in hatch success of Puffins than Razorbills, suggesting a greater carry-over effect on body condition of Puffins (Scopel *et al.* 2019, Diamond *et al.* 2020). The record low productivity of Puffins in 2013 suggests that they were not able to recover body condition in time to raise the chick.

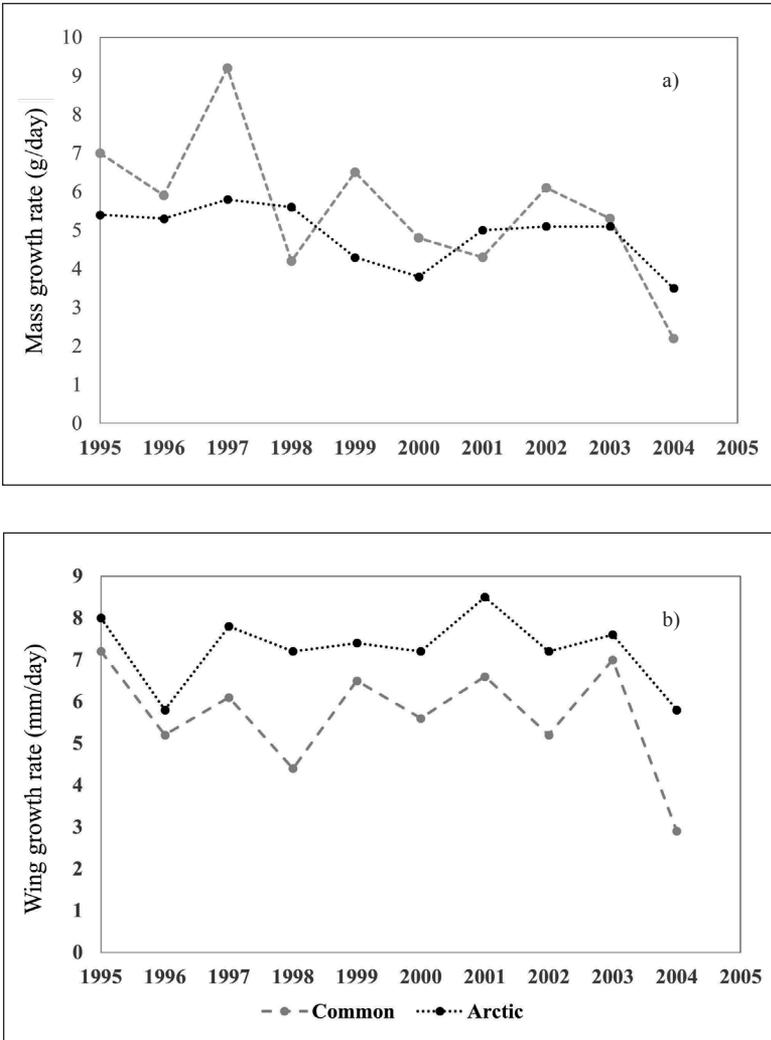


Fig 10 Growth of tern chicks. a) Mass growth is similar in the two species, varying around 4-6 g/day for nine years before dropping sharply in 2004. b) Wing growth patterns are similar to those of mass, except that Arctic Tern chick wings consistently grew faster than Common Terns.

Steady growth continued at 4-6 g/day until 2004, when it dropped sharply in both species; in that year, chick diet contained few herring and many butterfish, whose deep body makes it too wide for chicks to swallow (Kress *et al.* 2016, Scopel 2021). Too few chicks survived in 2005 to provide comparable data.

Wing growth shows a similar pattern, but whereas mass values were similar in the two species, Arctic Tern chick wings consistently grew faster than Common Terns, by about 1.5mm/day, despite adult wings of the two species being of very similar length.

**Auks** (Fig 11). Chick wing growth was similar in Puffins and Razorbills, varying inter-annually between 2 and 3.5 mm/day, and dropping sharply from 2005-2007 to 2.25 - 2.75. Mass growth was much more variable in both species (3-10 g/day), but they varied together more closely than in wing growth, except in 2011 when both mass and wing growth declined sharply in Razorbills but not Puffins. Wing growth also declined sharply in 2013, the season following the “heatwave” summer of 2012, when growth was maintained in wing chord but not in mass.

The sharp decline in growth rates, in both terns and auks, in 2004-2006 coincided with the inflow of cooler, low-salinity, nutrient-poor water entering the GOM from increased melting in the Arctic, by way of the Labrador Current (Townsend *et al.* 2010), and subsequent changes to circulation in the GOM (Greene and Pershing 2007, Smith *et al.* 2012). The beginning of this cooler-water regime appears in the SST records at MSI, where the mean SST in July 2005 was slightly below the June value (Fig 3), a situation which has not recurred. We tend to focus on increasing SST in the GOM since around 2000, and especially since that cooling period, but in the MSI record, that sudden cooling (accompanied by low salinity and nutrient content) was more clearly reflected in the seabird responses (productivity as well as growth) than the heatwave year of 2012.

## Diet

The prey consumed by these seabirds was dominated by juvenile forage fish, some of which are subject to a commercial fishery. Juvenile abundance is commonly not measured by fisheries managers, so our results could contribute to fishery management (Amey 1998, Scopel *et al.* 2018).

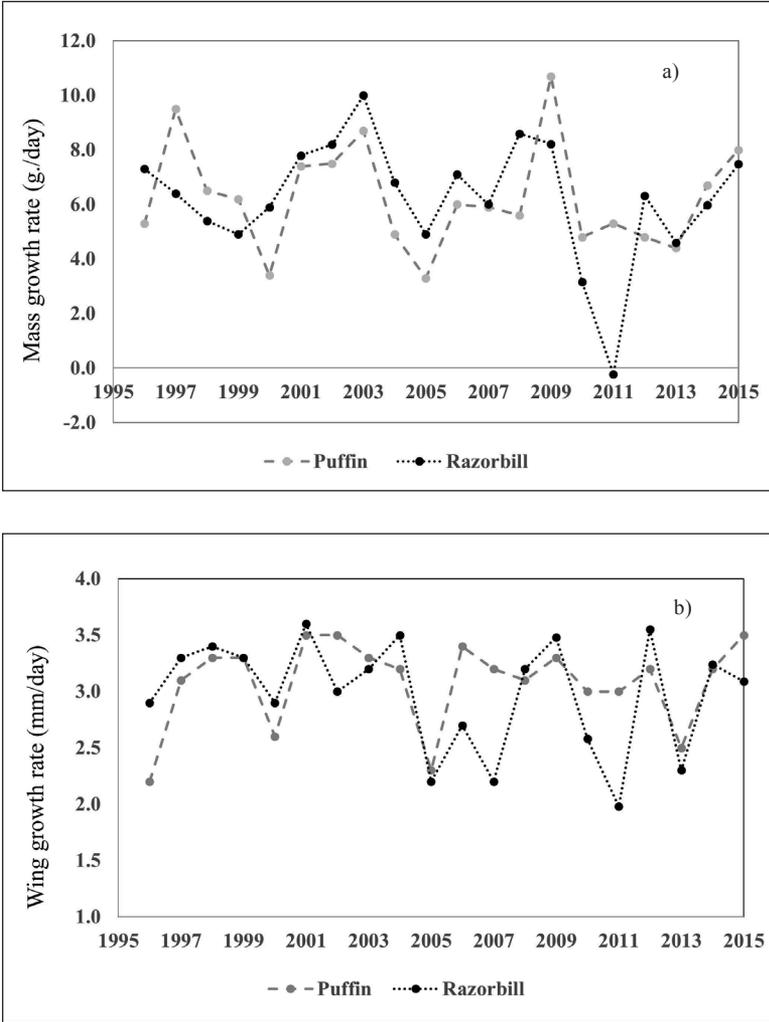


Fig 11 Growth of auk chicks. a) Mass growth varies in parallel in the two species in most years, except 1997 and especially 2011. b) Wing growth patterns are similar to those of mass, but less variable among years. In 2013, wing growth declined more than mass growth in both species. An unusual increase in herring in 2009 was reflected in mass growth rate of Puffins but not Razorbills. The lowest growth rate in Razorbills (2011) was not paralleled in Puffins.

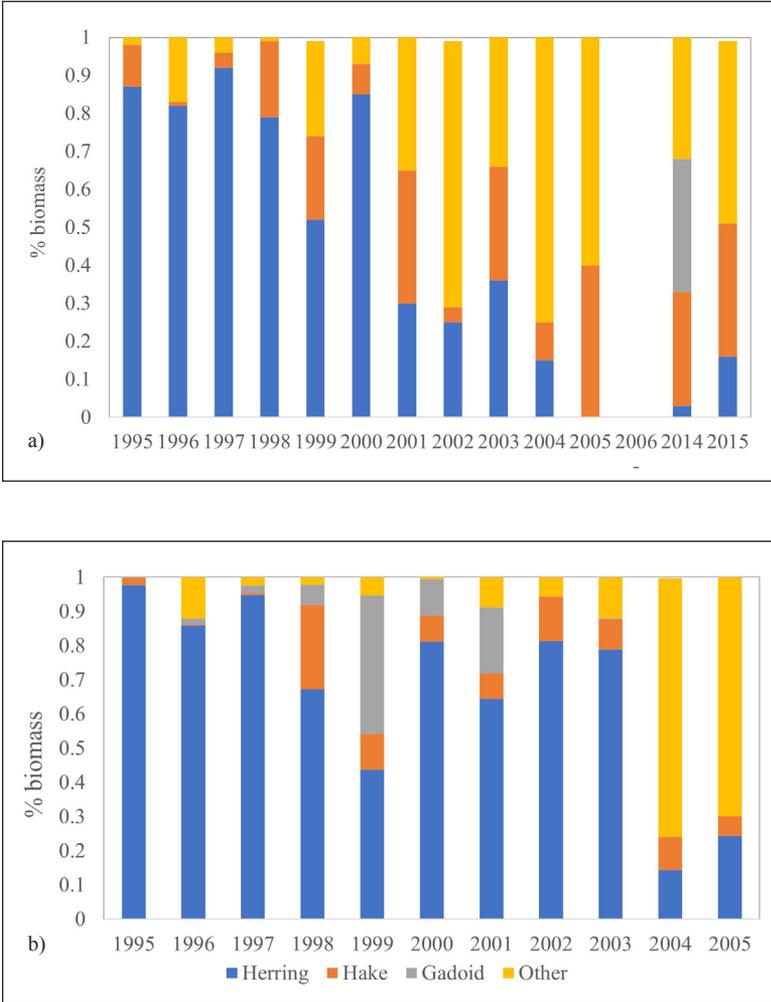
Terns and auks carry food for their chicks in the bill. The mass of each item was calculated using its estimated length and published mass:length relationships (Scopel *et al.* 2018) to allow for the great variation in size of the various items, e.g., small euphausiid shrimp, which can be very numerous in some years but still contribute very little to the diet compared with a single large herring. Table 4 shows an example of the difference in proportions by number and by mass. These data have revealed clear differences in diet between species, and changes over time. Changes in diet are the most obvious responses to changes in the marine ecosystem and have revealed several “regime changes” as reflected in the prey field for MSI seabirds (Scopel *et al.* 2018), notably around 2000 and again in 2010 (Kress *et al.* 2016, Johnson *et al.* 2018).

**Arctic Tern.** Both species of tern catch small prey at or within a few centimetres of the sea surface by shallow plunge-dives from the air. Changes in diet of both Arctic and Common Terns are described in detail by Scopel *et al.* (2018).

In the first few years of the study, diet was dominated by juvenile (“1-group” in fishery terminology) Atlantic herring (*Clupea harengus* Linnaeus, 1758) (Fig 12a), with much smaller proportions of butterfish *Peprilus triacanthus* (Peck, 1804), sandlance *Ammodytes sp.*, and white hake *Urophycis tenuis* (Mitchill, 1814), silver hake *Merluccius bilinearis* (Mitchill, 1814) and fourbeard rockling *Enchelyopus cimbrius* (Linnaeus, 1766). These last three species are difficult to distinguish in the field, at least in the size ranges taken by the seabirds, and are recorded in the field as ‘hake’. After 2000,

**Table 4** Comparison of differences between % by number and % by mass in krill (euphausiid shrimp) in prey delivered to Arctic Tern chicks on Machias Seal Island.

Year	% by number	Number of samples	% by mass
1995	0	97	0
1996	22.3	175	2.3
1997	10.0	209	<0.1
1998	4.7	169	0
1999	0.5	208	<0.1
2000	35.7	241	<0.1
2001	0.5	588	<0.1
2002	90.6	891	17.6
2003	65.9	414	1.4
2004	60.4	470	6.7



**Fig 12** Proportion by mass of selected prey types in chick diet of a) Arctic Tern and b) Common Tern on Machias Seal Island, 1995-2015. No chicks hatched 2006-2013, and there were too few Common Tern chicks in 2014-15 to provide data. “Other” includes sandlance (usually larval), larval fish, marine invertebrates or krill (largely *Meganyctiphanes norvegica*), of little nutritive value, and butterfish which has high energy density but is too deep-bodied for chicks to swallow. Both tern species took mostly herring until 2001, when the proportion of herring in Arctic Tern diet declined sharply and remained low while continuing to contribute substantially to Common Terns diet through 2003. From L.C. Scopel (unpub. UNB data).

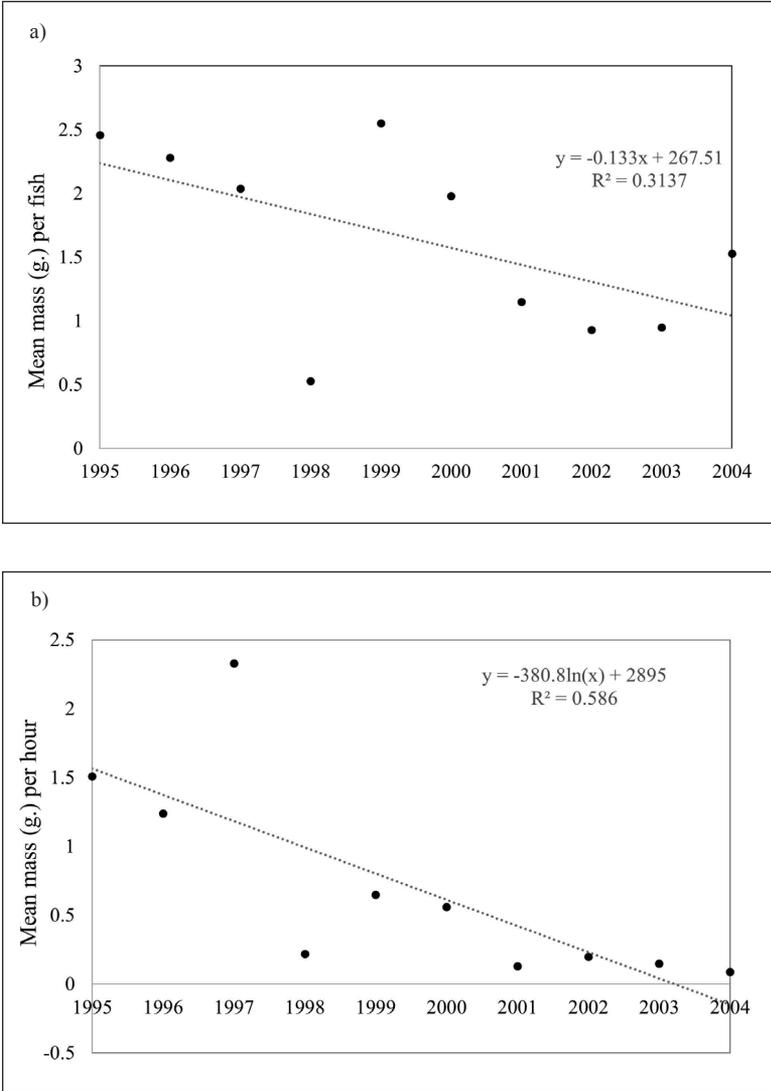
the proportion of herring declined quite sharply as more sandlance and “krill” (euphausiid shrimp, mostly *Meganyctiphanes norvegicus* (M. Sars, 1857)) and hake were taken; in 2005 there were no herring at all in chick diet, though there were few samples that year because many chicks died in prolonged rain. The rate of delivery of herring in the diet (Fig 13a) also declined after 2000, due only partly to a reduction in the size of the fish (Fig 13b); in 1999 and 2000, the rate of delivery declined while the size of herring did not, suggesting that reduced numbers of herring were mainly responsible for the decline in delivery rate, while from 2001 onward, the size and delivery rates were both reduced. There were no diet data after the collapse of the colony in 2006 because very few chicks hatched until 2014, and samples were small in that year and the next.

**Common Tern.** Common Terns are about 10% heavier than Arctic terns, but otherwise the species are very similar in appearance and nesting and feeding behaviour. The temporal decline of herring in the chick diets of the two species is roughly parallel, though in most years Common Terns had a higher proportion of herring than Arctic Terns, and much less hake; the species replacing herring in Common Tern diet were butterfish and pollock, rather than hake and krill (Fig 12b).

**Atlantic Puffin.** Changes in diet in Puffins, Razorbills and Murres are described in detail in Scopel *et al.* (2019). Here I compare broad patterns in Puffins and Razorbills (Fig 14).

Puffins are “pursuit-divers”, i.e., they dive below the surface and chase down their prey using the wings – they “fly through the water”. Adults bring several juvenile forage fish, usually below 16cm long, squid, and invertebrates especially krill, back to the burrow to feed the chick. They are known for carrying multiple prey items at the same time (“multiple-prey loaders”), in contrast with terns that usually bring one item at a time (“single-prey loaders”).

The range of prey taken by Puffins (Fig 14a) is similar to that of terns and also showed declines in herring in the early 2000s; 2009 was an exception to this trend but has not been repeated. Hake and sandlance have also been prevalent in the diet since the late 1990s, joined in 2010 by juvenile haddock (*Melanogrammus aeglefinus* (Linnaeus, 1758)) which have been the commonest prey item in several later years.



**Fig 13** a) Decline in the size of juvenile herring delivered to Arctic Tern chicks on Machias Seal Island, 1995-2004. b) Decline in the rate of delivery of herring. The highest rate of delivery by far was in 1997 when the prey size was average, suggesting prey was easy to find; and in the year with the largest prey (1999) the rate of delivery was slightly below average, so the herring were presumably less easily caught. The slope in (b) is almost three times steeper than in (a), showing that availability of herring declined more steeply than the size. Data from Lauren Scopel (unpublished UNB data).

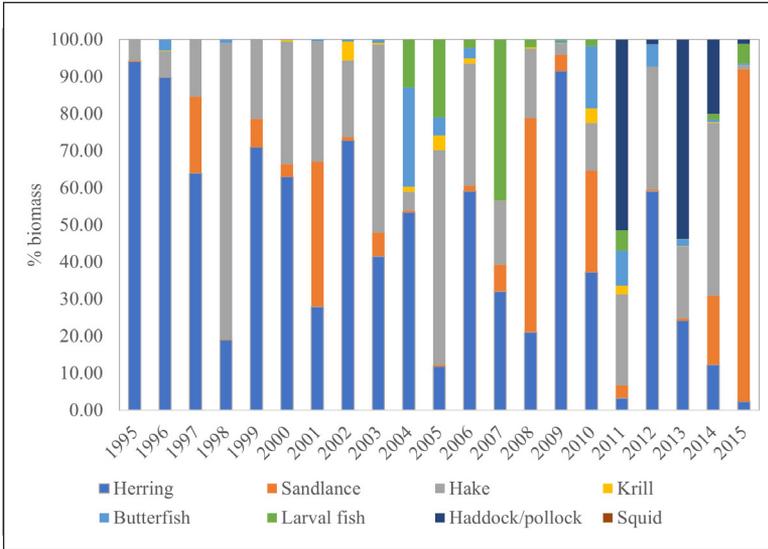
Our diet data come from prey brought to chicks, and there is uncertainty about the extent to which diet of chicks resembles adult diet. Kirsten Bowser explored this topic in Puffins using DNA barcoding of feces of both adults and chicks (Bowser *et al.* 2013), and found no significant difference between adult and chick diets in the year of field-work (2009). However, 2009 happened to be an exceptional year with a higher proportion of herring in chick diet than any year since 1995. There was no significant difference between the proportion of herring measured by the usual observational method, and the frequency of herring DNA detected in chick feces, a reassuring result that needs to be repeated in a year with a more varied diet.

**Razorbill.** Razorbills are also pursuit-divers, but are over 60% heavier than Puffins. They carry fewer prey items than Puffins, but are still multiple-prey loaders at this colony. They take larger items than Puffins, and more herring (Fig 14b); annual proportions of herring in chick diet are always greater in razorbills than in Puffins. Razorbills take a smaller variety of prey taxa than Puffins, *i.e.*, their diet is more specialised but they sample the same prey field.

**Common Murre.** Murres are the largest alcids at this colony, weighing 40% more than Razorbills and twice as much as Puffins. They are pursuit-diving single-prey loaders; we have diet data from only three years in this period (2013-15), but these show more herring and gadoids than Razorbills and Puffins (Scopel *et al.* 2019). The most striking dietary difference was in 2015, when Puffins and Razorbills took many sandlance but Murres took mainly herring, gadoids, butterfish and squid, but no sandlance. In all three years, Murres also took rock eel (*Pholis gunnellus*) which rarely shows up in the diet of other seabirds on MSI. The presence of this species in Murre diet reflects benthic feeding, common in murres elsewhere (Ainley *et al.* 2020).

### **Ecological segregation**

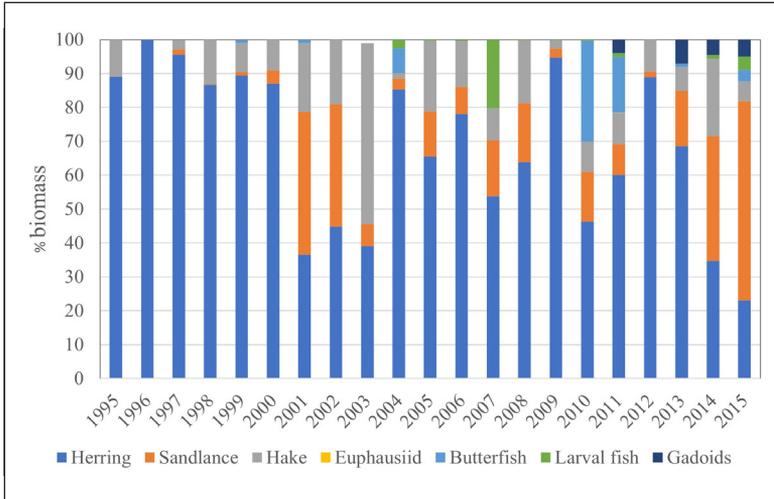
Differences in diet among these three auks, with similar feeding methods, sharing the same colony and surrounding waters, raise several obvious questions in the framework of competitive exclusion theory. Do they in fact hunt in the same oceanographic zones? Or at the same depths? At the same time of day? We have started



**Fig 14a** Percent by mass of prey types delivered to puffin chicks on MSI, 1995-2015. From L.C. Scopel (unpub. UNB data). “Other” includes sandlance (usually larval), larval fish, marine invertebrates or krill (largely *Meganyctiphanes norvegica*), of little nutritive value, and butterfish which has high energy density but is too deep-bodied for small chicks to swallow.

to address these questions by tracking movements of Puffins and Razorbills when feeding chicks, using GPS transmitters attached to the back of adults using tape and/or zip-ties. This was Stephanie Symons’ Master’s project, carried out in 2014 and 2015 (Symons 2018, Symons and Diamond 2019). The tags weighed less than 3% of body weight to minimise negative effects on the bird (Kenward 2001; also see Vandenabeele *et al.* 2012).

First, Razorbills and Puffins foraged in mostly different waters, Razorbills in shallow waters (mean depth 30 m) off the coast of Maine to the northwest of MSI, and off the south coast of Grand Manan Island to the east, and Puffins in deeper water (mean 104m) to the south and southeast of MSI, some as far as south of Brier Island, NS. They overlapped, inevitably, mainly in the 10 km or so immediately around the island. Second, the biggest surprise was in the depths to which they dived, Puffins somewhat (but not significantly) deeper ( $17.1 \pm 11.5$  m) than Razorbills ( $11.1 \pm 7.1$  m), in contravention of a generalisation among seabird biologists that



**Figure 14b** Percent by mass of prey types delivered to Razorbill chicks on MSI, 1995-2015. “Other” includes sandlance (usually larval), larval fish, marine invertebrates or krill (largely *Meganyctiphanes norvegica*), of little nutritive value, and butterfish which has high energy density but is too deep-bodied for small chicks to swallow. Gadoids were mostly haddock *Melanogrammus aeglefinus* after 2010. From L.C. Scopel (unpub. UNB data).

dive depths increase with body size in auks (Watanuki and Burger 1999). A reversal of expected dive depths has been found in these two species where they coexist elsewhere (Labrador – Pratte *et al.* 2017, and Wales – Shoji *et al.* 2015); in both cases, Puffins fed in deeper water than Razorbills, for whatever reason. Third, the two species both showed peaks of diving activity in the early morning (5-7 am) and late evening (7-9 pm), suggesting no obvious segregation in feeding times and a shared concentration of feeding at times of vertical migration of plankton and planktivores. Razorbills dived more than twice as often in a day as Puffins (661 vs. 290 dives/day), reflecting their larger body size and need for self-feeding. Feeding Puffins ranged on average twice as far from MSI (38 km) as Razorbills (19 km).

An unwelcome but important finding in Stephanie Symon’s study was that birds were unlikely to bring prey to their chick while carrying a tag, meaning that the diving locations recorded by the tag were for feeding the adult itself, not the chick (Symons and

Diamond 2019). The technology is moving fast though, and it would now be possible to repeat the study using devices that do not affect the behaviour of the bird (Fayet *et al.* 2021).

### **Seabird diet and the herring fishery**

Diet is evidently an important contributor to ecological segregation between Puffins and Razorbills. The other reason that we measure it is for possible insight into what it tells us about the availability of juveniles of commercially-exploited fish, especially herring. MSI's first graduate student, Krista Amey, devoted her thesis to exploring possible relationships between the proportion of herring in tern diet, and catches of juvenile herring in the weirs around Grand Manan. Because the terns eat herring too small to be caught in weirs (so-called 1-group herring, i.e., in the first calendar year after spawning), and weirs catch herring aged two years or more, Krista found a significant correlation between the proportion of herring in Arctic Tern diet and total catch of herring in the weirs two years later (Amey 1998). Although suggestive, the link disappeared in later years when the herring content of Arctic Tern diet declined steeply as both size (Fig 11a), and especially availability (Fig 11b), of herring declined; the herring weir fishery declined rapidly over the same period (DFO 2018).

More recent exploration of possible links between seabird diet data and herring fishery data by Lauren Scopel extended to include all of the seabird colonies of the Gulf of Maine as far west as Stratton Island (70.31W – Fig 1), and Arctic and Common Terns, Puffins and Razorbills. Scopel *et al.* (2018b) found several correlations between seabird and fishery data that suggested considerable spatial stratification of herring stocks as reflected in colony location. Perhaps most surprising, seabird diet data suggested that juvenile Bay of Fundy herring migrate with the Maine Coastal Current to the western seabird colonies in the Gulf of Maine, returning to the Bay of Fundy three years later. A similar pattern was proposed by Tupper (1998). Scopel also found stronger correlations of seabird diet data with some fishery measures, such as from acoustic surveys, than with the metrics commonly used in stock assessments, suggesting that the latter might not be the best fit for purpose. Correlations between mobile-gear landings and diets of Common Terns, Puffins, and Razorbills suggest that the seabirds select herring preferentially, as the fishery does, emphasising the need for

managing herring fisheries with the needs of these predators in mind (i.e., truly ecological-based fishery management (EBFM)).

Seabirds are commonly overlooked as predators by fishery biologists and managers, probably because they take a much smaller proportion of a fish stock than larger and more abundant predators such as other fish, and often prey on species that are fished lightly or not at all (Cairns *et al.* 1991); seabird consumption is often no threat to the human harvest. However, forage fish such as herring are critical to the reproductive success and survival of seabirds. This is true also at the global scale, where Cury *et al.* (2011) found that seabird reproductive success declined when the stock of forage fish on which they depended declined below one-third of the maximum long-term biomass of the stock. Both the Bay of Fundy and Gulf of Maine herring stocks have been below that threshold for most of our study.

### **Winter distribution**

One of the most exciting changes in technology over the lifetime of this study has been the appearance of diminutive digital devices for tracking movements of birds (Bridge *et al.* 2011). The GPS devices revealing the movements of Puffins and Razorbills, described above, have revolutionised our understanding of the lives of these birds in summer. But older (radio) technology has its uses too, and we took advantage of that to pursue mounting evidence that MSI Razorbills not only spent much of the winter in the Bay of Fundy, but were joined there by Razorbills from other colonies further north in Canada. This started with old-fashioned visual observations by Brian Dalzell of Grand Manan, and Ph.D. student Falk Huettmann, in the late 1990s. Brian's count of about 25,000 Razorbills off White Head Island, Grand Manan, in February, 1997, prompted Falk to organise regular counts by my lab from land and sea around Grand Manan in winter 1997/98. Together these proved that far more Razorbills used this area in winter than could be accounted for by the few hundred pairs (then) breeding at MSI and the Yellow Murre ledges nearby. We suggested that the Grand Manan area was an important wintering site for all North American Razorbill colonies, especially the Old Proprietor Shoals to the south-east and Long Eddy off the north end (Huettmann *et al.* 2005).

Notwithstanding the strength of these observational findings, scientists seem to find technological results more convincing than mere observation, so M.Sc. student Travis Clarke tried to confirm whether Razorbills from more distant colonies were indeed travelling to the Grand Manan area in winter. The largest colonies of Razorbills in Canada are in the Gulf of St Lawrence and in Labrador, so these were the focus of tracking efforts in summer 2007. Travis attached radio transmitters to plastic bands on Razorbills breeding on the Gannet Islands, Labrador, and colleagues from Quebec did the same on Corossol Island in Quebec, while the MSI crew equipped breeders on MSI. In the following winter, Travis listened for signals from those radios from a light aircraft flying over the seas around Grand Manan, and detected signals from birds from all three origins, confirming that at least some birds from all those colonies spent part of the winter in the Bay of Fundy (Clarke *et al.* 2010). This result is of considerable conservation importance for the species, showing that the outer Bay of Fundy is an important wintering area for the entire continental population, adding another dimension to the importance of a region already recognised for hosting long-distance migrants from as far away as Europe and the South Atlantic during summer (Diamond 2012).

## CONCLUSIONS

### **Environmental change**

Two years, 2006 and 2012, stand out as warmer than any during the previous decade. 2006 ended a short period of cool, fresh, nutrient-poor water entering the region via the Labrador Current, fed by increased melting of arctic ice (Townsend *et al.* 2010, Smith *et al.* 2012), and included the warmest SST yet measured followed by a sharp decline in the productivity of Puffins and Razorbills. 2012 was the first “marine heatwave” (five days of temperature above the 90th percentile of the day-specific climatology – Hobday *et al.* 2016) recorded in the region, with the annual SST 2 °C above the 1982-2011 average (Mills *et al.* 2013). Among a variety of sudden and unanticipated effects on the marine ecosystem of the Gulf of Maine, including record landings of lobsters and a consequent collapse in prices (Pershing *et al.* 2018), were negative consequences for seabirds, first in winter (Diamond *et al.* 2020) and the following

breeding season (especially Puffins - Scopel *et al.* 2019). Productivity of Puffins on MSI was normal in 2012 but declined drastically the following year, probably because the SST anomaly which began in summer 2012 lasted throughout the following winter, implicated in the first known “wreck” of Puffins at Cape Cod, MA, and much larger wrecks of Razorbills (Diamond *et al.* 2020) and demonstrably poor condition of Puffins starting the 2013 breeding season (Scopel *et al.* 2019). In Puffin colonies further south in the Gulf of Maine, breeding success was severely affected in both 2012 and 2013 (Kress *et al.* 2016).

The SST in the Gulf of Maine has been increasing ten times faster since 2004 (0.26 °C/year), than in the previous 30 years (0.026 °C/year) (Mills *et al.* 2013), though this rapid increase is amplified by starting in the unusually cool years of 2004-2006. Model projections over the rest of this century suggest that from 2070 onwards, annual SSTs in every year will be higher than the warmest year in the period 1976-2005 (Alexander *et al.* 2018). The effects of the marine heatwave of 2012 are thus likely to become the norm well before the end of the century.

### **Population trends**

The rapid increase in Razorbills, and rapid increase following colonisation of Murres, both cold-water species, was unexpected in a fast-warming ocean, particularly in comparison to the stability of Puffin numbers; these three species co-exist widely throughout their North Atlantic ranges and would be expected to show similar population trends. The general hypothesis that cold-water species should respond negatively to a warming ocean – especially at the southern limit of their range, where SSTs are warmer than anywhere else in their range – is supported in short-term demographic responses such as reduced occupancy and productivity, but not in population decline. Increasing populations of Canadian Razorbills and Murres are generally treated as delayed responses to protection from the Migratory Bird Act of 1918 (Gaston *et al.* 2009), but that was over 100 years ago, and a more recent factor seems necessary. One candidate is the closure of the cod fishery in Newfoundland in 1992; this fishery used to kill thousands of auks in gillnets around breeding colonies in Newfoundland, and populations of Razorbills, Puffins and Murres have increased significantly following the closure (Regular *et al.* 2013). Newfoundland and Labrador hold the

largest numbers of all three species in Atlantic Canada, so we suggest that increased survival there has supplied recruits to the Bay of Fundy, at least in Razorbills; the nearby colony of Murres on Yellow Ledge, where 424 individuals were counted in 2001 (Ronconi and Wong 2003), are a likely source of the colonisation of MSI by this species. It may not be coincidental that the relative percentage increase in these three species in Newfoundland colonies (Puffin < Murre < Razorbill) is the same as on MSI. The stability of the Puffin population on MSI is possibly due to the population reaching carrying capacity here; Razorbills and Murres may be close to that capacity too, as suggested by a few Razorbills taking over former Puffin burrows in recent years (A.W.D., pers. obs.) and the stable numbers of breeding Murres.

The overall metapopulation of Arctic Terns in the Bay of Fundy/Gulf of Maine has declined since 2006, by about the same number as used to nest on MSI prior to the collapse of the colony, illustrating the importance of the largest colony to the whole metapopulation. Nest success (productivity) of the terns at MSI has consistently been lower than on other islands in most years (Devlin 2006, Devlin *et al.* 2008) and the colony has acted, in terms of “source-sink dynamics” (Pulliam 1988), as a sink rather than a source despite being the largest colony by far until the mid-2000s (Scopel 2021).

### **Ecosystem-indicator implications**

Arctic and Common Tern numbers and productivity were poor indicators of bottom-up environmental change because of predation by gulls (Scopel and Diamond 2018, Scopel *et al.* 2018), i.e. top-down pressures. Gull predation is no doubt also subject to bottom-up influences, and the complexities of this relationship are under more detailed investigation by Scopel (2021). However, data on chick diet show considerable promise for assessing recruitment potential in forage-fisheries including herring (Scopel *et al.* 2018) and Acadian redfish (*Sebastes fasciatus*) (Depot *et al.* 2020).

The increase in numbers of two of the auks suggests improving environmental conditions, but as argued above, the population trends are more likely the delayed result of fishery closures far to the north, in Newfoundland. Further, several important environmental changes have been recorded at MSI including in SST and rainfall (Major *et al.* in press), accompanied by declines in several demographic parameters of Razorbills and Puffins

(Scopel *et al.* 2019). These changes, together with the increase in poor-quality prey (Scopel *et al.* 2018, 2019, Depot *et al.* 2020), suggest significant regime shifts in the Bay of Fundy and Gulf of Maine in 2005 and again in 2010, with negative consequences for the auks which are not reflected in recent population trends but are clear in annual monitoring of breeding success (Kress *et al.* 2016, Scopel *et al.* 2018, 2019).

### **Conservation implications**

As the most diverse seabird colony in the Maritimes, and a federally-designated Migratory Bird Sanctuary and nationally-recognised Important Bird Area (#NB019), there is obvious conservation interest in keeping this colony in a healthy condition. Regular population counts track the size of the colony, but seabirds are long-lived (up to 40 years) and, since each bird needs to produce only one offspring surviving to breeding age over its lifetime to maintain a stable breeding population, many years of failed breeding must occur before any decline is detected in the numbers of adults. Preserving the viability of a seabird community requires advance notice of emerging problems. Negative impacts of climate (or any other) change will show up sooner in such measures as low clutch size, poor breeding success, and reduced chick growth, acting as early warning signs of difficulties long before they become obvious in terms of population size. These signals are now clear in the seabirds of Machias Seal Island, beginning in the early 2000s and especially after the regime shift in 2005.

Overall, I conclude that these early warning signs of impending population decline have been clear in MSI seabirds since about 2005, in contrast to the stable or increasing populations of the three species of auk. The vulnerability of terns to predation by gulls makes their demographics unsuitable as indicators of ecosystem change, but the diets of four species (two auks and two terns) agree in suggesting a decline in availability of juvenile herring since the late 1990s and their replacement by a poorer-quality diet.

### **Future prospects**

This paper focuses on easily-measured responses of seabirds to changes in weather, oceanographic conditions, and food supply, and confirms that variables such as occupancy, clutch size, breeding success and chick growth do indeed reflect such changes, as

proposed long ago by Cairns (1987). By collaborating with researchers elsewhere in the Gulf of Maine region, spatial differences in these responses, and oceanic conditions, are also becoming clearer (Scopel *et al.* 2018, 2019; Depot *et al.* 2020). But as Cairns (1992) also pointed out, population changes of long-lived species such as seabirds respond more to changes in adult survival and recruitment than to these within-season variables. The banding and resighting program on MSI provides such data (Breton *et al.* 2006b, Breton & Diamond 2014, Devlin *et al.* 2008, Lavers *et al.* 2007, 2008a,b), but we have not been reporting on it annually despite annual changes revealing sometimes important fluctuations, such as in Puffins in relation to herring abundance (Breton & Diamond 2014), and reduced survival of juvenile Razorbills from a mass mortality event (Diamond *et al.* 2020). Survival estimates are currently being updated for Arctic Terns by Scopel (in progress) and Puffins and Razorbills by Durham (in progress), but devising a protocol to allow annual reporting of survival and recruitment should become a priority.

Another important feature of seabird biology that is becoming practicable to investigate using miniaturised digital technology is movement, both within the breeding season and outside of it. Symons (2018) has explored the former in Puffins and Razorbills, and Baran (2019) for Puffins and Dodds (in prep.) for Razorbills have documented winter movements. Other seabird tracking studies (Fayet *et al.* 2017, Dias *et al.* 2011) have shown important differences between individuals wintering in different areas, and differences between years, so winter tracking, like survival estimates, should probably be incorporated into regular monitoring, now that research projects have shown their potential value.

Long-term studies of auk biology at colonies elsewhere, notably at the Isle of Man off Scotland (Frederiksen *et al.* 2004), Triangle Island off the British Columbia coast (Hipfner *et al.* 2020), and Hornøya in Norway (Barrett 2015), have recorded changes in breeding success and diet comparable to those that we have seen on MSI. This confirms the value of such work not only to seabird conservation but also towards a more holistic perspective on changes in the ocean ecosystem. It bodes well that annual research and monitoring of seabirds on MSI continues under the supervision of Prof. Heather Major of UNB Saint John.

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