Long-term stability in the volume of Atlantic Puffin (*Fratercula arctica*) eggs in the western North Atlantic

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Abstract: In the eastern North Atlantic, declines in the volume of Atlantic Puffin (*Fratercula arctica* Linnaeus, 1758) eggs have been associated with shifts in the marine ecosystem, such as changes in the abundance of forage fishes and increasing sea-surface temperatures. In the western North Atlantic, where similar shifts in oceanographic conditions and changes in the abundance of forage fishes have presumably occurred, trends in the volume of Atlantic Puffin eggs remain unknown. In this study, we investigate Atlantic Puffin egg volume in the western North Atlantic. We compiled 140 years (1877–2016) of egg volume measurements (n = 1,805) and used general additive mixed-effects models to investigate temporal trends and regional variation. Our findings indicate that Atlantic Puffin egg volume differs regionally but has remained unchanged temporally in the western North Atlantic since at least the 1980s.

Key words: Alcidae, Atlantic Puffin, egg volume, *Fratercula arctica*, general additive models, seabirds, western North Atlantic

Introduction

Identifying climate change-related shifts to an ecosystem's structure is fundamental to ecosystem management, particularly in the face of a rapidly changing climate. Seabirds can be useful indicators of change in marine ecosystems as environmental fluctuations are often expressed in their demographics (e.g., Cairns 1987; Croxall et al. 2002; Descamps et al. 2013). Owing to their high energetic requirements, many seabirds optimize the timing of energetically demanding events (e.g., reproduction, migration) with periods of favorable environmental conditions and resource availability (Stenseth and Mysterud 2002). Thus, one might expect phenological shifts to match shifts in the timing of favorable environmental conditions. However, the phenological mismatch between seabird energy requirements and resource availability is common and is seemingly becoming more common in a changing climate (e.g., Durant et al. 2007; Hipfner 2008; Gaston et al. 2009; Keogan et al. 2018). To compensate for this mismatch, seabirds may regulate the energy invested into eggs in response to fluctuating resource availability, either by adjusting clutch size or, in the case of single-egg-laying species, egg size (Nisbet 1973; Drent and Daan 1980; Barrett et al. 2012; Bond et al. 2020; but see Christians 2002).

The Atlantic Puffin (*Fratercula arctica* Linnaeus, 1758) is a colony-nesting, single-egg-laying seabird whose distribution spans the North Atlantic Ocean (Lowther et al. 2020). Climate change has triggered shifts in the distribution and abundance of many marine species (Hoegh-Guldberg and Bruno 2010), presumably including the energy-rich forage fishes on which these seabirds rely during egg production. In the eastern North Atlantic, Barrett et al. (2012) documented declines in the volume of Atlantic Puffin eggs at two colonies driven by changes in the abundance of forage fishes and shifting climatic conditions, including rising sea-surface temperatures. Barrett et al. (2012) suggested that these changes to the ecosystem's structure imposed energetic constraints on egg-laying females through a mismatch between the energetic demands of egg production and pre-laying food availability. In this study, we compiled 140 years (1877–2016) of Atlantic Puffin egg volume measurements to investigate temporal trends and regional variation in the western North Atlantic where similar climate change-related shifts in the distribution and abundance of forage fishes have presumably occurred (Hoegh-Guldberg and Bruno 2010; e.g., Scopel et al. 2019). For example, Atlantic Puffins nesting at this study's southernmost colony (Machias Seal Island, Bay of Fundy, Canada) are in an area of unprecedented ocean warming (Pershing et al. 2015). Given the observed ocean warming and the link between climatic conditions, pre-laying food availability, and egg volume in the eastern North Atlantic (Barrett et al. 2012), we predicted declines in the volume of Atlantic Puffin eggs in the western North Atlantic.

Materials and methods

Study area and egg measurements

We obtained Atlantic Puffin egg measurements (n = 1,805) from nine western North Atlantic colonies between 1877 and 2016 (Fig. 1), ~85% of which (n = 1,536) were obtained between 1980 and 2016 (see Supplemental Material Table S1). These eggs were either measured at breeding colonies and returned to nesting burrows or collected and measured off-site. We assumed selection for measurement or collection was haphazard, and all eggs were viable when measured or collected. For statistical analyses, we grouped measurements from the nine colonies into four geographic regions: Bay of Fundy, Gulf of St Lawrence, Newfoundland, and Labrador. Colonies were grouped in this way because several colonies had small sample sizes or measurements recorded during only a single year. In all cases, the maximum length and breadth of individual eggs were recorded to the nearest 0.1 mm using calipers. Egg volume was estimated using the equation:

$$\text{Volume} = K \times L \times B^2 \text{ (Hoyt 1979)}$$

where the constant *K* = 0.507 (egg shape typical of Charadriiformes species; Hoyt 1979), *L* is egg length (mm), and *B* is maximum egg breadth (mm).

Statistical analyses

We tested the normality of the data using Shapiro-Wilk's test. Owing to the potential for non-linear relationships, we used general additive mixed-effects models (GAMMs; Wood 2011) to quantify trends in egg volume using the R package mgcv (Wood 2019). We tested region as a fixed factor, colony as a random effect, and a cubic spline for collection year using generalized cross-validation to set the number of knots (*k* = 10; Wood 2017). We completed one analysis using the entire dataset (1877–2016) and a second excluding pre-1980 data, the latter representing a range similar to the eastern North Atlantic study (Barrett et al. 2012). In the second analysis, each region was represented by eggs from a single colony (Supplemental Material Table S1); thus, we used a general additive model with colony as a fixed factor and a cubic spline as described above.

Ethical approvals

We received permits from the Canadian Wildlife Service, followed relevant provincial and federal guidelines, and received approval from the institutional animal care and use committees at the University of New Brunswick, the University of Saskatchewan, Memorial University of Newfoundland, and Environment and Climate Change Canada for all egg measurements and collections.

Results

We achieved data normality following the removal of a single outlying measurement. Mean ± standard deviation egg volume across all regions was 63.3 ± 4.7 cm^3 (range: 44.0–80.0 cm^3). Egg volume differed among regions: eggs were smallest in the Bay of Fundy (mean ± standard deviation: 61.5 ± 4.4 cm^3), followed by Newfoundland (62.7 ± 4.4 cm^3), the Gulf of St Lawrence (63.2 ± 4.4 cm^3; although not different from Newfoundland or Labrador), and largest in Labrador (64.0 ± 4.8 cm^3; all $F > 2.90$, all $p < 0.01$; Table 1). Egg volume was not related to year of collection across the entire dataset ($F = 0.62$, effective df = 1, $p = 0.43$; Fig. 2), nor was it across the 1980–2016 dataset ($F = 0.02$, effective df = 1, $p = 0.90$).

Discussion

Contrary to Barrett et al.'s (2012) findings in the eastern North Atlantic (1980–2011), Atlantic Puffin egg volume in the western North Atlantic has remained unchanged since at least the 1980s (the scarcity of pre-1980s data limits discussion of longer-term trends). Bond et al. (2020) described similar stability in the eggs of Atlantic Yellow-nosed Albatrosses (*Thalassarche chlororhynchos*) in the South Atlantic Ocean. In the eastern North Atlantic, Barrett et al. (2012) showed that declines in the volume of Atlantic Puffin eggs were driven by climatic conditions and changes in the abundance of forage fishes. Despite changing climatic conditions in the western North Atlantic (e.g., rising sea-surface temperatures), egg volume stability suggests that conditions during the pre-laying period did not exceed thresholds above which prey (more specifically, energy) availability was influenced (but see discussion on phenological shifts below). However, continued oceanographic change may influence the availability of forage fishes and trigger similar egg volume declines. If this is the case, Machias Seal Island, located near the southern edge of the species' range and in an area of rapid ocean warming (Pershing et al. 2015), may be among the first colonies to exhibit egg volume declines. Nevertheless, any climate change-related shift in oceanographic conditions (rising sea-surface temperatures or otherwise), which reduces the availability of forage fishes during the pre-laying period, will reduce the energy available for egg production and could consequently cause egg volume declines. However, we acknowledge the complex relationship between climate change and the distribution and abundance of marine fishes (Hoegh-Guldberg and Bruno 2010).

Seabirds that lay single-egg clutches have few mechanisms by which they can adjust their parental investment in the early stages of the breeding season; egg volume is one of the more plastic of these traits (but see Christians 2002) along with shifting the timing of breeding (e.g., Schroeder et al. 2009) and skipping breeding altogether (e.g., Reed et al. 2015). In Atlantic Puffins, the adjustment of parental investment through shifting egg-laying dates has been observed on Machias Seal Island where egg-laying is occurring later (Fana 2019; 1995–2018). In general, however, seabirds are poor at buffering climate change through phenological shifts (Keogan et al. 2018). On Machias Seal Island, the adjustment of parental investment through skipping breeding altogether is uncommon, although it has occurred more frequently in recent years (A.W. Diamond, unpublished data). Thus, phenological shifts (e.g., Fana 2019) may have been partially responsible for compensating for climate change in the western North Atlantic ecosystem.

We suggest the continued monitoring of North American Atlantic Puffin populations with a focus on improving our understanding of the relationships between resource availability and egg volume, constituent egg components, adult body mass, breeding success, and offspring fitness (Krist 2011). Furthermore, an improved understanding of wintering areas and migratory routes (see Guilford et al. 2011; Jessopp et al. 2013; Fayet et al. 2017; Baran 2019) is required to explore the relationship between egg volume and resource availability during the pre-laying period.

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Competing interests

None to declare

Contributors' statement

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Data availability

Data are provided in the Supplementary Information.

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Figure 1. Atlantic Puffin (*Fratercula arctica* Linnaeus, 1758) colonies in the western North Atlantic from which eggs were measured in the Bay of Fundy (Machias Seal Island [MSI]), the Gulf of St Lawrence (Bird Rocks [BR], Île Brion [IB], Île de Mingan [IM], Île Sainte-Marie [ISM]), Newfoundland (Baccalieu Island [BA], Wolf Island [WI], Witless Bay [WB]), and Labrador (Gannet Islands [GI]). Map created in R version 4.0.2 (R Core Team 2020). Map data: Natural Earth (available from https://www.naturalearthdata.com/).

Figure 2. Atlantic Puffin (*Fratercula arctica* Linnaeus, 1758) egg volume in the Bay of Fundy, the Gulf of St Lawrence, Newfoundland, and Labrador (1877–2016). Solid blue lines are cubic splines from general additive mixed-effects models with 95% confidence intervals in light blue. Figure created in R version 4.0.2 (R Core Team 2020).

Table 1. Mean ± standard deviation, median, and range of Atlantic Puffin (*Fratercula arctica* Linnaeus, 1758) egg volume (cm^3) in the Bay of Fundy, the Gulf of St Lawrence, Newfoundland, and Labrador (1877–2016).

Region	***n***	**Mean ± sd**	**Median**	**Range**
Bay of Fundy	157	61.5 ± 4.4	62.1	50.9–73.1
Gulf of St Lawrence	143	63.2 ± 4.4	63.2	50.3–76.8
Newfoundland	653	62.7 ± 4.4	63.0	44.0–80.0
Labrador	851	64.0 ± 4.8	63.8	45.0–77.9
All Regions	1804	63.3 ± 4.7	63.2	44.0–80.0

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