OCEAN HEAT WAVE INDUCES BREEDING FAILURE AT THE SOUTHERN BREEDING LIMIT OF THE NORTHERN GANNET *MORUS BASSANUS*

WILLIAM A. MONTEVECCHI[1*], PAUL M. REGULAR[1], JEAN-FRANÇOIS RAIL[2], KYRAN POWER[3], CHRIS MOONEY[3], KYLE J.N. D'ENTREMONT[1], STEFAN GARTHE[4], LEANNE GUZZWELL[1] & SABINA I. WILHELM[5]

[1]*Cognitive and Behavioural Ecology Program, Psychology Department, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador A1C 5X7, Canada *(mont@mun.ca)*
[2]*Canadian Wildlife Service, Quebec City, Quebec G1J 0C3, Canada*
[3]*NL Parks & Natural Areas Division, Holyrood, Newfoundland and Labrador A0B 2Z0, Canada*
[4]*Research & Technology Centre (FTZ), University of Kiel, Hafentörn 1, 25761 Büsum, Germany*
[5]*Canadian Wildlife Service, Mount Pearl, Newfoundland and Labrador, Canada*

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ABSTRACT

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We document unprecedented abandonments and breeding failures by Northern Gannets in eastern Canada at Cape St. Mary's, Bonaventure Island, and the Magdalen Islands. These events were associated with a marine heat wave during chick rearing in the late summer of 2012. The rapid onset of abandonment at Cape St. Mary's also coincided with intense lightning and thunder during an overnight storm. Parental desertions at all colonies were transient, resolving over a period of weeks, and appeared to be food-related, resulting in the poorest breeding success on record for each of these colonies. The Northern Gannet's primary prey during the breeding season is Atlantic mackerel *Scomber scombrus*, which was at historically low levels in 2012; a 2018 assessment by Fisheries and Oceans Canada classified the population in the Critical Zone. Researchers studying the effects of ocean heat waves are noticing widespread changes in marine food webs, and longer-term biophysical relationships are under investigation.

Key words: Atlantic mackerel, Cape St. Mary's, seabird breeding success, ocean climate variability, western Atlantic

INTRODUCTION

Climate change models forecast increases in the frequency of extreme weather events that are likely to escalate acute-onset biological consequences for many marine organisms (Oliver *et al.* 2019). For seabirds, these consequences can include reproductive failures and colony abandonments (e.g., Schreiber 2002, Newell *et al.* 2015, Piatt *et al.* 2020). Here, we document an unprecedented synchronous colony abandonment and widespread reproductive failure among Northern Gannets *Morus bassanus* in 2012 at the southern limit of their breeding range. These unusual events were associated with abnormally warm water and extreme weather, which together likely altered prey availability and parental vigilance (Mills *et al.* 2013, Hobday *et al.* 2018).

METHODS

Study sites

Our first study site in eastern Canada was the Cape St. Mary's Ecological Reserve (46.81°N, 054.21°W) on the Avalon Peninsula in Newfoundland, which has approximately 15 000 Northern Gannet nesting pairs and is the third largest of the six North American colonies (Fig. 1; Chardine *et al.* 2013). The gannets

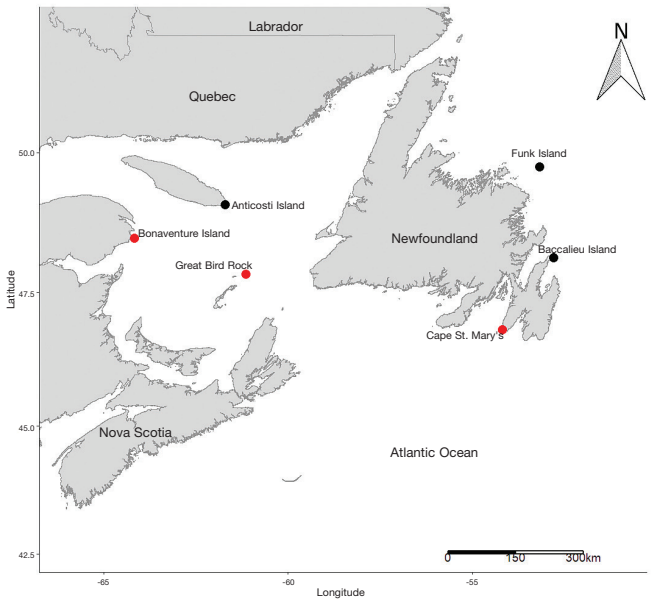

Fig. 1. The six Northern Gannet *Morus bassanus* colonies in North America. Our study sites at Cape St. Mary's, Bonaventure Island, and Great Bird Rock are denoted in red.

at Cape St. Mary's nest on Bird Rock (a sea stack, see centre of Fig. 2A, 2B) and the adjacent cliffs. Our second site was Bonaventure Island (48.49°N, 064.16°W), which is at the eastern tip of the Gaspé Peninsula in Quebec, Canada (Rail *et al.* 2013; JFR unpubl. data); it has approximately 48 000 nesting pairs and is the species' largest North American colony. Our third site was

Fig. 2. Cape St. Mary's. (A) 06 August 2012: white adult gannets nesting on Bird Rock and the adjacent cliffs. (B) 08 August 2012: the bare rock and nesting cliffs speckled with white chicks and a small number of adult gannets show that well over 90% of breeding adults had abandoned the colony. Heavy fog precluded photography on 07 August. (Photos: KP)

Great Bird Rock (47.84°N, 061.15°W) in the Magdalen Islands in the Gulf of St. Lawrence, Canada (JFR unpubl. data), which had about 25 000 pairs as of 2019 and is the second-largest North American colony.

Colony abandonments

While taking periodic photographs of the Northern Gannet colony in the course of their regular duties, natural history interpreters at Cape St. Mary's documented a mass colony abandonment on 08 August 2012 and alerted us (WAM pers. comm.). Intepreters were also able to observe the behaviour of parents and chicks. Researchers from Memorial University visited the Cape St. Mary's site on 12 August, 24 August, and 28 September to estimate the number of unattended chicks. At the Bonaventure colony, federal and provincial biologists observed partial parental abandonments throughout the season. No observers were able to access the colony on Great Bird Rock.

Breeding success and behavioural observations

At Cape St. Mary's, systematic studies of breeding success (defined here as birds fledged per active nest) at four study plots [two on the plateau, two on the cliff face of Bird Rock] have been underway annually since 2009 (LG & KJND unpubl. data). At Bonaventure Island, breeding success was assessed every five years between 1974 and 2009, with estimates also made in 1976, 2005, 2011, 2012, 2013, 2016, 2017, 2018, and 2019 (Rail *et al.* 2013). Observations of study plots at both colonies were used to estimate breeding success, while the behaviour of parents and nestlings was also observed periodically throughout the nesting season at Cape St. Mary's (30 May–14 September 2012) and on Bonaventure Island (02 June–19 September 2012). At Great Bird Rock, high-resolution aerial photos of the entire colony were used to estimate breeding success by dividing the number of pre-fledglings in photographs taken on 12 September 2012 (just before they began leaving the colony) by the number of apparently occupied territories counted on photos from 14 July 2012. The number of pre-fledglings present could have been slightly underestimated, owing to the lack of contrast between their color and the surrounding environment. As well, a few chicks may have fledged before 12 September, though these possibilities would not alter the overall estimated breeding success.

Ocean temperature

Global 1-km sea surface temperatures (SST) anomalies and absolute data were obtained from the NASA Jet Propulsion Lab at the California Institute of Technology (JPL 2014).

RESULTS

Colony abandonment

Cape St. Mary's

On the morning of 08 August 2012, interpreters at the Cape St. Mary's Ecological Reserve found that virtually all adult gannets had abandoned the colony (Fig. 2). Parental abandonments proved to be temporary, and gannets began returning within 3–4 days. By 14 August, based on counts in different areas of the colony, approximately 40% of the chicks were still unattended, though adults continued to return.

Bonaventure Island

Observations of parental abandonment were made during 14–20 August. The abandonment was not as sudden or striking as at Cape St. Mary's, but an unusually large and growing proportion (30%–50%) of the chicks were seen unattended for most of the day (T. Richard, pers. comm.); normally, Northern Gannet chicks are always attended by at least one parent, except at times when chicks attain fledging age at 12–13 weeks.

Breeding success and behavioural observations

Cape St. Mary's

In 2012, the breeding success of 133 active nests on the four study plots averaged 41% (55/133). Chicks begged for food from parents who had nothing to regurgitate, and dead chicks were seen in the colony.

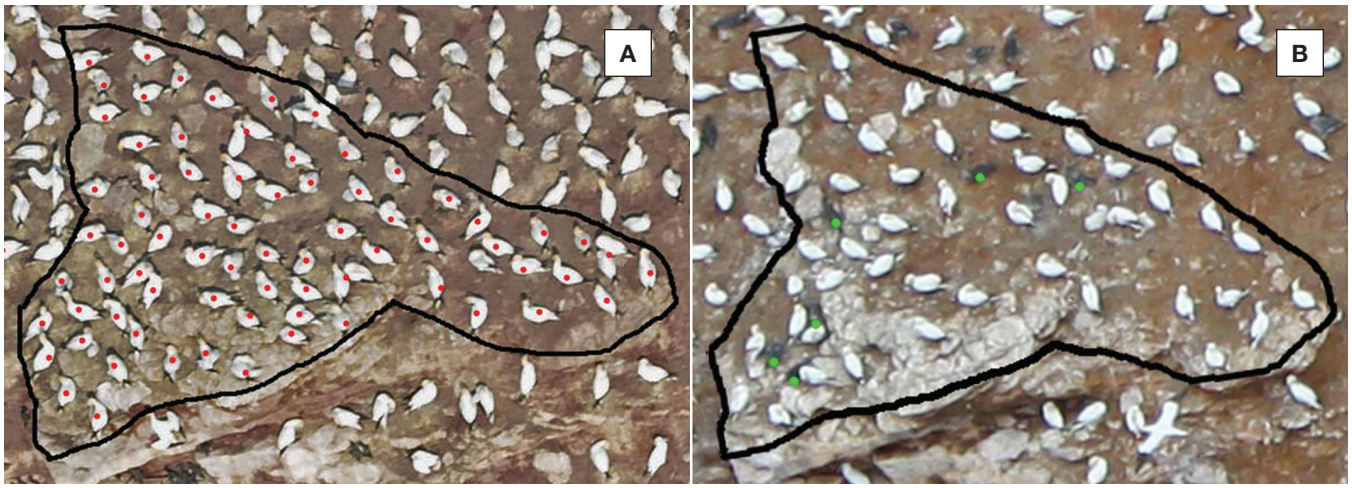

Fig. 3. View of an area with well-defined landmarks on the plateau of Great Bird Rock, Magdalen Islands. (A) Aerial photographs taken 14 July 2012 show 73 apparently occupied territories of Northern Gannet *Morus bassanus* (red dots). (B) Aerial photographs taken on 12 September 2012 show six dark grey pre-fledgling gannets (green dots) in the same plot. (Photos: J. Chardine, JFR).

Bonaventure Island

In 2012, the breeding success of 399 nests with eggs on six study plots on the plateau of the island was estimated at 8% (32 chicks reached fledging age). From the outset, the 2012 nesting season showed negative indications, as 15% of nests remained empty and only 42% of the eggs hatched. Matters worsened in August, when chicks begged from parents who had nothing to regurgitate; they were left unattended and eventually died. Dead chicks were often five to seven weeks of age, an age-class that usually has high survival (Mowbray 2020); most of the younger chicks had disappeared, likely being depredated, scavenged, or covered over in nest material and other debris.

Great Bird Rock

On 14 July 2012, 73 nest-site holding pairs were demarcated in a discrete area on the plateau of the island (Fig. 3A). When the study plot was re-photographed on 12 September 2012, only six pre-fledgling birds were identified (Fig. 3B), indicating a breeding success of ~8%. This estimate corroborated a colony-wide estimate. A high-resolution aerial photographic count of 26 366 apparently occupied territories (AOT) in the colony on 14 July 2012 was compared with a replicate count of 1 696 pre-fledglings in photos taken on 12 September 2012. This yielded an estimated breeding success of 7% (chicks fledged per AOT). It is possible that a few pre-fledglings were missed or had fledged before 12 September. However, this would not alter the finding of extremely poor breeding success, comparable to Bonaventure Island at the same time.

Ocean temperature

Low-Arctic waters in the Newfoundland and Gulf of St. Lawrence regions were anomalously warm on 08 August 2012 (Fig. 4A). As is usual in the region, SSTs increased through summer, but both the SST and the SST anomaly (i.e., the difference between the daily SST in 2012 and its corresponding average value for all recorded years) exhibited a steep spike (Fig. 4B) just before the colony abandonment at Cape St. Mary's. Warmer-than-average values (3.0–4.5 °C above normal) continued throughout most of August, with evidence of a northward shift of the 16 °C SST isotherm during 06–10 August 2012, relative to 2011 and 2013 (Fig. 5). In 2012, surface water > 16 °C encompassed the foraging ranges of breeding gannets at Cape St. Mary's, Bonaventure Island, and Great Bird Rock.

DISCUSSION

Anomalously warm water and prey availability

During August 2012, SST was 3.0–4.5 °C higher than the long-term average in the Newfoundland region, the Gulf of St. Lawrence, and throughout the Northwest Atlantic. The SST on the Grand Banks was the warmest since satellite records became available in 1985, and the cold intermediate layer (i.e., 0 °C water) was at record depths (Bernier *et al.* 2018). In the Gulf of St. Lawrence, the 8 °C isotherm was at an average depth of 15 m, the deepest level in decades (Galbraith & Grégoire 2015).

Northern Gannets feed on a broad spectrum of cold- and warm-water pelagic fishes, including small forage species like capelin *Mallotus villosus* and the much larger Atlantic mackerel *Scomber scombrus* (Montevecchi 2007). The gannets are quite flexible in prey exploitation and often switch among alternate prey with seasonal and inter-annual variability. During late summer, gannets provision offspring with migratory warm-water pelagic prey, primarily Atlantic mackerel, Atlantic saury *Scomberesox saurus*, and short-finned squid *Illex illecebrosus* (Montevecchi 2007). Atlantic mackerel, a key prey species that is associated with the

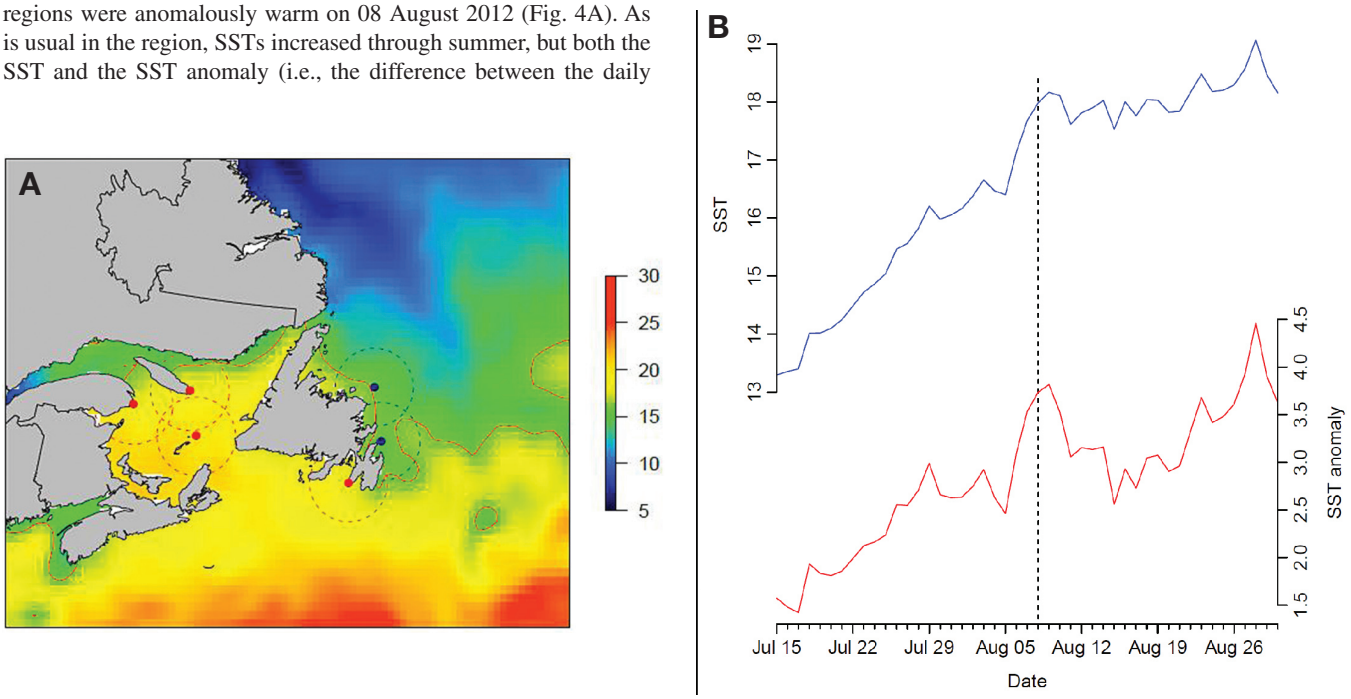

Fig. 4. (A) Heat map of sea surface temperatures (SST) on 08 August 2012, in degrees Celsius. The solid red line represents the 16 °C isotherm. Dotted circles are the estimated 200-km foraging ranges around each colony, showing colonies in the Gulf of St. Lawrence and at Cape St. Mary's in anomalously hot water. Data are global 1-km SSTs. (B) SST and SST anomalies in the gannets' 200-km foraging range around Cape St. Mary's during the two weeks immediately before and after the colony abandonment (dashed vertical line).

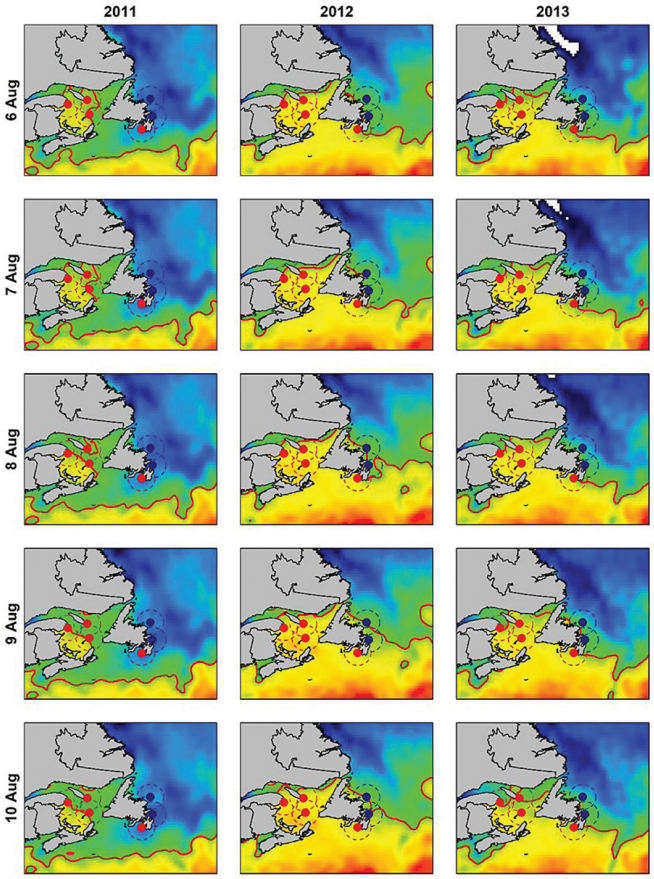

Fig. 5. Charts comparing the position of the 16 °C isotherm (red line) during 06–10 August 2011–2013. The dotted circles around colony locations represent the approximate maximum gannet foraging range of 200 km. Colony locations in red were exposed to warm water caused by the heat wave.

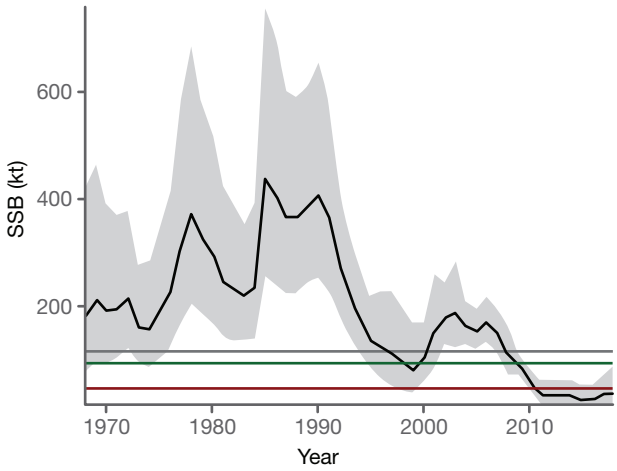

Fig. 6. Standing stock biomass (SSB, or the amount of Atlantic mackerel) in eastern Canada, estimated from a catch-at-age model. The red line is the Limit Reference Point (the point at which continued commercial fishing may harm the stock's ability to maintain itself), the green line is the Upper Stock Reference Point (the point above which stocks are considered to be robust), and the horizontal black line is the size of the SSB at which 40% of the stock can be exploited sustainably by a commercial fishery. The shaded area represents the 95% confidence interval (DFO 2019).

gannets' breeding success at Bonaventure Island (Guillemette *et al.* 2018) and at Cape St. Mary's (KJND & WAM unpubl. data), have thermal preferences of 9–13 °C and avoid waters over 15 °C (Olla *et al.* 1976, Studholme *et al.* 1999, Olafsdottir *et al.* 2019), as was the case in the gannets' foraging ranges in 2012 (Fig. 5). Since 2011, the spawning stock biomass of Atlantic mackerel in eastern Canada has been in the Critical Zone of Canada's Precautionary Approach framework for fisheries assessment (DFO 2019); i.e., it is below the Limit Reference Point, or the point at which continued commercial fishing harms the stock's ability to maintain itself (Fig. 6).

Rapidly heating surface water could have caused pelagic fish and squid to move deeper in the water column (Galbraith & Grégoire 2015), suggested by some fishermen who reported instances of "very deep bait." Northern Gannets have a maximum dive depth of 20 m (Garthe *et al.* 2000), and their primary prey often swim in deeper water (e.g., Nøttestad *et al.* 2016). These circumstances would be expected to be most acute when surface waters exceeded the thermal preferences of prey, as occurred during August 2012.

Colony abandonment

The rapid and spontaneous colony abandonment was unprecedented at Cape St. Mary's, where colony observations were first made in the 1870s and have been ongoing intermittently since the 1970s (Montevecchi & Wells 1984). To the best of our knowledge, no similar colony abandonment has occurred at any other Northern Gannet colony in the North Atlantic, which is remarkable given the long history of observations at colonies in the northeastern Atlantic Ocean (Gurney 1913, Nelson 1978).

Other instances of seabird colony abandonment and reproductive failure have long been documented during extreme oceanographic and weather events (Murphy 1981, Ainley *et al.* 2018). One of the best known in recent times was associated with an El Niño Southern Oscillation event in the central Pacific during the early 1980s that generated anomalously hot SSTs and torrential rainfalls (Schreiber & Schreiber 1984). More recently, Common Murres *Uria aalge* completely abandoned attempts to breed at several colonies in the northeastern Pacific during the powerful marine heat wave of 2014–2016 (Piatt *et al.* 2020).

Besides food shortages, abiotic factors could have also contributed to initiating the rapid-onset abandonment. An intense thunder and lightning storm during the night of 07/08 August, likely generated by the rapidly changing thermal conditions, could have triggered the spontaneous abandonment. The acute response at Cape St. Mary's suggests a rapid-onset event rather than a more gradually driven influence. Ultimately, nutritional stress was likely a key determinant in the colony abandonment. Parental abandonments subsequently occurred at Bonaventure Island and increased noticeably throughout August.

Gannets at Cape St. Mary's began returning to their chicks within a week or so of the abandonment, though almost half of the chicks were still unattended one week following the egress. While no other complete colony abandonment has occurred since 2012, partial

parental abandonments involving about one third to one half of the breeding adults occurred during August in 2014, 2015, and 2018. The 2018 event is the most extensive and best documented of these, involving 52% of the birds with chicks (142/275; Table 1). These abandonments were temporary, with birds returning to chicks within 3–7 days.

TABLE 1
Details of a partial parental abandonment at Cape St. Mary's on 18 August 2018

Nesting site	Parent attending	No parent attending	Dead chicks
Top, Bird Rock	29	54	2
Cliff face, Bird Rock	88	60	-
Mainland East	6	14	1
Mainland West	10	14	-
Totals	133	142	3

Breeding success

Although breeding success has been generally decreasing at gannet colonies in eastern North America during the 2000s, the reproductive failures at the Northern Gannet colonies in 2012 were unprecedented. Breeding success (41%) at Cape St. Mary's in 2012 was lower than in all previously (2009–2011) and subsequently (2013–2019) monitored years except for 2017, when comparably poor breeding success (39%) occurred (LG & KJND unpubl. data). From 2009 to 2020, breeding success at Cape St. Mary's was highest (81%) in 2010 and averaged 53.9% ± 16.1% (standard deviation).

The massive failure (8% success) on Bonaventure Island in 2012 was the most extreme in all the years that breeding success has been monitored since the 1970s (Chapdelaine & Rail 2013; JFR unpubl. data). Success dropped from a mean of 72.5% ± 3.1% during 1974–2005 to 50% in 2009 and 22% in 2011. Breeding success has subsequently rebounded somewhat but remained low in 2013 (37%), 2014 (44%), 2016 (43%), 2017 (50%), and 2018 (64%) before dropping again in 2019 (14%). Overall, breeding success from 1966 through 2019 on Bonaventure Island ranged from a low of 8% in 2012 to a high of 77% in 1977, and it averaged 53%, which is essentially equivalent to the long-term average at Cape St. Mary's.

No other measurements of breeding success exist for Great Bird Rock. Despite the high mortality of Northern Gannets from eastern Canada during the DeepWater Horizon disaster in the Gulf of Mexico in 2010 (Montevecchi *et al.* 2011), this colony has increased to approximately 25 000 pairs from 7 640 pairs in 1989. This population growth followed the decommissioning of the staffed light station in 1987, and the colony expanded spatially from the cliffs to cover the island's plateau as well.

Connection between prey availability and gannet foraging patterns

Central-place foraging constraints restrict the distances that seabirds can travel and return with provisions for offspring (Orians & Pearson 1979). Periods of elevated ocean temperature have been associated with expanded foraging ranges for Northern Gannets (Garthe *et al.* 2011) and Black-legged Kittiwakes *Rissa tridactyla* (Osborne *et al.* 2020). Gannets at Cape St. Mary's have an average foraging range during chick rearing of ~100 km and maximum distances of ~250 km (KJND unpubl. data). Mackerel (and likely other fish with similar tolerances) may have moved both northward outside the gannets' foraging range and into deeper, cooler waters, resulting in prey scarcity for breeding gannets (Nye *et al.* 2009). Consistent with this possibility, high numbers of gannets were observed beyond their foraging ranges in 2012: (1) notably high numbers of gannets were reported flying northeastward through the Strait of Belle Isle past southern Labrador, peaking during the week of 13 August (P. Ploughman pers. comm.); (2) hundreds of gannets foraged with humpback whales *Megaptera novaeangliae* in Battle Harbour, Labrador on 18 August (G. Slade pers. comm.); and (3) the highest number of gannets ever recorded at Torngat Mountains National Park in northern Labrador was made in August (D. Whitaker pers. comm.). In addition, feeding aggregations of gannets were reported in Tadoussac, Quebec on the St. Lawrence River (N. Ménard pers. comm.); Halifax, Nova Scotia (A. Boyne, pers. comm.); and the Bay of Fundy. Commercial fishermen working in the Gulf of St. Lawrence and south of Cape St. Mary's reported gannets diving extremely close to their boats for deck washings and at times diving into the bubble streams of outboard motors (never witnessed before). Dead gannets were found along northern shore of the Gulf of St. Lawrence, on the Gaspé Peninsula, on the Magdalen Islands, and in western Newfoundland during August 2012.

It is notable that not all subsequent partial colony abandonments have been associated with warm-water occurrences. For instance, SSTs during the 2013 nesting season were similar to those of 2012 but no parental abandonment was observed; in this case, gannets might have foraged in the cooler waters along eastern Newfoundland (Fig. 5). Partial parental abandonment occurred in 2014, when SSTs were similar to the long-term average. Our investigations of longer-term relationships between Northern Gannet breeding success, foraging behaviour, prey conditions, and oceanography are ongoing.

Extreme weather events and climate change

Biophysical events reflected an acute-onset meteorological perturbation that began in early August 2012 and continued throughout the month, affecting waters influenced by the Gulf Stream; the rapid-onset warm-water pulse was a component of a large-scale climate anomaly throughout the Northwest Atlantic. The negative consequences for the gannets' reproductive success were significant and were mirrored in the responses of other top marine predators and prey throughout the region (Kress *et al.* 2016). The impacts of marine heat waves on seabirds and a range of other taxa and fisheries have become global phenomena (e.g., Mills *et al.* 2013, Piatt *et al.* 2020), with forecasts of increasing frequency (Frölicher *et al.* 2018). Our ongoing studies of marine birds will help provide information about the rapidly changing ocean environment and its varied and novel biological consequences (e.g., Buren *et al.* 2019).

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