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Nutritional stress in Northern gannets during an unprecedented low reproductive success year: Can extreme sea surface temperature event and dietary change be the cause?



Cynthia D. François Vézina b,c, François Grégoire d, Jean-François Rail e, Jonathan Verreault a,*

- ^a Centre de recherche en toxicologie de l'environnement (TOXEN), Département des sciences biologiques, Université du Québec à Montréal, C.P. 8888, Succursale Centre-ville, Montreal, OC H3C 3P8, Canada
- ^b Département de Biologie, Chimie et Géographie, Université du Québec à Rimouski, 300 Allée des Ursulines, Rimouski, QC G5L 3A1, Canada
- ^c Centre d'études nordiques, Centre de la science de la biodiversité du Québec, 300 Allée des Ursulines, Rimouski, QC G5L 3A1, Canada
- ^d Maurice Lamontagne Institute, Fisheries and Oceans Canada, 850 Route de la Mer, Mont-Joli, QC G5H 3Z4, Canada
- ^e Canadian Wildlife Service, Environment Canada, 801-1550 ave. d'Estimauville, Quebec, QC G1J 0C3, Canada

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ABSTRACT

Reproductive success of seabirds is tightly associated with availability of their prey for which the spatiotemporal distribution may be influenced by sea surface temperature (SST) fluctuations. The objective of this study was to investigate whether Northern gannets (Morus bassanus) from the largest colony in North America (Bonaventure Island, Quebec, Canada) were in negative nutritional state during the unprecedented low reproductive success year of 2012, and whether this was associated with changes in SST anomalies and diet. The incubation period of gannets in 2012 was characterized by a significant decline, from early to late incubation, in plasma triglyceride levels that was associated with an increase in plasma corticosterone levels. However, no changes in plasma glycerol and β -hydroxybutyrate levels were noted. SST anomalies recorded in this area (south of the Gulf of St. Lawrence) during the breeding period were consistently higher in 2012 compared to the previous year (a better reproductive success year). Based on signatures of stable carbon (δ^{13} C) and nitrogen (δ^{15} N) isotopes in gannet red blood cells and in whole fish homogenates of three major preys (mackerel, herring, and capelin), a minor dietary shift was noted between those years and incubation periods. In light of these findings, it is suggested that the extreme warm-water perturbation event that prevailed in the Gulf of St. Lawrence during summer 2012 was associated with a rapid deterioration of nutritional condition of Bonaventure Island gannets during the incubation. These suboptimal physiological changes likely contributed to the dramatic decline in reproductive success reported in this colony.

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1. Introduction

Long considered as limitless resources, oceans are now facing large-scale changes induced by anthropogenic activities. These changes may cause extensive stress on marine ecosystems worldwide (Halpern et al., 2008) and modulate food web interactions (e.g. predator–prey dynamics), which can have profound consequences on top predators such as seabirds (Schreiber and Burger, 2002; Grémillet and Boulinier, 2009). A growing number of studies have suggested that climate change may contribute, along with overfishing and environmental pollution, to severe impacts on reproductive success and long-term population

E-mail address: verreault.jonathan@uqam.ca (J. Verreault).

stability of seabirds as well as their survival (Frederiksen et al., 2004; Jenssen, 2006; Ainley and Blight, 2009).

An unprecedented low reproductive success of 8% (i.e., chick survival to fledging age) was recorded in 2012 for Northern gannets (*Morus bassanus*) breeding in a colony in the Gulf of St. Lawrence (Bonaventure Island, Quebec, Canada) (Montevecchi et al., 2013). Bonaventure Island is a migratory bird sanctuary (Rail, 2009), which hosts the most important breeding Northern gannet sub-population in North America (Chardine et al., 2013). A general declining trend in the reproductive success of Northern gannets from this colony has also been observed during the last decade, from around 74% between 1979 and 2004 (range: 72–77%; Rail et al., 2013) to 22% in 2011 (Montevecchi et al., 2013). A consistent decline, although less severe, has also been observed in Cape St. Mary's Northern gannet colony (Newfoundland and Labrador, Canada) with a reported reproductive success averaging 68% in 2011 and 39% in 2012 (Montevecchi et al., 2013). These observations led Montevecchi et al. (2013) to postulate that abnormally warmer sea

^{*} Corresponding author at: Département des sciences biologiques, Université du Québec à Montréal, C.P. 8888, Succursale Centre-ville, Montréal, Québec H3C 3P8, Canada. Tel. + 1514 987 3000x1070; fax: +1514 987 4647.

surface temperatures (SSTs) recorded in the Gulf of St. Lawrence and throughout the entire Northwest Atlantic combined with limited fish prey availability might have been the driving factors behind this dramatic nest failure.

Prey fish distribution is directly affected by climate-induced warming of sea surface when exceeding the thermal tolerance of the species (Perry et al., 2005). Suboptimal variations in SST may therefore represent an important factor limiting fish availability for diving seabirds by influencing the depth at which prey are found (Ropert-Coudert et al., 2009; Kokubun et al., 2010). Roberts and Hatch (1993) have shown that poor feeding conditions may result in extended foraging bouts in black-legged kittiwakes (Rissa tridactyla), thus increasing the amount of time that chicks are left unattended and exposed to predation. This has also been observed in other seabird species, e.g., Northern gannets (Hamer et al., 2007), great skuas (Catharacta skua) (Hamer et al., 1991), and common guillemots (Uria aalge) (Wanless et al., 2005). Therefore, low prey availability below a certain threshold may compromise seabird's reproductive success (Harding et al., 2007) as foraging behavior and effort during the breeding season are tightly associated with prey distribution (Ropert-Coudert et al., 2004; Wilson et al., 2005).

In seabirds with long breeding period, body fat storage represents essential reserves for self-maintenance. In food deprivation condition (fasting), however, the physiological response of seabirds can be described in three phases that can be detected by variations of certain blood nutritional markers (Jenni-Eiermann and Jenni, 1998). In the first phase, readily available glycogen is used as main energy source (Alonso-Alvarez and Ferrer, 2001). The second phase implies lipid oxidation as alternative source of energy (Cherel and LeMaho, 1985; Caloin, 2004), which is reflected in blood by an increase in glycerol and β-hydroxybutyrate levels, and a decrease in triglyceride levels (Castellini and Rea, 1992). In the last phase, as the bird begins to degrade proteins for fuel, nitrogenous waste levels increase in blood, while lipid metabolites are at their lowest (Cherel et al., 1988; Castellini and Rea, 1992; Caloin, 2004). Corticosterone, the primary glucocorticoid released by the adrenal gland cortex in birds, plays an essential role in energy metabolism (Romero and Remage-Healey, 2000; Love et al., 2004; Chastel et al., 2005) and regulation of body maintenance processes through the modification of foraging behaviors (Astheimer et al., 1992; Bray, 1993). As lipid reserves decrease, corticosterone secretion has been shown to increase in several breeding seabirds (Cherel et al., 1988; Kitaysky et al., 1999a,b), which is thought to promote foraging activities (Astheimer et al., 1995) and elicit mobilization of stored energy resources (Romero and Remage-Healey, 2000). However, high corticosterone levels in a low food supply situation has also been associated with impaired breeding success and low survival in seabirds as shown, for example, in common guillemots (Kitaysky et al., 2007).

The objective of the present study was to investigate whether Northern gannets from Bonaventure Island were in negative nutritional state during the unprecedented low reproductive success year of 2012 (Montevecchi et al., 2013), and whether this was associated with changes in SST and diet. In order to address this question, plasma levels of selected nutritional markers (glycerol, triglycerides, and β-hydroxybutyrate) and corticosterone of Northern gannets as well as SST anomalies were compared between 2012 and 2011 (a year with higher reproductive success) during two periods in the incubation (early and late). The diet of Northern gannets was compared based on the estimated contribution of three major forage fish (Atlantic mackerel [Scomber scombrus], Atlantic herring [Clupea harengus harengus], and capelin [Mallotus villosus]; Jackson et al., 2009) using signatures of stable carbon (δ^{13} C) and nitrogen (δ^{15} N) isotopes in Northern gannet blood and whole fish. We hypothesized that Northern gannets from Bonaventure Island in 2012 were in a poorer nutritional status relative to 2011 and experienced warmer than average SSTs, which was associated with a different diet composition. More specifically, birds sampled in 2012 were hypothesized to have higher plasma glycerol and β-hydroxybutyrate levels and lower triglyceride levels combined with higher plasma corticosterone levels in both incubation periods. The present study provides essential insights onto the challenges Northern gannets and potentially other seabirds from the Northwest Atlantic may face when experiencing extreme events in a changing ocean climate.

2. Materials and methods

2.1. Ethical procedures

Bird capture and handling methods were approved by the institutional animal care committee of the Université du Québec à Rimouski (Rimouski, Quebec, Canada), and complied with the guidelines of the Canadian Council on Animal Care (CCAC).

2.2. Study area and sample collection

Fieldwork was conducted from May through July 2011 and 2012 at Bonaventure Island (48° 30′ N, 64° 10′ W) located in the Île-Bonaventure-et-du-Rocher-Percé National Park (Quebec, Canada) in the Gulf of St. Lawrence. Breeding male (n=26) and female (n=10) Northern gannets (hereafter called gannets) were captured twice during the breeding period (early incubation: end of May to early June; late incubation: end of June to early July) from the peripheral section of the colony in both years using a noose-pole. A subset of ten birds (n=8 males and 2 females) were selected from this sub-population for the purpose of the present study as these were the only birds that were successfully sampled (blood; see below) in both incubation periods (early and late) and years (2011 and 2012). All birds included in the present study were identified with a US Fish & Wildlife Service stainless steel ring and a color-coded plastic band.

Blood samples (10-15 mL, which corresponds to less than 0.5% of this species' body mass [mean \pm SD: 3050 \pm 293 g]) were collected from the brachial vein of all birds using butterfly needles, 5 mL syringes, and heparinized vacutainer tubes. In order to minimize changes of corticosterone levels related to the circadian cycle, samples were all collected between 10 AM and 4 PM. Moreover, blood sample collection was performed immediately following capture (mean \pm SD: 2.90 \pm 0.30 min) to avoid handling-related stress effects on corticosterone secretion, and thus corticosterone levels corresponded to baseline levels. An aliquot (1–2 drops) of this blood sample was used for subsequent DNA sexing of the individuals. The birds were immediately released near their nesting site after blood sampling. While in the field, blood samples were kept on ice in a cooler before they were processed in the laboratory within 8 h of collection. In the laboratory, blood samples were centrifuged (7 min; $2500 \times g$), and the resulting plasma was stored in liquid nitrogen, and subsequently in a -80 °C freezer until nutritional marker and corticosterone analyses (Sections 2.3 and 2.4, respectively), while red blood cells were kept in a regular freezer (-20 °C) until stable isotope analysis (Section 2.5).

The three major fish preys of gannets were all collected in the south of the Gulf of St. Lawrence. More specifically, mackerels (n=5) were caught using a conventional fishing rod at Percé wharf (Percé, Quebec, Canada) in July 2013. Capelins (n=5) were collected by hand on the shore in the Bay of Chaleurs (Grande-Rivière, Quebec, Canada) during spawning in June 2013. Herrings (n=5) were collected using fixed gillnets in September 2013 (Saint-Isidore, New Brunswick, Canada). All fish were of sizes and weights that are commonly found in gannet regurgitations that have been monitored in this breeding colony over the years (Rail J.-F., unpublished data). Whole fish were kept at $-20\,^{\circ}$ C until stable isotope analysis (Section 2.5).

SST anomaly data for the south of the Gulf of St. Lawrence were obtained from the National Oceanic and Atmospheric Administration's Office of Satellite and Product Operations, National Environmental Satellite, Data and Information Service website (http://www.ospo.noaa.gov/Products/ocean/sst/anomaly/index.html). SST anomalies are

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