



# Pursuit-diving seabird endures regime shift involving a three-decade decline in forage fish mass and abundance

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**ABSTRACT:** Forage species availability is a key determinant of seabird success, survival, and population change. In the Northwest Atlantic Ocean, capelin *Mallotus villosus*, a keystone forage species, experienced a stock collapse in the early 1990s that was a pivotal component of a regional regime shift. Since then, capelin have exhibited delayed protracted spawning, younger spawning age, distribution shifts, and smaller size. As capelin specialists, pursuit-diving common murre *Uria aalge* have had to adjust to these changes. We show that the masses of capelin provisioned to murre chicks at the species' largest colony declined steadily from 1990–2017. We predicted that the parental provisioning of lower quality prey would reduce offspring condition, lower parental body mass, and increase foraging effort. Offspring condition declined, and while no negative effects were found on adult body mass, parental murre worked substantially harder in 2016, when capelin were dispersed and availability was low and when offspring and parental mass were the lowest in the time-series. These circumstances suggest that the murre neared a behavioral tolerance of parental effort. Despite the multi-decadal order-of-magnitude reduction in the regional capelin stock, parental murre coped by exploiting local prey availability at persistent shallow-water spawning sites and by increasing foraging effort. Even while the keystone forage fish stock remained at extremely low levels, the murre population increased, a likely consequence of enhanced adult survival due to amelioration of anthropogenic risk factors.

**KEY WORDS:** Forage fish · Seabirds · Prey availability · Prey quality · Foraging behavior · Provisioning · Predator · Resiliency

## 1. INTRODUCTION

How marine top predators respond to ocean climate change is a focal research question that challenges biologists, oceanographers, and fishers alike. Ocean climate influences on top predators are mediated almost exclusively through bottom-up influences on prey availability (Oro 2014), and forage species on which many top predators depend are often the conduit of food web perturbations which can generate complex species interactions (Sydeman et al. 2015).

Capelin *Mallotus villosus*, a keystone forage species in the Northwest Atlantic Low Arctic ecosystem, collapsed by an order of magnitude during a regime shift in the early 1990s (Buren et al. 2014). In Northwest Atlantic Fisheries Organization (NAFO) Divisions 3KL, stock biomass declined from approximately 3000–6000 kt before 1991 to 23–983 kt from 1991–2017 (DFO 2018, Buren et al. 2019). Subsequently, capelin have exhibited delayed and protracted seasonal spawning, spawned at younger ages, and shown spatial shifts and decreased size

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owing to the disappearance of older age classes (Buren et al. 2019).

Given these changes in capelin availability and behavior, breeding seabirds are predicted to exhibit non-linear responses across a range of behavioral and population parameters before reaching a tipping point (Cairns 1987). For example, breeding success can be nearly constant over a wide range of prey abundances, in part because seabirds often exhibit behavioral flexibility to counter prey base deterioration, e.g. by increasing foraging time through reduction in discretionary time at the colony (Burger & Piatt 1990, Grémillet et al. 2012, Regular et al. 2014). However, below a certain level of prey availability, breeding success can decline precipitously (Harding et al. 2007, Piatt et al. 2007).

A global meta-analysis has suggested that a threshold for seabird productivity occurs at approximately of the long-term maximum biomass of the key prey species (Cury et al. 2011). For central place foragers like colonial nesting seabirds, however, it is necessary to consider fish stocks assessed at large scales and actual food supply (i.e. locally available prey within the predators' foraging range; Guillemette et al. 2018), as large changes in stock size may not be realized at local scales due to range contractions (Worm & Tittensor 2011) or to locally persistent high-abundance aggregations related to key life history events such as spawning (Penton & Davoren 2012, Davoren 2013b). Hence, the prey base around a seabird colony could remain locally abundant even if the fish stock declined regionally. In addition to food availability, prey quality can also influence breeding success by compelling predators to catch more prey to compensate for less energetically beneficial food (junk food hypothesis; Österblom et al. 2008, Kadin et al. 2016). Interactions between local prey availability and quality can therefore complicate the relationship between seabird breeding productivity and regional stock size.

The largest North American colony of the common murre *Uria aalge* (hereafter murre), on Funk Island, Newfoundland, Canada (Nettleship & Evans 1985), is an excellent site to examine how seabirds respond to marked differences in food supply and prey quality. Murres are the primary seabird predator of capelin in the Northwest Atlantic (Montevecchi 2000) and are capelin specialists (Davoren & Montevecchi 2003). Their breeding season overlaps with the inshore spawning period of capelin (Regular et al. 2014), and they are sensitive samplers of inter-annual variation in capelin availability (Davoren & Montevecchi 2003, Burke & Montevecchi 2009, Buren et al. 2012, Davoren et al. 2012).

Despite the collapse of the capelin stock, spawning sites in shallow water (15–40 m) that are accessible to murres have been persistent within the murres' foraging range (60–80 km) around Funk Island (Burke & Montevecchi 2009, Hedd et al. 2009, Penton & Davoren 2012, Davoren 2013a). These sites, where capelin can be predictably located, are key foraging areas for marine birds and mammals (Davoren 2013b).

Here, we investigated how the order-of-magnitude decrease in capelin biomass and changing fish mass influenced the murres' parental food deliveries, offspring condition, and adult body mass over 3 decades (1990–2017; see Davoren & Montevecchi 2003). To assess parental effort, we compared the foraging tracks of the murres during 2014 — when capelin exhibited multiple spawning waves and biomass was higher in the study area, relative to 2016 — when capelin did not spawn during the study period, biomass was lower, and the fish were more scattered.

## 2. MATERIALS AND METHODS

### 2.1. Study site

Research was carried out on the Funk Island Ecological Seabird Reserve (49° 45' N, 53° 11' W), a small (800 × 400 m), relatively flat granite rock about 40 km off the northeast coast of Newfoundland, Canada (see Montevecchi & Tuck 1987). In 2009, ~500 000 pairs of common murres bred on the islet (Wilhelm et al. 2015).

### 2.2. Capelin sampling from parental prey loads

Prey were collected from food-carrying parental murres that were captured with pole nets as they flew into the center of the colony. The species, sex, maturity (gravid, spent, immature capelin), digested condition (fresh progressing through eyeless, snoutless, headless), mass (g), and fork length (cm) of each fish were determined in the hand and recorded using a measuring board and Pesola spring scales during late July/early August 1990 through 2017 (Table S1 in Supplement 1 at [www.int-res.com/articles/suppl/m627p171\\_supp.pdf](http://www.int-res.com/articles/suppl/m627p171_supp.pdf)). We used all capelin (male and female) that were whole (i.e. digestion = fresh or eyeless) and excluded years when, owing to field logistics, there were fewer than 10 prey samples (1991, 1994, 2010). We analyzed capelin mass, length, and Fulton's condition factor ( $K$ ; a weight-length relationship, see Davoren & Montevecchi 2003) as a func-

tion of year (see Supplement 2). To avoid the introduction of biases associated with Fulton's  $K$ , we decided not to report trends in condition, and because most of the variability in the energy content of capelin delivered to murre chicks is due to the mass of the fish, we focused the analyses on capelin mass (see Supplement 2 for data assessment and rationale). Capelin mass was used as a proxy for prey quality, as this metric reflects the calorific content received by offspring in each prey delivery.

### 2.3. Chick and fledgling condition

Chicks were captured at the same centrally located sub-colony site (1980, 1991–1995, 1997–1998), and fledglings moving to the water with adults at dusk and after dark were captured with dip-nets (1980, 1982–1984, 2000–2005, 2009, 2010, 2012–2014, 2016, 2017; Table S1). Mass was measured to the nearest 2 or 5 g using 300 or 600 g Pesola spring scales respectively, and flattened wing lengths were measured to the tip of longest primary wing covert to the nearest 1 mm. Young were banded with US Fish and Wildlife Service (USFWS) metal bands on their right leg and released immediately. The condition of young was calculated by dividing body mass by wing length (Davoren & Montevecchi 2003). Chick and fledgling data were combined to calculate overall offspring condition (provided as mass per wing length,  $\text{g mm}^{-1}$ ); chicks with wings less than 30 mm were excluded from analysis (Fig. S1).

### 2.4. Adult mass

Murres carrying capelin and flying in to the central area of the colony were captured with pole nets, weighed with 1000 or 1500 g Pesola spring scales, and banded (USFWS) on the right leg before immediate release in 1990, 2000, 2005, and 2008–2017 (Table S1). Data from 1990 and 2000 were excluded from analysis owing to differences in data collection (1990) and small sample size (2000;  $n = 3$ ).

### 2.5. Tracking foraging parents

On 31 July 2014, each of 10 parental murres with chicks were captured by noose pole at a centrally located sub-colony and had an Ecotone Telemetry GPS-UFH Uria-60 data logger (26 × 16 × 11 mm; 6 g) taped (~2 g) to scapular and back feathers. Tracking

data were downloaded to a base station on the island each time a bird returned to the colony following a foraging trip. Data collection began on 31 July; the base station (containing downloaded data) was removed on 7 August. Due to a logger malfunction during 2014, GPS positions were obtained from 9 birds. In 2016, 6 parental murres with chicks had Ecotone Telemetry GPS-UFH Uria-300 loggers (36 × 22 × 12.5 mm; 13.5 g) taped (~2 g) to scapular and back feathers and data were downloaded to a base station on the island during 18–27 July. Devices (<1% [2014] and <2% [2016] mean annual adult body mass) recorded latitude, longitude, and speed data every 10 min; dive frequency and duration were recorded whenever devices were submerged for 10 s or more. Data collected from each individual were partitioned into trips by splitting the track between periods when the bird was known to be at the colony. Trips greater than 2 km (72% of all trips) from the colony were considered foraging trips; trips less than that were excluded from analysis because these trips are likely related to bathing and rafting behavior near the colony (Burger 1997).

### 2.6. Capelin biomass and spawning dates

A fine-scale (~15 km) hydro-acoustic survey was conducted approximately weekly during July and August 2014 (11, 14, 18, 24 July) and 2016 (14 July, 3, 16 August) over 4 persistently used shallow-water (15–40 m) capelin spawning sites (Penton & Davoren 2012) as part of an annual monitoring program of the timing and magnitude of peak capelin biomass in the study area. The survey area represents an annually persistent biological hotspot of multiple seabird and whale species, including high abundances of murres (Davoren 2013b). The survey followed a zig-zag design to include each shallow-water spawning site within the survey. Along the survey line, capelin biomass was quantified using a DTX 6000 (BioSonic) scientific echo-sounding system, operated through a 70 kHz split-beam transducer (see Davoren et al. 2006). To quantify capelin biomass ( $\text{g m}^{-2}$ ) per survey, backscatter volume ( $s_v$ ) was converted into backscatter area ( $s_a$ ), which was then combined with biometrics of capelin in the study area and a published target strength–length relationship for capelin in Newfoundland (Rose 1998). The survey that detected peak average capelin biomass ( $\text{g m}^{-2}$ ) within a year has been used as the most robust metric of inter-annual differences in forage fish abundance in the seabird foraging areas. Additionally, shallow-water

spawning sites were monitored for capelin spawning activity (presence of eggs) following methods described in previous studies in the area (Davoren et al. 2012, Penton & Davoren 2012, Davoren 2013a,b, Crook et al. 2017).

## 2.7. Data processing and statistical analysis

Data processing, analyses, and plotting were conducted using R version 3.4.2 (R Core Team 2017). In addition to base R, the 'data.table' (Dowle & Srinivasan 2017) package was used to aid data processing and the 'sf' (Pebesma 2017) and 'ggplot2' (Wickham 2016) packages were used for plotting and mapping. Linear mixed models were run using the 'lme4' package (Bates et al. 2015).

Linear trends in capelin mass, murre offspring condition, and adult murre mass were assessed using a regression of the annual means of each metric and weighted by the inverse of the variance of the annual measurements—a standard approach for accounting for varying quality of point estimates (Faraway 2016).

Total and maximum distances travelled during each foraging trip were extracted from the GPS data. Total distance was simply the cumulative point-to-point distance traveled within a foraging trip, and maximum distance was the maximum point-to-colony distance recorded within a foraging trip. Note that these metrics were underestimated in 2016, especially total distance, because several foraging trips were only partially recorded by the devices. Differences between total and maximum distances travelled per foraging trip across these 2 yr were assessed using a linear mixed model with individual as a random effect.

Means ( $\pm$ SD) are presented throughout and parameter estimates from linear models are presented with 95% confidence intervals in square brackets. Trends are considered significant if the 95% confidence intervals did not bound zero.

## 3. RESULTS

### 3.1. Parental prey deliveries

Murres on Funk Island specialize on capelin to provision offspring. Over 3 decades (1990–2017), parental food loads consisted almost exclusively of capelin (93.9  $\pm$  10.9%) of which almost all were females (95.2  $\pm$  5.2%; Fig. 1). The mean annual mass of fresh capelin delivered to chicks declined significantly between 1990 and 2017 ( $-0.10$  [ $-0.19, -0.017$ ] g yr<sup>-1</sup>; Fig. 2A).

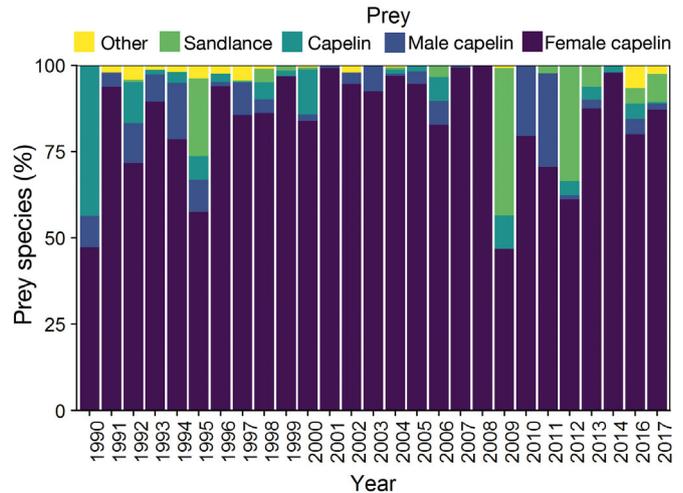


Fig. 1. Percentage of prey species provisioned to common murre chicks on Funk Island, NL, 1990–2017

### 3.2. Offspring condition and adult mass

Murre offspring condition also declined over the time series ( $-0.032$  [ $-0.055, -0.010$ ] g mm<sup>-1</sup> yr<sup>-1</sup>; Fig. 2B). The mean body mass of food-provisioning parental murres exhibited considerable variation and did not change systematically from 2005–2017 ( $-0.92$  [ $-2.77, 0.93$ ] g yr<sup>-1</sup>; Fig. 2C).

### 3.3. Parental foraging and diving effort

Compared to 2014, parental murres doubled their maximum and total foraging distances from the colony in 2016 (Table 1, Fig. 3). The average maximum distance travelled from the colony per foraging trip in 2016 was 28.7 [8.6–50.2] km further than parental murres traveled in 2014 (i.e. a 102% increase). Likewise, total distance traveled per foraging trip in 2016 was significantly longer than in 2014 (difference = 61.6 [15.0–109.1] km; a 94% increase). As well as traveling farther to forage in 2016, parental murres also dove much more frequently in 2016 (108.1  $\pm$  30 dives per foraging trip) than in 2014 (44.6  $\pm$  13 dives per foraging trip;  $t = 3.91$ ,  $df = 53.81$ ,  $p = 0.0003$ ; Fig. 4), and mean maximum dive duration was also significantly longer in 2016 (216.8  $\pm$  22.5 s [3.6 min]) than in 2014 (162.3  $\pm$  20.31 s [2.7 min];  $t = 3.61$ ,  $df = 85.64$ ,  $p = 0.0005$ ; Fig. 5).

Coincident with the inter-annual differences in foraging behavior and parental effort, in 2014 average fledgling condition (3.28  $\pm$  0.72 g mm<sup>-1</sup>) and parental mass (934.6  $\pm$  6.1 g) were significantly higher than fledgling condition (2.49  $\pm$  0.36 g mm<sup>-1</sup>) and parental

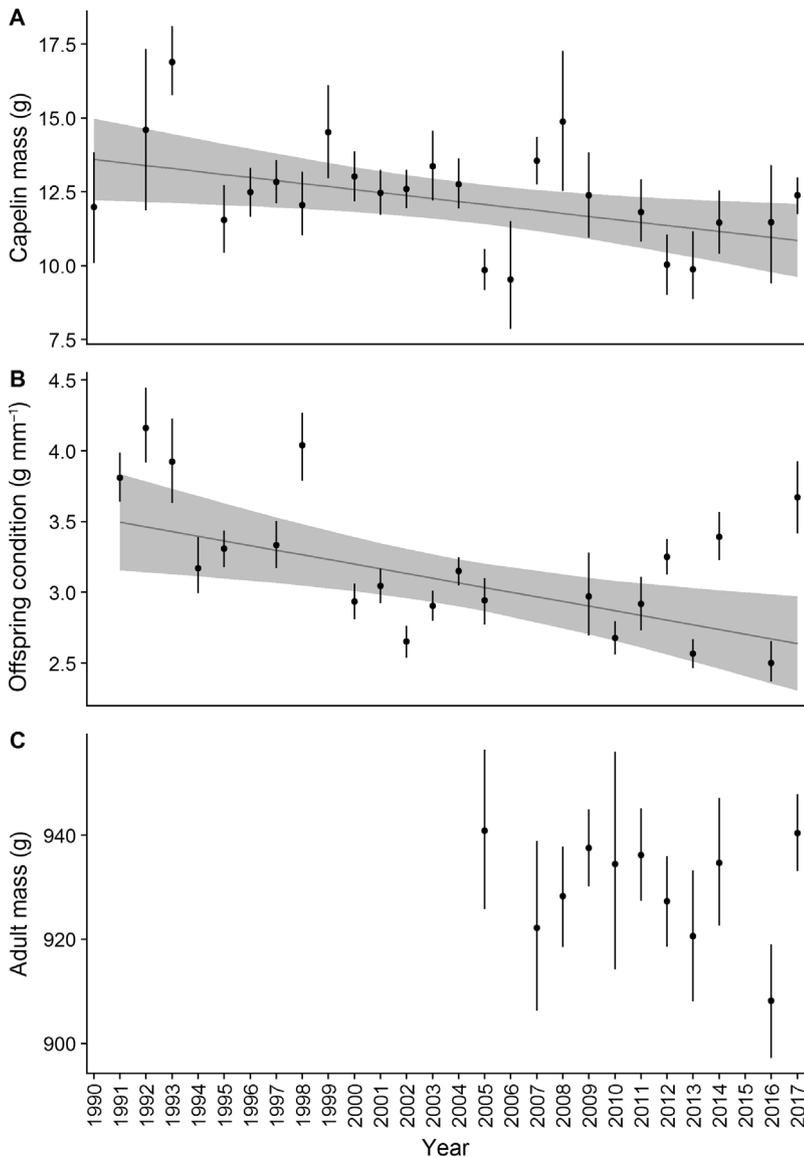


Fig. 2. (A) Capelin mass and (B) common murre offspring condition and (C) adult mass on Funk Island. Error bars = SDs; grey shading = 95 % CI of the slope of the linear regression

mass ( $908.2 \pm 5.6$  g) in 2016, when both factors were the lowest in their respective data series. For the 5 yr for which we have both offspring condition and local level prey data (2010, 2012, 2014, 2016, 2017), there is a suggestive positive correlation between offspring

and delivering larger capelin when prey availability is low (Burke & Montevecchi 2009, Buren et al. 2012), parents provisioned offspring with smaller capelin over the past 3 decades with concordant decreases in offspring condition.

condition and peak capelin biomass ( $r = 0.44$ ,  $R^2 = 0.19$ ). The mean masses of GPS-carrying birds in 2014 ( $912.8 \pm 34.6$ ) were less than those in 2016 ( $985.8 \pm 64.7$ ;  $t_{13} = 2.86$ ,  $df = 13$ ,  $p = 0.13$ ). The masses of the capelin provisioned to chicks did not differ between the 2 yr (2014:  $11.5 \pm 3.5$  g; 2016:  $11.5 \pm 4.1$  g).

The timing of fine-scale capelin surveys overlapped during 2014 (11 July–24,  $n = 4$  surveys) and 2016 (14 July–16 August,  $n = 3$  surveys) as did monitoring for capelin spawning activity (2014: 1 July–20 August; 2016: 1 July–16 August). The survey with the peak average capelin biomass in the study area occurred on the same date in both years (14 July) but was higher in 2014 ( $0.254$  g  $m^{-2}$ ) relative to 2016 ( $0.027$  g  $m^{-2}$ ). Capelin spawned in the study area from 16–24 July 2014, but capelin did not spawn or spawned much later (i.e. after 16 August) in the study area during 2016.

#### 4. DISCUSSION

Parental flexibility can be crucial for successful reproduction by seabirds, especially when coping with fluxes in prey availability (Harding et al. 2007, Pettex et al. 2012). Single-prey loading parental murre breeding in the species' largest North American colony specialize on capelin for provisioning offspring but also exhibit foraging flexibility to adjust to variable prey conditions. Yet despite the parental murre's ability to adjust to adverse conditions by foraging farther

Table 1. Mean (95 % confidence intervals) of mean maximum and mean total foraging trip distances, offspring condition and adult mass of common murre breeding on Funk Island during 2014 and 2016

Year	Max. foraging distance trip <sup>-1</sup> (km)	Total foraging distance trip <sup>-1</sup> (km)	Fledgling condition (g mm <sup>-1</sup> )	Adult mass (g)
2014	28.1 (14.9–40.4)	65.5 (36.9–94.4)	3.39 (3.23–3.57)	934.7 (922.6–947.1)
2016	56.8 (23.5–90.6)	127.0 (52.0–203.5)	2.49 (2.37–2.65)	908.2 (897.2–919.0)

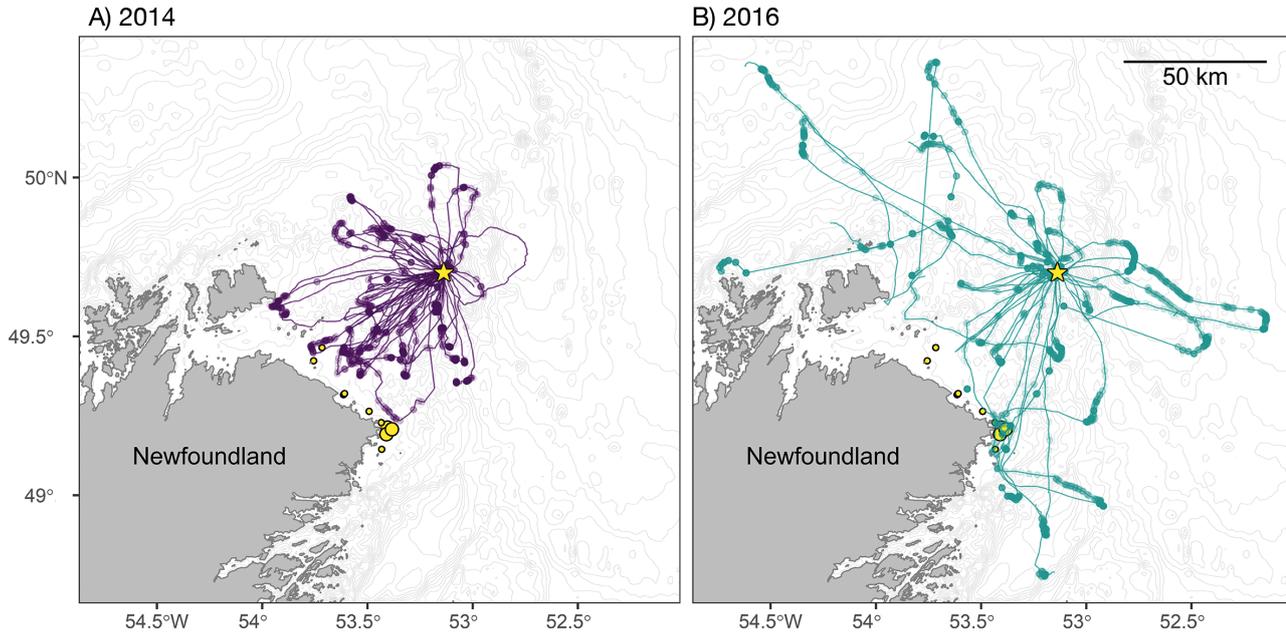


Fig. 3. Common murre foraging trips and dive locations obtained from GPS data for (A) 2014 (n = 9), when capelin spawned within the murre’s foraging range and (B) 2016 (n = 6), when no spawning was recorded and capelin were more dispersed. Yellow star: Funk Island; yellow circles: locations of shallow-water spawning sites scaled to relative abundance indices (larger circles indicate persistent sites)

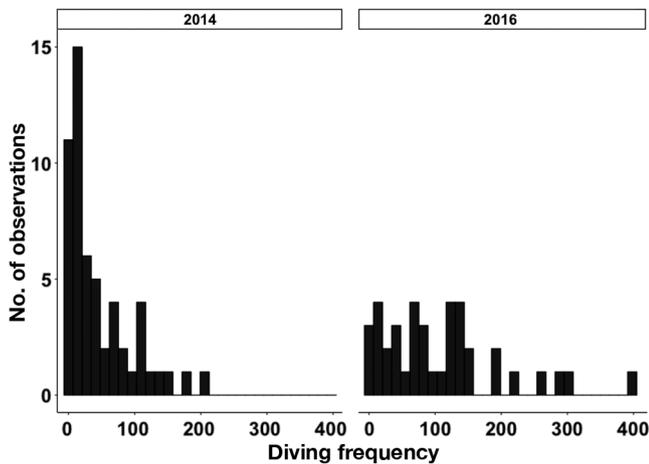


Fig. 4. Diving frequency per foraging trip by parental common murre’s foraging from Funk Island in 2014 and 2016

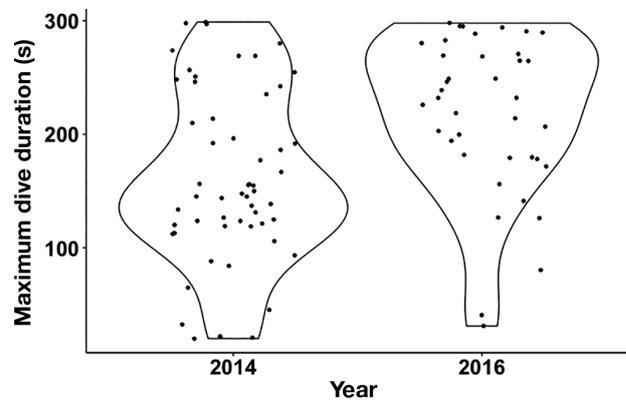


Fig. 5. Violin plot of the maximum dive duration per foraging trip by parental common murre’s breeding on Funk Island in 2014 and 2016

The decline in the mass of capelin provisioned to chicks reflects the regional trend, i.e. spawning capelin have become smaller since the early 1990s owing to the disappearance of older age classes (DFO 2018, Buren et al. 2019). Parental murre’s responded proactively to changes in prey availability by doubling foraging trip lengths, increasing both the frequency and duration of diving in 2016, when capelin biomass was low in key foraging areas compared to 2014. Both offspring condition and adult mass were the lowest on record during 2016, suggesting that the behavioral

tolerance of parents was challenged by decreases in capelin availability and mass.

The murre’s performance at Funk Island appears to be maintained by nearby predictable and annually persistent high-biomass shoals of spawning capelin (Davoren et al. 2003, Davoren 2013a,b, Gulka et al. 2017). In related circumstances, enhanced foraging effort on locally available prey allowed northern gannets *Morus bassanus* to maintain breeding success until the availability of its primary prey (Atlantic mackerel *Scomber scombrus*)

was only about 8% of local maximum abundance (Guillemette et al. 2018).

Despite deteriorating offspring condition, the murre's breeding population has increased over the past 35 yr (Wilhelm et al. 2015) following the collapse of the capelin stock. The increase in murre numbers indicates that seabirds can, at times, overcome major declines in fish stocks which, in the current circumstances, was associated with release from gillnet bycatch mortality following the northern cod *Gadus morhua* and Atlantic salmon *Salmo salar* fishery closures in the early 1990s (Regular et al. 2013) and with the easement of other negative anthropogenic influences associated with hunting and ship source oil pollution (Wilhelm et al. 2009).

The timing of prey availability can be a key determinant of seabird reproductive success (Regular et al. 2014), and parental deliveries of high quality gravid capelin have been linked to the timing of spawning (Davoren et al. 2012). Temporal mismatches between chick rearing and the peak of abundance in locally spawning capelin likely negatively affect breeding success (Regular et al. 2014, Storey et al. 2017). Owing to the highly variable timing of capelin spawning in our study area (Crook et al. 2017), our temporally restricted sampling period could not adequately assess the potential influence of spawning time on murre responses, though these interactions are likely at play (Davoren et al. 2012).

Despite the apparent resiliency of the common murre population, we caution that the massive colony on Funk Island is quite vulnerable given its size, concentration of breeding adults, and dependency on local capelin spawning sites. As capelin biomass declines, capelin spawn at fewer sites (Crook et al. 2017), resulting in a contraction of critical foraging area for murre and other marine birds, mammals, and fishes. It is uncertain whether the murre on Funk Island are approaching a threshold of parental foraging ability. However, the increased parental foraging efforts and the lowest levels of fledgling condition and adult mass in our 29 yr data series during 2016 suggest that years with low capelin biomass have direct, measurable influences on murre and their offspring. Efforts to monitor breeding success are underway (J. Gulka et al. unpubl. data), and long-term monitoring of prey catches and offspring and adult conditions in comparison with changing capelin conditions are continuing.

## 5. CONCLUSIONS

Our findings document the resiliency of a pursuit-diving seabird in the face of an extreme and prolonged reduction in regional forage fish abundance, mass, and condition. The changes since the early 1990s have imposed costs on breeding murre. Despite these costs, the population has increased at the common murre's largest North American colony—likely due to a local, dependable source of persistent, predictable prey during the breeding season, as well as flexible parental behavior and reductions in adult mortality outside the breeding season. These results underscore the murre's behavioral tolerance, vulnerability, and risk.

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