NON-BREEDING MOVEMENTS AND FORAGING ECOLOGY OF THE BLACK GUILLEMOT *CEPPHUS GRYLLE* IN ATLANTIC CANADA

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ABSTRACT

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Understanding the movements of seabirds, which are important ecological indicators, can provide new insights into physical and biological aspects of the marine environment. This information can also be used in planning marine conservation and oil spill response strategies. Though Black Guillemots *Cepphus grylle* are widely distributed in the coastal waters of eastern and arctic Canada, little is known about their movements during the non-breeding season. We used a combination of global location sensors and stable-isotope analyses on Black Guillemots breeding on Country Island, Nova Scotia, Canada and on Kent Island, New Brunswick, Canada to examine their non-breeding movements and trophic ecology in 2017–2018. Overall, the two populations dispersed an average of 157 km from their breeding colonies (max. 494 km) throughout the region, reaching areas that included the Scotian Shelf, Gulf of St. Lawrence, Bay of Fundy, and Gulf of Maine; both populations overlapped in the Bay of Fundy during the winter. Trophic levels (δ^{15}N) and foraging locations (δ^{13}C) differed between the colonies. Birds from Country Island foraged at higher trophic levels and in less benthic waters than Kent Island birds overall, and birds from both colonies foraged at higher trophic levels in autumn than in winter. This indicates that foraging strategies differ between Black Guillemot populations and that diet varies between seasons, even when foraging habitats do not. Our findings, combined with other seabird, fish, and marine mammal tracking studies, can inform marine management decisions in Atlantic Canada.

Key words: alcid, distribution, geolocator, migration, stable isotopes, tracking

INTRODUCTION

Seabirds are sensitive to physical and biological changes in the marine environment and can be important indicators of marine ecosystem health (Parsons *et al.* 2008, Vandenabeele *et al.* 2011). However, seabirds spend most of the year at sea and only return to land to breed, making it difficult to study their non-breeding ecology. Advancements in tracking technology (Burger & Shaffer 2008), combined with data on prey availability or seasonal oceanic productivity, can help identify drivers of seabird movements (Takahashi *et al.* 2015). Further, information on distribution can be used for conservation planning, such as delineating marine protected areas, tidal energy development, or oil spill response strategies (Lascelles *et al.* 2012).

As tracking devices, such as geolocators, have decreased in size during the last 30 years, they have been increasingly used to track seabird movements (Bridge *et al.* 2011, Vandenabeele *et al.* 2011). The resulting data have been used to measure seabird foraging distances, map migration routes, and identify important offshore wintering areas (Montevecchi *et al.* 2012, McFarlane Tranquilla *et al.* 2014, Takahashi *et al.* 2015). However, tracking devices may have negative impacts on seabirds such as decreased reproductive success, return rates, and adult and/or chick mass, depending on the degree to which they encumber the birds (Adams *et al.* 2009, Robinson & Jones 2014, Schacter & Jones 2017). Data from tracking devices are useful only if the acquired information also represents the untagged population. Therefore, the effect on the individual and the validity of the data from these tracking devices must be assessed to ensure devices are not affecting the tagged bird itself or the parameters measured (Barron *et al.* 2010, Vandenabeele *et al.* 2011, Robinson & Jones 2014, Schacter & Jones 2017).

Recently, tracking devices have been used in conjunction with stable-isotope analyses (Phillips *et al.* 2009, Takahashi *et al.* 2015) to interpret or confirm spatial differences in geolocation data. Stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) are also frequently used to examine seabird food webs and trophic relationships (Hobson & Clark 1992, Bearhop *et al.* 2006). Measurements of δ^{13}C can identify foraging location or habitat because δ^{13}C reflects primary producers, and δ^{13}C values are more enriched in inshore benthic food sources compared to offshore pelagic ones (Hobson *et al.* 1994, Kelly 2000). Similarly, δ^{15}N increases with dietary trophic levels and can therefore be used to assess diet (Hobson & Clark 1992, Bearhop *et al.* 2006). Information on seasonal differences in foraging location and trophic level among individuals, populations, or species enhances our understanding of regional year-round movements and foraging ecology.

The Black Guillemot *Cepphus grylle* is a Holarctic alcid that is common along the Atlantic coast of Canada. During the breeding season, it is known to feed on rock gunnel *Pholis gunnellus*, sculpin *Cottidae* spp., cod *Gadidae* spp., sandlance *Ammodytidae* spp. and Atlantic herring *Clupea harengus* (Bradstreet 1979, Nol &

Gaskin 1987, Butler & Buckley 2002). During the breeding season, extensive research indicates that Black Guillemots prefer inshore benthic foraging locations (Nol & Gaskin 1987, Prach & Smith 1992, Huettmann *et al.* 2005). However, less is known about their habitat use during the non-breeding period, which composes most of their annual cycle (Nol & Gaskin 1987, Prach & Smith 1992, Butler & Buckley 2002, Divoky *et al.* 2016). In the western North Atlantic, particularly the Gulf of Maine, waters have been warming faster than in many other areas; effects on fish stocks (Mills *et al.* 2013, Pershing *et al.* 2015) have had corresponding effects on breeding seabirds (Scopel *et al.* 2019). Further, like other alcids, Black Guillemots are affected by threats such as vessel disturbance (Ronconi & St. Clair 2002), tidal energy development (Karsten *et al.* 2008, Furness *et al.* 2012), and oil spills (Lieske *et al.* 2019). Therefore, tracking studies on Black Guillemots during the non-breeding season are necessary to understand their distribution and movements away from their breeding colonies.

Here, we use a combination of geolocators and stable-isotope analyses to: (1) identify the non-breeding movements of Black Guillemots along the Canadian coast of the western Atlantic; (2) determine if inter-seasonal or inter-colony differences exist in foraging ecology; and (3) assess the effect of tagging on hatching success and adult mass.

STUDY AREA AND METHODS

Study area

Black Guillemots were studied at nesting colonies on Country Island, Nova Scotia, Canada and Kent Island, New Brunswick, Canada from June 2017 to July 2018 (Fig. 1). Country Island (44°58′N, 066°75′W) is located off the eastern shore of Nova Scotia and has a breeding population of 500–600 Black Guillemots (Trottier-Paquet & Rock 2018). This 19-ha (0.19 km^2) island is located along the Scotian Shelf and is in an area of high productivity due to upwelling near the outer shelf and shelf break (Yoder *et al.* 1983). Kent Island (45°10′N, 061°54′W) is 75 ha (0.75 km^2) in size, is located in the Grand Manan Archipelago (Bay of Fundy), and supports *ca.* 250 Black Guillemots, which includes 61 breeding pairs (Cannell & Maddox 1983, Ronconi & Wong 2003). Owing to the high tides of the Bay of Fundy, the Grand Manan Archipelago experiences substantial tidal mixing, which results in high productivity (Gran & Braarud 1935). Both Country Island and the Grand Manan Archipelago are

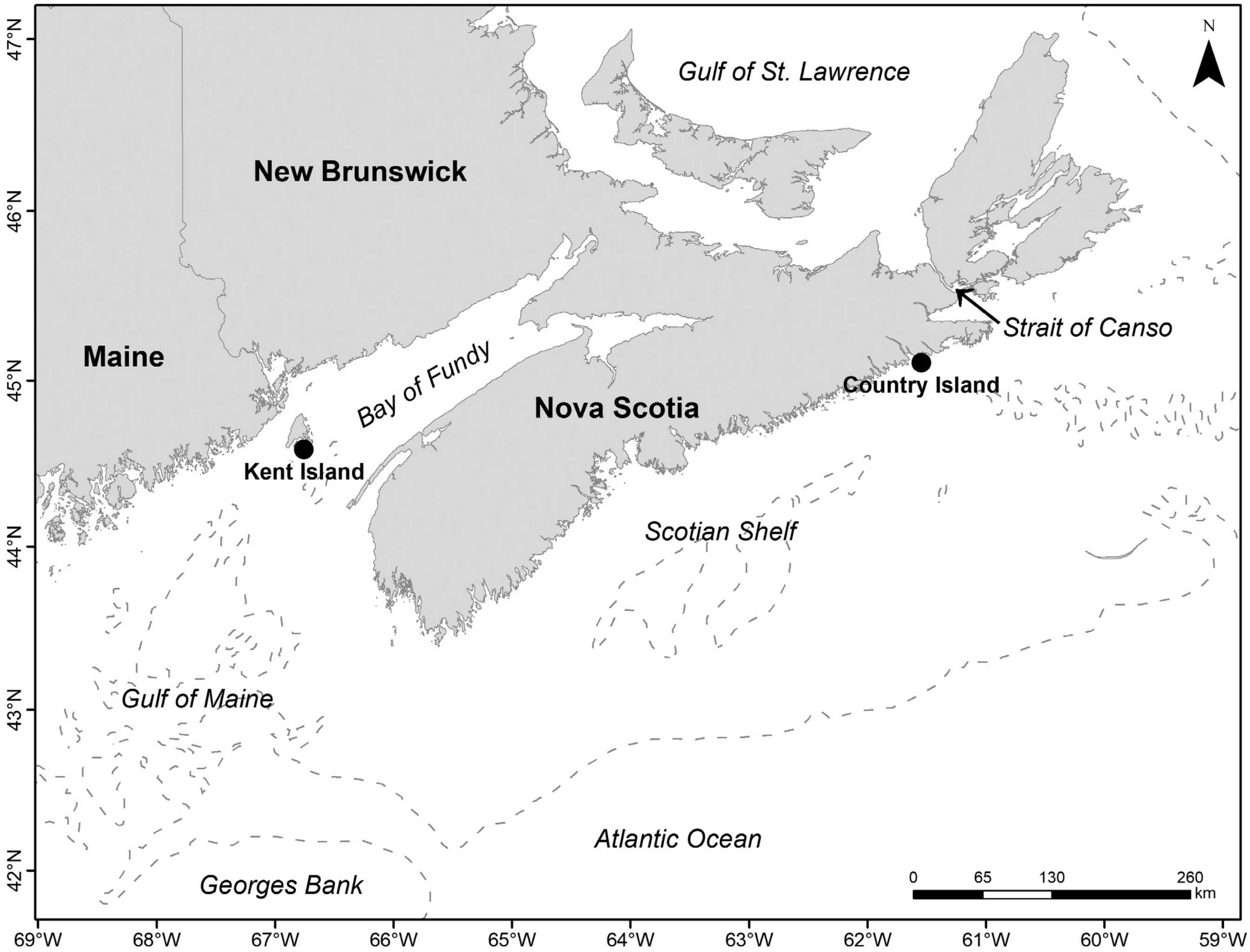

Fig. 1. Map of southeastern Atlantic Canada showing the location of Country Island, Nova Scotia and Kent Island, New Brunswick, where global location sensors were deployed on Black Guillemots *Cepphus grylle* in June 2017. Dashed lines represent the 200-m bathymetric contour, illustrating the continental shelf break line and basins on the shelf. Sources: base map from GADM (www.gadm.org); shelf-break lines from GEBCO (www.gebco.net)

designated as Important Bird Areas due to the variety of nesting seabird species (Huettmann & Diamond 2000; Huettmann *et al*. 2005; Wong *et al*. 2018; Birds Canada 2019a, 2019b).

Tag deployment and recapture

Black Guillemots on both islands return to their breeding colony in April, begin courtship in May, and lay eggs in June (Winn 1950). We captured Black Guillemots in mid to late June, which is approximately halfway through the 29-day incubation period (Butler & Buckley 2002). In June 2017, we captured breeding adults from Country Island (n = 10) and Kent Island (n = 7) on-nest by hand and recorded egg number, adult mass, and natural wing chord. At the time of capture, we attached a size-4 stainless steel band to the right tarsus and a MK4093 Global Location Sensor (GLS; 15 mm × 10 mm × 6 mm; from Biotrack Ltd. in Wareham, UK) to the left tarsus using a plastic leg ring, as per McFarlane Tranquilla *et al.* (2014) and Takahashi *et al.* (2015). This GLS model included a wet/dry sensor that recorded every 10 minutes, but it had no temperature sensor. Measurements (mass in g and wing chord in mm), banding, and GLS attachment took less than 10 minutes per bird, and birds were returned to their nest site.

In 2018, we recaptured birds during the incubation period and measured them again. When possible, we collected blood samples at the time of recapture for sex determination (see Results). From recaptured birds, we also removed from both wings the first secondary feather, which is moulted between August and September (hereafter "autumn"), along with approximately five breast feathers, which are moulted between February and April (hereafter "winter"; Pyle 2008). The feathers were used to quantify stable-isotope values (δ^{13}C, δ^{15}N) for these two periods. In 2018, we also captured an additional 10 untagged birds from Country Island and five untagged birds from Kent Island; these were sampled as described above to assess tag effects.

Geolocation data analysis

We downloaded and decompressed data from the GLS tags using BAS-Trak software (Biotrack Ltd., Wareham, UK). We analyzed light-level data in R (version 3.4.3, R Development Core Team 2017) using the "TwilightFree" package (version 0.1.0, Bindoff *et al.* 2018), which uses a Hidden Markov Model (Rabiner 1989) to produce daily position estimates from a hidden sequence of geographic locations and the pattern of light intensity measured by the tag (Bindoff *et al.* 2018). We omitted light-level data from 10 September 2017 to 18 October 2017 and from 20 February 2018 to 05 April 2018 *a priori* to exclude latitudes that cannot be accurately assessed due to the equinox (Hill 1994); the greatest variability in readings precedes the vernal equinox and follows the autumnal equinox (Hill & Braun 2001). Using pre-deployment calibration periods, we determined zenith angles and twilight threshold values for each tag using the "TwilightFree" calibrate function (Bindoff *et al.* 2018).

The "TwilightFree" model relies on shading likelihood and cell transition parameters to determine the most likely position occupied by the tag. Therefore, we examined individual twilight events for each tag using the R package "TwGeos" (version 0.0.1; Wotherspoon *et al.* 2016, R Development Core Team 2017). In turn, we calculated the shading likelihood parameter, which is an estimation of sensor obstruction, as the proportion of obscured twilights over the total number of twilights throughout the deployment period. We determined the cell transition parameter using tag immersion data. The GLS tags recorded a wet/dry state every three seconds and categorized the total number of "wet" samples into 10-minute bins. We filtered immersion records such that consecutive bins with < 2% wet samples were interpreted as periods of sustained flight (Fifield *et al.* 2009, Fayet *et al.* 2016). Then we applied a speed filter of 58 km/h (Ewins 1986) to total daily sustained flight times to estimate the proportion of each day a bird could have flown beyond the bounds of one cell in the "TwilightFree" spatial domain (0.5° or ~55.5 km), assuming it was flying in a straight line. We calculated the cell transition parameter as the proportion of days that sustained flight exceeded 55.5 km over the total number of days recorded during the deployment period.

We focused our analyses on movements during the non-breeding period, as determined by colony attendance. We filtered immersion data and interpreted uninterrupted dry periods of ≥ 6 h as colony attendance (McFarlane Tranquilla *et al.* 2014). On Kent Island, guillemots come ashore in mid-April to early May but do not lay eggs until late May or early June (Winn 1950). Courtship in April and May occurs both on land and in water (Butler & Buckley 2002), thus colony attendance periods of ≥ 6 h likely represents incubation onset. We then incorporated a sea mask to restrict analysis to movements in the marine environment. We smoothed validated data once, with raw position estimates retained around periods of missing data (see Phillips *et al.* 2004, Hedd *et al.* 2011). Two data points from 02 and 03 June 2018 were excluded from analyses due to presumed light-level errors. Finally, because GLS position estimates typically have a mean error of approximately 200 km (Phillips *et al.* 2004, Shaffer *et al.* 2005), we averaged positions for each bird by week to reduce error and investigate seasonal movement patterns.

Once data were processed, we calculated distance from colony and distance from shore (closest land mass) for each weekly location (including islands; CanCoast Geodatabase, Environment and Climate Change Canada, unpubl. data). Additionally, we calculated distance from shore for at-sea observations of Black Guillemots using data from the Programme intégré de recherches sur les oiseaux pélagiques (PIROP) from 1965 to 1992 (plus an additional survey in 2001 using the same methods) and the Eastern Canada Seabirds at Sea (ECSAS) from 2006 to 2019 (CWS 2019). We restricted ECSAS/PIROP records to those occurring within the range of Black Guillemots tracked in the current study area (bound by 40°N, 48°N, 059°W, and 069°W) to compare GLS location data with at-sea observations, so we could examine similarities and potential error in GLS data. We summarized the distance from colony by individual and month, and we summarized distance from shore by month (as ECSAS and PIROP data do not have individual data).

Stable-isotope analysis

We soaked feathers in 10-mm vials using a 2:1 ratio of chloroform:methanol and air-dried them for 48 hours (Hobson & Bond 2012). We then weighed the feather samples to the nearest 1.000 mg using a high-precision microbalance (readability of 0.001 mg) and sent them to the Stable Isotopes in Nature Laboratory at the University of New Brunswick (Fredericton, New Brunswick, Canada) to determine carbon (δ^{13}C) and nitrogen (δ^{15}N) stable-isotope values. Stable isotopes were quantified using the deviation from standards (parts per thousand) according to the following equation:

$$\delta X = \left(\frac{R\ sample\ \text{-}1}{R\ standard}\right) \times 1000$$

where X was ^{13}C or ^{15}N and R was the corresponding respective $^{13}C/^{12}C$ or $^{15}N/^{14}N$ value (Hobson & Bond 2012, Takahashi *et al.* 2015).

To compare diet between colonies (Country Island and Kent Island), time periods (autumn and winter moult), and treatments (tagged and untagged), we compared stable isotopes $\delta^{13}C$ and $\delta^{15}N$ using two-way Analysis of Variance (ANOVAs) with colony, feather type, and treatment as predictors, as well as a colony-feather type interaction term. We carried out normality checks and Levene's tests, meeting the assumptions of normality and equality of variances. We computed all post-hoc comparisons using Tukey tests, and we report results as means ± one standard deviation.

Tag effects

We used two methods to determine the potential effect of tagging on adult mass. First, we compared the mass of tagged adults (n = 6) at time of deployment (2017) and recovery (2018) using paired t-tests. Second, we compared adult mass between tagged (Country Island n = 4; Kent Island n = 3) and untagged (Country Island n = 10; Kent Island n = 5) individuals in 2018 using unpaired t-tests.

We also compared hatching success at nest sites on Country Island between nests where adults were handled and tagged (2017, n = 10; 2018, n = 4), handled but not tagged (2017, n = 11; 2018, n = 9), and neither handled nor tagged ("control"; 2017, n = 30; 2018, n = 45) using Kruskal-Wallis rank sum tests. Nests of all three groups were distributed randomly throughout the colony (i.e., treatment types were not spatially clustered) and sample sizes varied across treatments due to the logistical constraints of finding nests that could be readily monitored. Time restrictions and logistical limitations prevented the monitoring of nests on Kent Island. We checked nests on Country Island every two weeks and recorded clutch size and number of eggs hatched. We defined "hatching success" as the proportion of nests that hatched at least one chick. Finally, we compared stable isotopes $\delta^{13}C$ and $\delta^{15}N$ between tagged and untagged birds using two-way ANOVAs to assess tag effects (see above).

RESULTS

Four tags were retrieved from Country Island birds and three tags were retrieved from Kent Island birds (total n = 7; 41% recovery rate). Two additional tagged birds from Country Island were observed in 2018 but could not be recaptured. With these birds included, the return rate rises to nine tagged birds (minimum return rate = 53%) across both sites. This total is conservative because some tagged birds likely went undetected. From these individuals, the total number of location points was 1479, with an average of 211 ± 53 points per bird (where D323 and D355 had 100 and 185, respectively, due to weak electrical connections; partial sets of light data were recovered). Sex determination from blood samples was successful for only two tagged individuals (D354 and D355 from Kent Island were females).

Movement and distribution

On Country Island, all four birds left the colony between 07 and 28 July 2017 (mean: 12 July 2017 ± 4.9 d) following breeding and moved to the Scotian Shelf. For the July/August period, two of these birds remained in the area, while the other two moved through the Strait of Canso into the Gulf of St. Lawrence before returning to the Scotian Shelf (Figs. 2, 3). In September/October, three birds moved from the Scotian Shelf south to waters off the continental shelf; from there, one returned to the Scotian Shelf, one circled north to the Gulf of St. Lawrence and then returned to the Scotian Shelf, while the other returned to the Scotian Shelf then proceeded west to the Gulf of Maine. The fourth bird remained on the Scotian Shelf during this period. In November/December and January/February, the three birds on the Scotian Shelf either travelled to the Bay of Fundy and Gulf of Maine (n = 1), travelled back and forth between the Scotian Shelf and the Gulf of St. Lawrence (n = 1), or remained on the Scotian Shelf (n = 1). The bird that travelled to the Gulf of Maine in September/October moved back and forth between the Gulf of Maine and the Bay of Fundy during the winter months. Finally, in April/May/June, two of the three birds on the Scotian Shelf appeared to move from the Scotian Shelf/Gulf of St. Lawrence off the continental shelf, the third moved from the Scotian Shelf to the Gulf of St. Lawrence, and the fourth moved from the Bay of Fundy/Gulf of Maine back to the Scotian Shelf. Return dates to the breeding colony could not be precisely determined by GLS, but dry periods of > 6 hours (measured by wet/dry sensors) indicated incubation onset between 29 May and 04 June 2018 (mean: 01 June 2018 ± 2.6 d).

On Kent Island, the three birds left the colony on 13, 16, and 25 July 2017 following breeding. In July/August all three birds moved out of the Bay of Fundy to the Gulf of Maine; one bird moved south through the Gulf of Maine to the eastern tip of George's Bank, while the other two remained in the Gulf of Maine (Figs. 2, 3). From September until April, all three birds remained in the lower Bay of Fundy or northeastern portion of the Gulf of Maine. (Note, however, that only partial tracks are available for two individuals: D323 and D355 have no data for January–June and April–June, respectively.) The one bird that was tracked to the onset of breeding (D354) likely began incubation on 09 June 2018. Return/incubation dates for the other two birds are unknown due to partial data loss.

Across individuals and seasons, the mean distances from the colony were 185 ± 144 km and 104 ± 79 km for Country Island and Kent Island, respectively, with 90% of location points occurring within 409 and 260 km of the colonies on Country Island and Kent Island, respectively (Fig. 4). Country Island birds were furthest from the colony near the end of the non-breeding period (mean distance: 268 ± 175 km in January/February), with a maximum distance of 494 km. During this period, Country Island birds appeared to have a bimodal distribution in dispersal distance, where some birds remained on the Scotian Shelf while others migrated to the Bay of Fundy and Gulf of Maine (Fig. 4). By contrast, Kent Island birds dispersed the greatest distance from the colony at the beginning of the non-breeding period (mean distance: 147 ± 103 km in September/October), with a maximum dispersal distance of 360 km (Figs. 2, 4).

Across individuals and seasons, the mean distances from shore were 74 ± 83 km and 52 ± 47 km for Country Island and Kent Island, respectively, with 90% of location points occurring within

193 and 122 km of any shoreline for birds from Country Island and Kent Island, respectively (Fig. 5). Country Island birds were furthest from shore near the end of the non-breeding period (mean distance: 96 ± 117 km in January/February) with a maximum distance of 392 km from shore. In contrast, Kent Island birds dispersed the furthest from shore at the beginning of the non-breeding period (mean distance: 81 ± 61 km in September/October), with a maximum distance of 222 km from shore. For at-sea observations, birds were observed furthest from shore in April/May/June (maximum of 84 km from shore) by ECSAS observers and September/October (maximum of 55 km from shore) by PIROP observers. The mean distances from shore across seasons were 7 ± 10 km and 10.9 ± 14.1 km for Black Guillemots observed during ECSAS and PIROP surveys, respectively.

Stable isotopes

There were no significant differences in δ^{13}C values for breast feathers (winter diet) and secondary feathers (autumn diet) (ANOVA; $F_{1,33} = 1.37$, $P = 0.25$; Table 1, Fig. 6) among birds from either colony. However, δ^{13}C values did differ between colonies ($F_{1,33} = 101.50$, $P < 0.0001$; Table 1, Fig. 6), with higher δ^{13}C values among birds of Kent Island compared to Country Island (Tukey HSD multiple comparison tests; both $P < 0.001$; Table 1, Fig. 6). Additionally, the colony-feather type interaction was significant ($F_{1,33} = 6.08$, $P = 0.02$), with secondary feathers on Kent Island having significantly higher δ^{13}C than breast feathers on Country Island and breast feathers on Kent Island having higher δ^{13}C than secondary feathers on Country Island (both $P < 0.0001$).

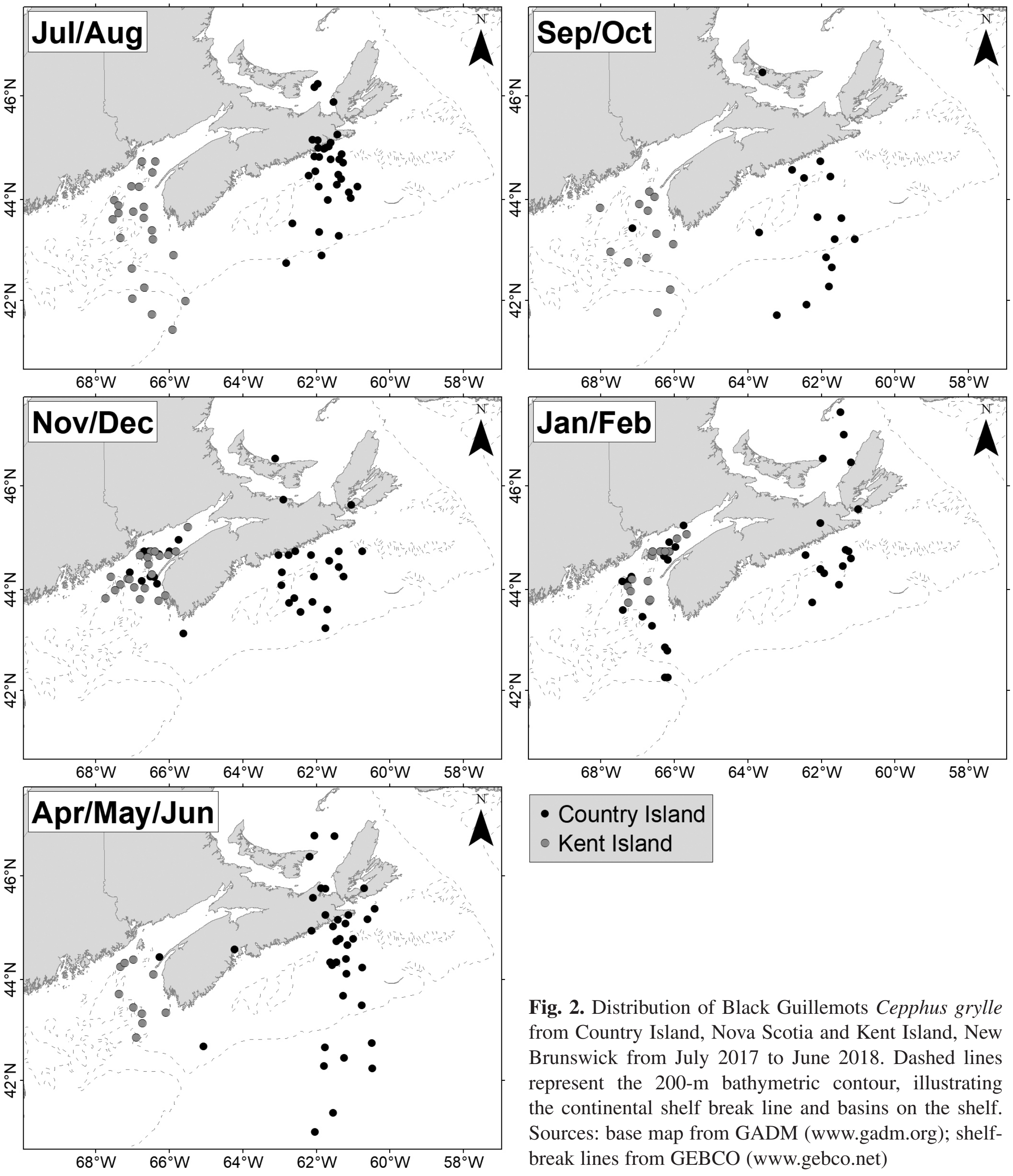

Fig. 2. Distribution of Black Guillemots *Cepphus grylle* from Country Island, Nova Scotia and Kent Island, New Brunswick from July 2017 to June 2018. Dashed lines represent the 200-m bathymetric contour, illustrating the continental shelf break line and basins on the shelf. Sources: base map from GADM (www.gadm.org); shelf-break lines from GEBCO (www.gebco.net)

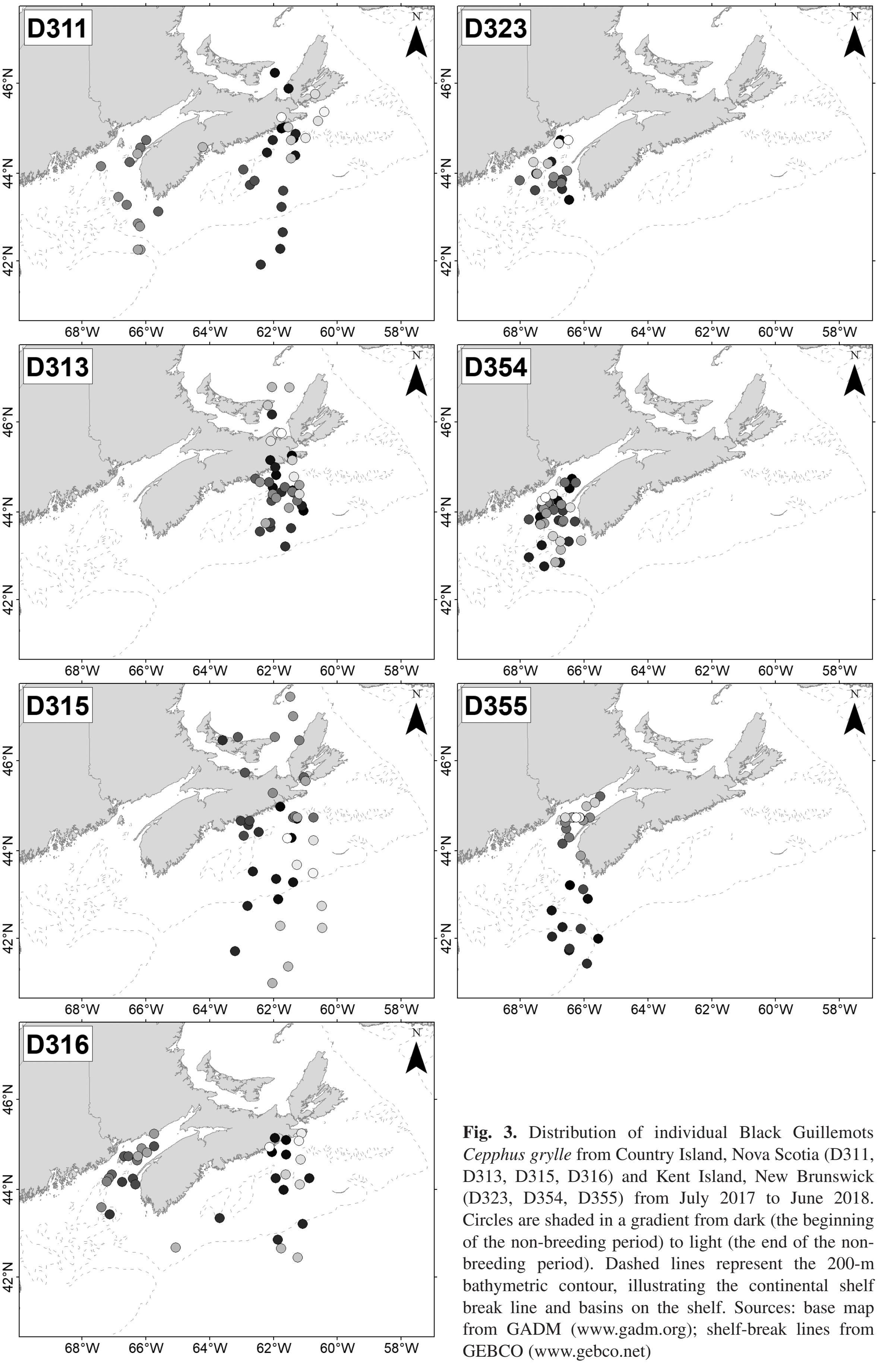

Fig. 3. Distribution of individual Black Guillemots *Cepphus grylle* from Country Island, Nova Scotia (D311, D313, D315, D316) and Kent Island, New Brunswick (D323, D354, D355) from July 2017 to June 2018. Circles are shaded in a gradient from dark (the beginning of the non-breeding period) to light (the end of the non-breeding period). Dashed lines represent the 200-m bathymetric contour, illustrating the continental shelf break line and basins on the shelf. Sources: base map from GADM (www.gadm.org); shelf-break lines from GEBCO (www.gebco.net)

There were significant differences in $\delta^{15}N$ values for breast (winter) and secondary (autumn) feathers (ANOVA; $F_{1,33} = 165.85$, $P < 0.0001$), with breast feathers showing significantly lower $\delta^{15}N$ values than secondary feathers (Tukey HSD multiple comparison tests; both $P < 0.0001$, Fig. 6). Similarly, $\delta^{15}N$ values differed significantly among the two colonies ($F_{1,33} = 77.31$, $P < 0.0001$), with Kent Island breast and secondary feathers having significantly lower $\delta^{15}N$ values than Country Island breast and secondary feathers (both $P < 0.0001$). Finally, the colony-feather type interaction was not significant ($F_{1,33} = 0.94$, $P = 0.34$).

Tag effects

On all tagged birds that were recaptured, the skin at the site of tag attachment appeared uninjured with no obvious scarring. The average mass of adult Black Guillemots on Country Island and Kent Island upon deployment was 390 ± 21 g (range: 360–435 g) and the total mass of the GLS (1.52 g) and plastic leg ring (1 g) was approximately 0.65% of body mass, less than the recommended 3% maximum for marine birds (Phillips *et al.* 2003). The mean mass of tagged birds did not differ significantly between tag deployment in 2017 and tag retrieval in 2018 (paired *t*-test: $t(5) = 0.38$, $P = 0.72$, $n = 6$). Similarly, the mean mass of tagged birds (388 ± 14 g, $n = 7$) did not differ significantly from untagged birds (375 ± 30 g, $n = 15$; Welch's two sample *t*-test; $t(20) = -1.29$; $P = 0.21$) in 2018. Hatching success did not differ significantly between handled and tagged, handled but not tagged, and control nests in either 2017 or 2018 (Table 2). Finally, $\delta^{13}C$ and $\delta^{15}N$ values did not differ between tagged and untagged birds ($F_{1,33} = 1.22$, $P = 0.28$).

DISCUSSION

Movement and distribution

We obtained full or partial tracks for seven Black Guillemots from two breeding colonies in Nova Scotia and New Brunswick, Canada, providing new information on non-breeding distribution and movement patterns of this species. Black Guillemots from Country Island and Kent Island were distributed across a broad area during the non-breeding season. Country Island birds either remained on the Scotian Shelf or travelled to the Gulf of St. Lawrence, Bay of Fundy, or Gulf of Maine, whereas birds from Kent Island remained in the Bay of Fundy or Gulf of Maine (Figs. 2, 3). This demonstrates that guillemots from the different colonies have different movement strategies in the non-breeding season, and that guillemots from the same colony have different migration strategies (see also Divoky

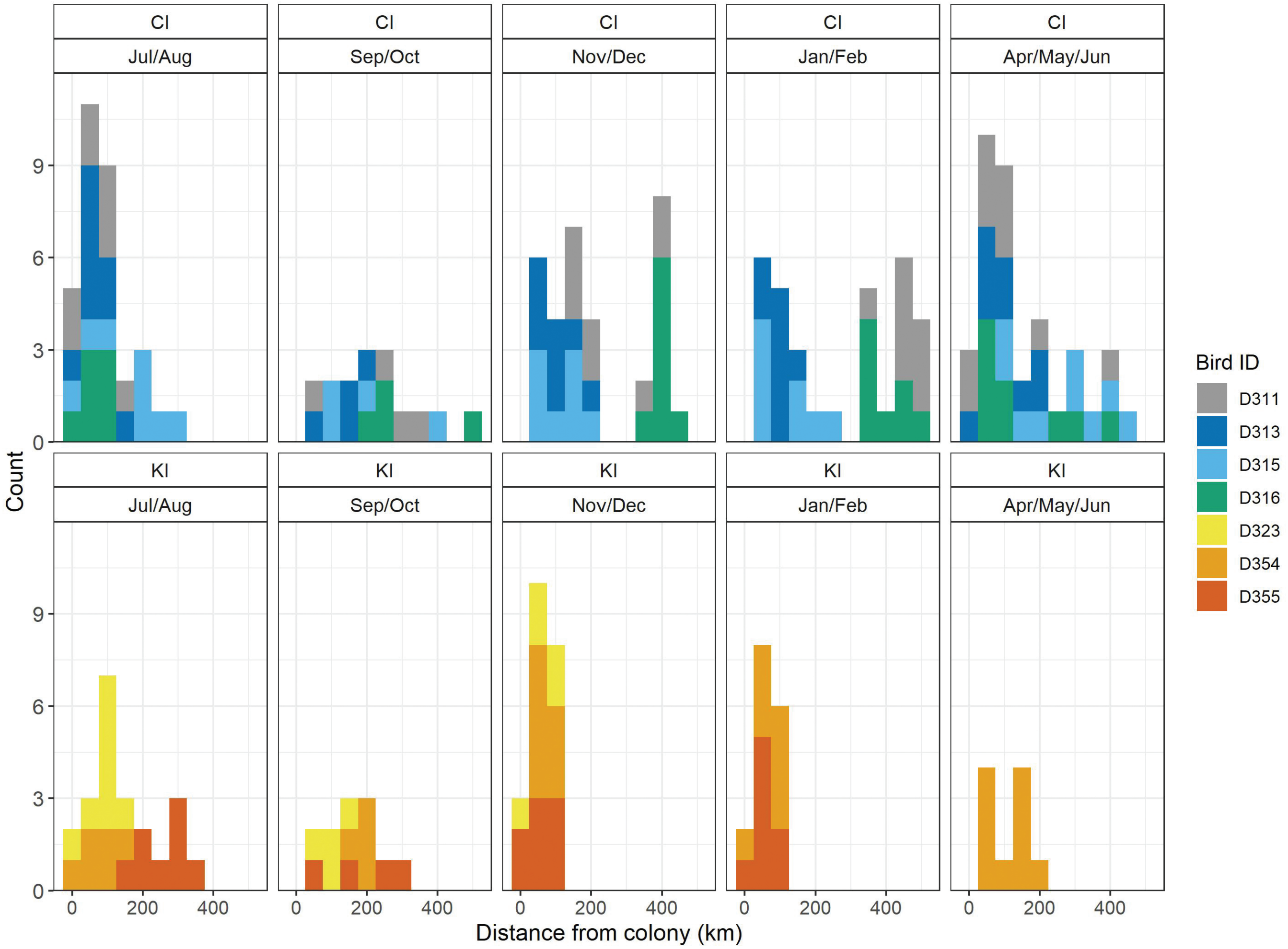

Fig. 4. Histogram of the distance from colony (km) for Black Guillemots *Cepphus grylle* from Country Island (CI), Nova Scotia and Kent Island (KI), New Brunswick from July 2017 to June 2018. Data collected from 10 September 2017 to 18 October 2017 and from 20 February 2018 to 05 April 2018 were omitted to exclude latitudes that cannot be accurately assessed due to the autumnal and vernal equinox, respectively.

et al. 2016). This pattern has also been observed in Common Murres *Uria aalge* and Thick-billed Murres *U. lomvia* (McFarlane Tranquilla *et al.* 2013), where birds from the same colony were distributed in different areas during the non-breeding period.

Location estimates also showed that guillemots dispersed up to 392 km offshore and past the continental shelf break (Figs. 2, 5) during the non-breeding season. These distances contrast with the coastal inshore distribution of guillemots during the breeding season (Nol & Gaskin 1987, Huettmann *et al.* 2005), as well as with the ECSAS and PIROP at-sea observations, in which birds were observed a maximum of 84 km and 55 km offshore, respectively, during the non-breeding season. It is possible that at-sea data are missing detections of guillemots further offshore or that the GLS data are providing incorrect locations. While at-sea survey programs rely on ships of opportunity and, therefore, have variable

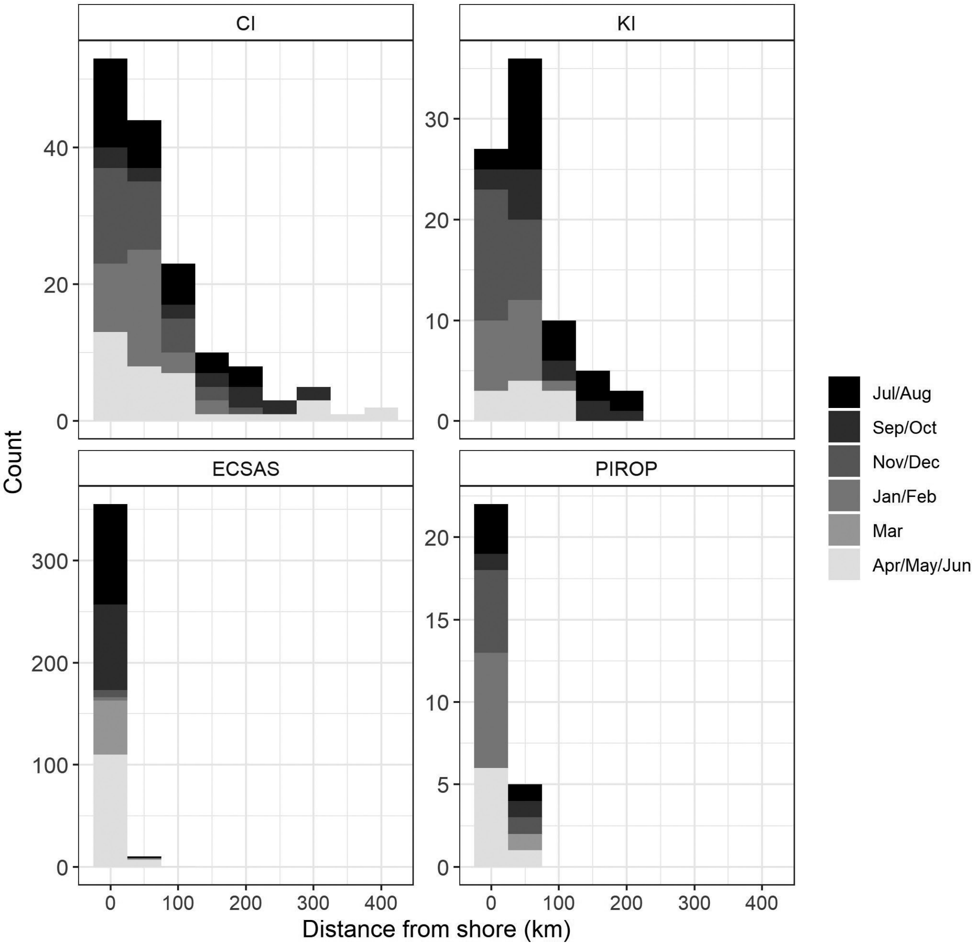

Fig. 5. Histogram of the distance from shore (km) for Black Guillemots *Cepphus grylle* from Country Island (CI), Nova Scotia from July 2017 to June 2018; from Kent Island (KI), New Brunswick from July 2017 to June 2018; as observed by the Eastern Canada Seabirds at Sea (ECSAS) program in our study area from 2006 to 2019; and as observed by the Programme intégré de recherches sur les oiseaux pélagiques (PIROP) in our study area from 1969 to 2001. Data collected for tagged birds from 10 September 2017 to 18 October 2017 and from 20 February 2018 to 05 April 2018 were omitted to exclude latitudes that cannot be accurately assessed due to the autumnal and vernal equinox, respectively.

TABLE 1
Mean, standard deviation (SD), minimum and maximum of δ^{13}C and δ^{15}N values (‰) from breast (winter moult) and secondary (autumn moult) feathers of Black Guillemots *Cepphus grylle* sampled on Country Island (CI), Nova Scotia and Kent Island (KI), New Brunswick in 2018

		δ^{13}C				δ^{15}N			
Colony	**Feather**	**Mean**	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**
CI	Breast	−18.8	0.9	−20.4	−17.1	16.3	0.5	15.5	17.1
	Secondary	−18.1	0.6	−18.9	−16.9	17.5	0.4	16.9	18.0
KI	Breast	−16.1	0.4	−16.6	−15.5	14.6	0.2	14.3	14.8
	Secondary	−16.1	0.4	−16.6	−15.5	15.6	0.2	15.3	15.9

survey effort, both ECSAS and PIROP data include considerable survey coverage beyond 50 km from shore and in deep waters off the Scotian Shelf (Huettmann & Diamond 2000, Gjerdrum & Bolduc 2016). Thus, the absence of any offshore sightings in ECSAS or PIROP data indicates that GLS error is the likely cause of these offshore location estimates. Though we made efforts to smooth and average our data, these methods reduce but do not eliminate locational error (Phillips *et al.* 2004). Thus, our study may be at a scale that can demonstrate general movement patterns but not precise dispersal distances from colonies and shore. This, in addition to our relatively small sample size, indicates that our results should be treated with caution. Nonetheless, despite GLS error rates of *ca*. 200 km (Phillips *et al.* 2004, Shaffer *et al.* 2005), the persistent appearance of offshore locations among seasons and individuals in our study (even after averaging locations weekly), presents an intriguing result that this species may in fact venture further from coastlines than previously thought. Future studies with more accurate tags, such as those using Global Positioning System (GPS) (Bridge *et al.* 2011), are needed to confirm non-breeding movements and habitat use by Black Guillemots.

Black Guillemot locations from Country Island and Kent Island also overlapped during the non-breeding period. In particular, Country Island birds moved into the same areas as some Kent Island birds, although the reverse was not the case with the Kent Island birds (Fig. 2). While neighbouring seabird colonies frequently show spatial segregation during the breeding season as a result of competition (Furness & Birkhead 1984, Grémillet *et al.* 2004, Hedd *et al.* 2018), overlapping distributions during the non-breeding season have also been observed for alcids from different colonies (McFarlane Tranquilla *et al.* 2013, McFarlane Tranquilla *et al.* 2014, Ratcliffe *et al.* 2014). This overlap may be the result of a common prey resource (Cairns 1987, Nol & Gaskin 1987, Divoky *et al.* 2016, Waggitt *et al.* 2016) or birds following migration routes learned from parents that previously moved between colonies (Dearborn *et al.* 2003, McFarlane Tranquilla *et al.* 2013). Overall, various factors may influence these differences in distribution, including ice cover, prey availability, or marine productivity levels (Nol & Gaskin 1987, Prach & Smith 1992, Montevecchi *et al.* 2012, Divoky *et al.* 2016, Waggitt *et al.* 2016).

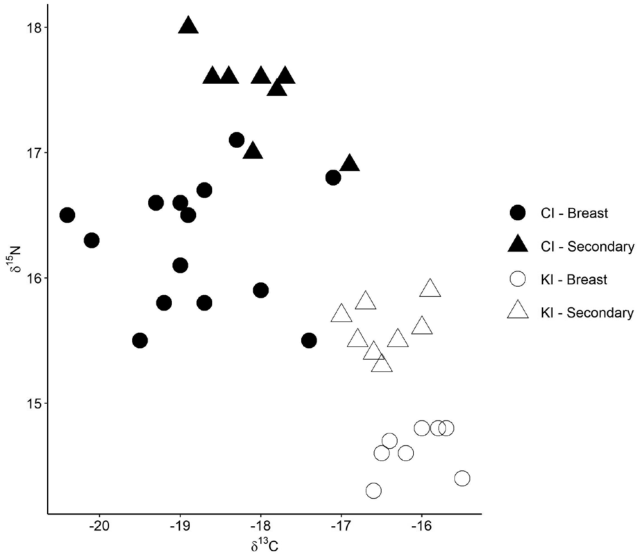

Fig. 6. Relationship between stable carbon (δ^{13}C) and stable nitrogen (δ^{15}N) isotope values in winter (breast feathers) and autumn (first secondary feathers) for Black Guillemots *Cepphus grylle* sampled on Country Island (CI), Nova Scotia and Kent Island (KI), New Brunswick in 2018.

Distributions of Black Guillemots in the Arctic during both breeding and non-breeding seasons are primarily influenced by ice cover (Bradstreet 1979, Nol & Gaskin 1987, Prach & Smith 1992, Divoky *et al.* 2016). In ice-free areas, however, guillemots are thought to remain relatively close to the colony (Brown 1985, Butler & Buckley 2002) or regularly visit it (Greenwood 1987) during the non-breeding season. There is little ice activity during winter in the Bay of Fundy, Gulf of Maine, and Scotian Shelf (Canadian Ice Service 2019), thus allowing guillemots to remain close to the breeding colony and shore. By contrast, Black Guillemots tracked with GLS from northern Alaska moved in association with ice formations to areas more than 1 000 km from their breeding site (Divoky *et al.* 2016).

The distribution of guillemots and other alcid species are also associated with prey availability (Cairns 1987, Nol & Gaskin 1987, Divoky *et al.* 2016, Waggitt *et al.* 2016) and areas of high productivity (e.g., high surface chlorophyll concentrations and surface water temperatures; Gaston *et al.* 2011, Montevecchi *et al.* 2012). Atlantic herring, cod, and sandlance, all of which are primary food sources for Black Guillemots (Nol & Gaskin 1987, Butler & Buckley 2002), are concentrated in the Bay of Fundy and Gulf of Maine (Tibbo *et al.* 1958, Scott 1980, Shackell *et al.* 1999), where Kent Island birds remain year-round and Country Island birds visit during the winter. Productivity levels on the Scotian Shelf are lowest in winter (Campbell & O'Reilly 1988) but remain high in the Bay of Fundy due to high tidal ranges and vertical mixing (Gran & Braarud 1935). Thus, Country Island birds likely moved to this area in winter following changes in prey or productivity. Likewise, the Bay of Fundy provides important winter habitat for other alcids, such as Razorbills *Alca torda* that occur in high abundance (Huettmann *et al.* 2005) and come to this area from numerous colonies (Clarke *et al.* 2010). This area also supports a variety of migratory species during the autumn (Wong *et al*. 2018). Thus, the area supports a variety of seabirds during the non-breeding period.

Age, sex, and experience can influence the distribution and movement of seabirds (Phillips *et al.* 2017). In this study, we were

TABLE 2
Hatching success (proportion of nests that hatched at least one chick) in Black Guillemots *Cepphus grylle* nests where parents were handled and tagged, handled but not tagged, or neither handled nor tagged (control), as sampled on Country Island, Nova Scotia in 2017 and 2018

Year	Treatment	*n*	Hatching success (%)	X^2	*df*	*P* value
2017	Handled and tagged	10	83.3			
	Handled but not tagged	11	54.6	3.72	2	0.16
	Control	30	80.0			
2018	Handled and tagged	4	50.0			
	Handled but not tagged	9	11.1	4.81	2	0.09
	Control	45	51.1			

unable to determine the age or experience of tracked adults, and though we collected data on sex for two individuals (both females), our sample size was too small to analyze. Thus, some variation in our data could be the result of differences in these variables. Additional tracking is required to more fully describe Black Guillemot distribution and movements during the non-breeding period in Atlantic Canada.

Stable isotopes

Our results indicated no seasonal differences in foraging location (δ^{13}C) of Black Guillemots, but we did find that foraging trophic level (δ^{15}N) is considerably higher in autumn than in winter. These results are consistent with the results of our tracking data, which showed that birds remain relatively close to the colonies (Figs. 2, 4) and do not show strong seasonal differences in distance from shore (Fig. 5). Thus, Black Guillemots sometimes change foraging trophic level (prey types) between seasons, even when they do not change foraging habitats. These results differ from alcids in other regions. For example, Cassin's Auklets *Ptychoramphus aleuticus* in British Columbia (Sorensen *et al.* 2009) and Razorbills in the North Sea (St. John Glew *et al.* 2018) had similar foraging trophic levels between seasons but differed in foraging location across seasons. However, Atlantic Puffins *Fratercula arctica* in the North Sea did not have seasonal differences in foraging locations (St. John Glew *et al.* 2018). Isotopic signatures can vary among species, diet, or location (Hobson *et al.* 1994, Quillfeldt *et al.* 2005, Bearhop *et al.* 2006, Cherel *et al.* 2006, Phillips *et al.* 2011), thus additional research on Black Guillemots and their prey in Atlantic Canada is warranted.

There were also inter-colony differences in both δ^{15}N and δ^{13}C, where Kent Island birds had lower δ^{15}N values and higher δ^{13}C values than Country Island birds. Thus, Kent Island birds foraged at lower trophic levels and in more benthic inshore waters than Country Island birds. This is consistent with the tracking data, which showed that Country Island birds spent more time at a greater distance from shore than Kent Island birds (see Figs. 2, 5). These results are also consistent with other alcid species that have inter-colony differences in foraging location (Bearhop *et al.* 2006). Additionally, birds on Country Island showed a large range in δ^{15}N (15.5‰ to 18.0‰) and δ^{13}C (−20.4‰ to −16.9‰), which indicates that there is considerable variability in trophic level and foraging location within this colony. This is consistent with the geolocation data, as Country Island birds spent time in a variety of locations (Scotian Shelf, Gulf of St. Lawrence, Bay of Fundy, Gulf of Maine) during the non-breeding period.

Overall, we observed significant differences in δ^{15}N between colonies and seasons, as well as significant differences in δ^{13}C between colonies. Discrimination factors for δ^{13}C and δ^{15}N range from 0‰–2‰ and 2‰–5‰, respectively, and differ depending on the species, tissue, and prey combination (Peterson & Fry 1987, Kelly 2000). For example, in Common Murres, the isotopic discrimination of δ^{15}N from capelin muscle to murre feathers is 3.6‰ ± 0.2‰ in breast feathers and 3.7‰ ± 0.2‰ in primary feathers; for δ^{13}C, it is 2.5‰ ± 0.2‰ in breast feathers and 1.9‰ ± 0.3‰ in primary feathers. The observed differences between seasons (δ^{15}N) and between colonies (δ^{13}C and δ^{15}N) are above the range of these discrimination factors, which suggests that despite our small sample size, Black Guillemot foraging strategies vary between colonies and seasons. However, we lack data on carbon and nitrogen isotope gradients in this region and on Black Guillemot prey species during the non-breeding period in this region. Additionally, various other factors may influence isotopic composition of Black Guillemots, such as sex (Phillips *et al.* 2011) or body condition (Hobson *et al.* 1994).

Tag effects

We found no difference in adult mass between tagged and untagged adults or between years. Further, neither δ^{13}C nor δ^{15}N values differed between tagged and untagged birds. In other alcid species, effects of tags on adult mass have been variable (Paredes *et al.* 2005, Robinson & Jones 2014), which may be attributed to differences in species, colonies, tag attachment location (back-mounted vs. leg-mounted), or the weight of the tag. We also found no effect of tags on hatching success. Although the effect of tags on alcid hatching success has not been previously examined, tags have been associated with decreased chick growth rate in Whiskered Auklets *Aethia pygmaea* (Schacter & Jones 2017) and Cassin's Auklets (Ackerman *et al.* 2004) as well as decreased fledgling success in Tufted Puffins *Fratercula cirrhata* (Whidden *et al.* 2007). By contrast, tags appeared not to affect fledgling success in Parakeet Auklets *A. psittacula* (Paredes *et al.* 2005). These differences may be due to physiological and behavioural differences in the species, such as mass, wing-loading, or migration distances (Schacter & Jones 2017). Because effects vary, species must be assessed individually in a given region (Burger & Shaffer 2008).

Our results suggest that there were no significant tagging effects on Black Guillemot adult mass or hatching success. Although not statistically significant, there appeared to be lower hatching success for birds that were handled but not tagged in both years. Our sample size and measured parameters were limited, and because birds were caught by convenience (non-random), a bird's catchability as it relates to their life experience may play a role in our results: when we arrived at the colony, we captured, banded, and tagged (handled and tagged) the first birds we could catch. Once all tags were deployed, any birds that remained on site were caught and banded (handled but not tagged); they may not have flushed during the initial disturbance because they were inexperienced. Additional research on potential handling and tagging effects on Black Guillemots is recommended.

CONCLUSION

We provide new information on the non-breeding movements of the Black Guillemot in coastal western North Atlantic. Most individuals showed moderate (< 350 km) seasonal movement away from breeding colonies and remained predominantly near shore (< 150 km) but showed a strong change in diet between autumn and winter. Black Guillemots from Country Island, Nova Scotia and Kent Island, New Brunswick were distributed in the Gulf of St. Lawrence, Scotian Shelf, Bay of Fundy, and Gulf of Maine during the non-breeding period. This research, combined with other seabird, fish, and marine mammal tracking studies, can inform marine management decisions in this region. The North Atlantic continental shelf has previously been identified as an important biological hotspot that should be protected (Montevecchi *et al.* 2012). In particular, the Bay of Fundy has high productivity levels (Gran & Braarud 1935) and is an important habitat for a variety of seabirds (Huettmann & Diamond 2000, Huettmann *et al.* 2005, Wong *et al.* 2018). Coastal areas of the Bay of Fundy are being explored for tidal energy development (Karsten *et al.* 2008), which may increase the risk of disturbance or direct harm for guillemots due to their diving and benthic foraging behaviour (Furness *et al.* 2012, Johnston *et al.* 2018). These foraging behaviours also make Black Guillemots vulnerable to oil pollution (Lieske *et al.* 2019) from continued exploration of exploitable oil and gas reserves on the Scotian Shelf (Grant *et al.* 1986) and from ships operating near shore and in the Bay of Fundy (Lieske *et al.* 2020). Thus, information on Black Guillemot distribution in Atlantic Canada can be used to inform decisions on marine spatial planning and oil spill response strategies to mitigate potential impacts of these anthropogenic activities on seabird species.

Although our sample of tracked birds was limited and may not fully represent species behaviour in this part of their range, these results provide new information on year-round movements and new insights on the life-history of this poorly studied species. Notwithstanding the relevance of the anthropogenic activities discussed above, it is noteworthy that our study and the non-breeding distribution of these populations overlap entirely with marine areas that are warming faster than most other parts of the world's oceans (Pershing *et al.* 2015). Our study occurred during a non-breeding period leading up to an atypically warm year in the region (Poppick 2018). This warming is changing fish populations and ecosystem functioning (Mills *et al.* 2013, Pershing *et al.* 2015, Scopel *et al.* 2019). Further tracking studies with more accurate devices would allow for modelling of species-habitat associations, enabling researchers to predict how this species will respond to changes in climate and habitat over time. Additional tracking studies and stable-isotope analyses of more populations over several non-breeding seasons would develop a better understanding of Black Guillemot wintering locations, habitat use, diet, and connectivity among populations in Atlantic Canada.

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REFERENCES

ACKERMAN, J.T., ADAMS, J., TAKEKAWA, J.Y. ET AL. 2004. Effects of radiotransmitters on the reproductive performance of Cassin's auklets. *Wildlife Society Bulletin* 32: 1229–1241. doi:10.2193/0091-7648(2004)032[1229:EOROTR]2.0.CO;2

ADAMS, J., SCOTT, D., MCKECHNIE, S., BLACKWELL, G., SHAFFER, S.A. & MOLLER, H. 2009. Effects of geolocation archival tags on reproduction and adult body mass of Sooty Shearwaters (*Puffinus griseus*). *New Zealand Journal of Zoology* 36: 355–366. doi:10.1080/03014220909510160

BARRON, D.G., BRAWN, J.D. & WEATHERHEAD, P.J. 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods in Ecology and Evolution* 1: 180–187. doi:10.1111/j.2041-210X.2010.00013.x

BEARHOP, S., PHILLIPS, R.A., MCGILL, R., CHEREL, Y., DAWSON, D.A. & CROXALL, J.P. 2006. Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. *Marine Ecology Progress Series* 311: 157–164. doi:10.3354/meps311157

BINDOFF, A.D., WOTHERSPOON, S.J., GUINET, C. & HINDELL, M.A. 2018. Twilight-free geolocation from noisy light data. *Methods in Ecology and Evolution* 9: 1190–1198. doi:10.1111/2041-210X.12953

BIRDS CANADA 2019a. *Important Bird Areas Canada—Grand Manan Archipelago: Grand Manan, New Brunswick.* Ottawa, Canada: Birds Canada, Nature Canada.

BIRDS CANADA 2019b. *Important Bird Areas Canada—Country Island Complex: Country Harbour/Tor Bay, Nova Scotia.* Ottawa, Canada: Birds Canada, Nature Canada.

BRADSTREET, M.S.W. 1979. Thick-billed murres and black guillemots in the Barrow Strait area, N.W.T., during spring: distribution and habitat use. *Canadian Journal of Zoology* 57: 1789–1802. doi:10.1139/z79-233

BRIDGE, E.S., THORUP, K., BOWLIN, M.S. ET AL. 2011. Technology on the Move: Recent and Forthcoming Innovations for Tracking Migratory Birds. *BioScience* 61: 689–698. doi:10.1525/bio.2011.61.9.7

BROWN, R.G.B. 1985. The Atlantic Alcidae at sea. In: NETTLESHIP, D.N. & BIRKHEAD, T.R. (Eds.) *The Atlantic Alcidae: The Evolution, Distribution and Biology of the Auks Inhabiting the Atlantic Ocean and Adjacent Water Areas.* London, UK: Academic Press

BURGER, A.E. & SHAFFER, S.A. 2008. Perspectives in Ornithology - Application of Tracking and Data-Logging Technology in Research and Conservation of Seabirds. *The Auk* 125: 253–264. doi:10.1525/auk.2008.1408

BUTLER, R.G. & BUCKLEY, D.E. 2002. Black Guillemot (*Cepphus grylle*), version 2.0. In: POOLE, A.F. & GILL, F.B. (Eds.) *The Birds of North America Online*. Ithaca, USA: Cornell Lab of Ornithology. doi:10.2173/bna.675

CAIRNS, D.K. 1987. Diet and foraging ecology of Black Guillemots in northeastern Hudson Bay. *Canadian Journal of Zoology* 65: 1257–1263. doi:10.1139/z87-196

CAMPBELL, J.W. & O'REILLY, J.E. 1988. Role of satellites in estimating primary productivity on the northwest Atlantic continental shelf. *Continental Shelf Research* 8: 179–204. doi:10.1016/0278-4343(88)90053-2

CANADIAN ICE SERVICE 2019. *Seasonal Summary: Eastern Canada, Winter 2017–2018.* Ottawa, Canada: Environment and Climate Change Canada.

CANNELL, P.F. & MADDOX, G.D. 1983. Population Change in Three Species of Seabirds at Kent Island, New Brunswick. *Journal of Field Ornithology* 54: 29–35.

CHEREL, Y., PHILLIPS, R.A., HOBSON, K.A. & MCGILL, R. 2006. Stable isotope evidence of diverse species-specific and individual wintering strategies in seabirds. *Biology Letters* 2: 301–303. doi:10.1098/rsbl.2006.0445

CLARKE, T.C.R., DIAMOND, A.W. & CHARDINE, J.W. 2010. Origin of Canadian Razorbills (*Alca torda*) Wintering in the Outer Bay of Fundy Confirmed by Radio-Tracking. *Waterbirds* 33: 541–545. doi:10.1675/063.033.0414

CWS (CANADIAN WILDLIFE SERVICE) 2019. *Eastern Canada Seabirds at Sea (ECSAS) database.* Sackville, Canada: Environment and Climate Change Canada, Canadian Wildlife Service, Atlantic Region. Information provided in response to data request on 20 February 2020.

DEARBORN, D.C., ANDERS, A.D., SCHREIBER, E.A., ADAMS, R.M.M. & MUELLER, U.G. 2003. Inter-island movements and population differentiation in a pelagic seabird. *Molecular Ecology* 12: 2835–2843. doi:10.1046/j.1365-294X.2003.01931.x

DIVOKY, G.J., DOUGLAS, D.C. & STENHOUSE, I.J. 2016. Arctic sea ice a major determinant in Mandt's black guillemot movement and distribution during non-breeding season. *Biology Letters* 12: 20160275. doi:10.1098/rsbl.2016.0275

EWINS, P.J. 1986. *The Ecology of Black Guillemots* Cepphus grylle *in Shetland.* Oxford, UK: University of Oxford.

FAYET, A.L., FREEMAN, R., SHOJI, A. ET AL. 2016. Drivers and fitness consequences of dispersive migration in a pelagic seabird. *Behavioral Ecology* 27: 1061–1072.

FIFIELD, D.A., BAKER K.D., BYRNE, R. ET AL. 2009. *Modelling Seabird Oil Spill Mortality Using Flight and Swim Behaviour.* Environmental Studies Research Funds Report No. 186. Dartmouth, Canada: Canadian Wildlife Service, Environment Canada.

FURNESS, R.W. & BIRKHEAD T.R. 1984. Seabird colony distributions suggest competition for food supplies during the breeding season. *Nature* 311: 655–656. doi:10.1038/311655a0

FURNESS, R.W., WADE, H.M., ROBBINS, A.M.C. & MASDEN, E.A. 2012. Assessing the sensitivity of seabird populations to adverse effects from tidal stream turbines and wave energy devices. *ICES Journal of Marine Science* 69: 1466–1479. doi:10.1093/icesjms/fss131

GASTON, A.J., SMITH, P.A., MCFARLANE TRANQUILLA, L. ET AL. 2011. Movements and wintering areas of breeding age Thick-billed Murre *Uria lomvia* from two colonies in Nunavut, Canada. *Marine Biology* 158: 1929–1941. doi:10.1007/s00227-011-1704-9

GJERDRUM, C. & BOLDUC, F. 2016. Non-breeding distribution of Herring Gull (*Larus argentatus*) and Great Black-backed Gull (*Larus marinus*) in eastern Canada from ship-based surveys. *Waterbirds* 39: 202–219.

GRAN, H.H. & BRAARUD, T. 1935. A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine (including observations on hydrography, chemistry and turbidity). *Journal of the Biological Board of Canada* 1: 279–467. doi:10.1139/f35-012

GRANT, A.C., MCALPINE, K.D. & WADE, J.A. 1986. The Continental Margin of Eastern Canada: Geological Framework and Petroleum Potential. In: HALBOUTY, M.T. (Ed.) *Future Petroleum Provinces of the World.* Volume 40. Tulsa, USA: American Association of Petroleum Geologists. doi:10.1306/M40454

GREENWOOD, J.G. 1987. Winter visits by Black Guillemots *Cepphus grylle* to an Irish breeding site. *Bird Study* 34: 135–136. doi:10.1080/00063658709476949

GRÉMILLET, D., DELL'OMO, G., RYAN, P.G., PETERS, G., ROPERT-COUDERT, Y. & WEEKS, S.J. 2004. Offshore diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS tracking of Cape gannets from neighbouring colonies. *Marine Ecology Progress Series* 268: 265–279. doi:10.3354/meps268265

HEDD, A., MONTEVECCHI, W.A., MCFARLANE TRANQUILLA, L. ET AL. 2011. Reducing uncertainty on the Grand Bank: tracking and vessel surveys indicate mortality risks for common murres in the North-West Atlantic. *Animal Conservation* 14: 630–641. doi:10.1111/j.1469-1795.2011.00479.x

HEDD, A., POLLET, I.L., MAUCK, R.A. ET AL. 2018. Foraging areas, offshore habitat use, and colony overlap by incubating Leach's storm-petrels *Oceanodroma leucorhoa* in the Northwest Atlantic. *PLoS One* 13: e0194389. doi:10.1371/journal.pone.0194389

HILL, R.D. 1994. Theory of Geolocation by Light Levels. In: LE BOEUF, J. & LAWS, R.M. (Eds.) *Elephant Seals: Population Ecology, Behavior, and Physiology*. Berkeley, USA: University of California Press.

HILL, R.D. & BRAUN, M.J. 2001. Geolocation by Light Level—The Next Step: Latitude. In: SIBERT, J. & NIELSEN, J. (Eds.) *Electronic Tagging and Tracking in Marine Fisheries*. Dordrecht, Netherlands: Springer Netherlands.

HOBSON, K.A. & BOND, A.L. 2012. Extending an indicator: year-round information on seabird trophic ecology from multiple-tissue stable-isotope analyses. *Marine Ecology Progress Series* 461: 233–243. doi:10.3354/meps09835

HOBSON, K.A. & CLARK, R.G. 1992. Assessing avian diets using stable isotopes I: Turnover of ^{13}C in tissues. *The Condor* 94: 181–188.

HOBSON, K.A., PIATT, J.F. & PITOCCHELLI, J. 1994. Using stable isotopes to determine seabird trophic relationships. *Journal of Animal Ecology* 63: 786–798. doi:10.2307/5256

HUETTMANN, F. & DIAMOND, A.W. 2000. Seabird migration in the Canadian northwest Atlantic Ocean: moulting locations and movement patterns of immature birds. *Canadian Journal of Zoology* 78: 624–647. doi:10.1139/z99-239

HUETTMANN, F., DIAMOND, A.W., DALZELL, B. & MACINTOSH, K. 2005. Winter distribution, ecology and movements of Razorbills *Alca torda* and other auks in the outer Bay of Fundy, Atlantic Canada. *Marine Ornithology* 33: 161–171.

JOHNSTON, D.T., FURNESS, R.W., ROBBINS, A.M.C., TYLER, G., TAGGART, M.A. & MASDEN, E.A. 2018. Black guillemot ecology in relation to tidal stream energy generation: An evaluation of current knowledge and information gaps. *Marine Environmental Research* 134: 121–129. doi:10.1016/j.marenvres.2018.01.007

KARSTEN, R.H., MCMILLAN, J.M., LICKLEY, M.J. & HAYNES, R.D. 2008. Assessment of tidal current energy in the Minas Passage, Bay of Fundy. *Journal of Power and Energy* 222: 493–507. doi:10.1243/09576509JPE555

KELLY, J.F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology* 78: 1–27.

LASCELLES, B.G., LANGHAM, G.M., RONCONI, R.A. & REID, J.B. 2012. From hotspots to site protection: Identifying Marine Protected Areas for seabirds around the globe. *Biological Conservation* 156: 5–14. doi:10.1016/j.biocon.2011.12.008

LIESKE, D.J., MCFARLANE TRANQUILLA, L., RONCONI, R.A. & ABBOTT, S. 2019. Synthesizing expert opinion to assess the at-sea risks to seabirds in the western North Atlantic. *Biological Conservation* 233: 41–50. doi:10.1016/j.biocon.2019.02.026

LIESKE, D.J., MCFARLANE TRANQUILLA, L., RONCONI, R.A. & ABBOTT, S. 2020. "Seas of risk": Assessing the threats to colonial-nesting seabirds in Eastern Canada. *Marine Policy* 115: 103863. doi:10.1016/j.marpol.2020.103863

MCFARLANE TRANQUILLA, L.A., MONTEVECCHI, W.A., FIFIELD, D.A. ET AL. 2014. Individual winter movement strategies in two species of murre (*Uria* spp.) in the Northwest Atlantic. *PLoS One* 9: e90583. doi:10.1371/journal.pone.0090583

MCFARLANE TRANQUILLA, L.A., MONTEVECCHI, W.A., HEDD, A. ET AL. 2013. Multiple-colony winter habitat use by murres *Uria* spp. in the Northwest Atlantic Ocean: implications for marine risk assessment. *Marine Ecology Progress Series* 472: 287–303. doi:10.3354/meps10053

MILLS, K.E., PERSHING, A., BROWN, C. ET AL. 2013. Fisheries management in a changing climate: Lessons from the 2012 ocean heat wave in the Northwest Atlantic. *Oceanography* 26: 191–195.

MONTEVECCHI, W.A., HEDD, A., MCFARLANE TRANQUILLA, L. ET AL. 2012. Tracking seabirds to identify ecologically important and high risk marine areas in the western North Atlantic. *Biological Conservation* 156: 62–71. doi:10.1016/j.biocon.2011.12.001

NOL, E. & GASKIN, D.E. 1987. Distribution and movements of Black Guillemots (*Cepphus grylle*) in coastal waters of the southwestern Bay of Fundy, Canada. *Canadian Journal of Zoology* 65: 2682–2689. doi:10.1139/z87-407

PAREDES, R., JONES, I.L. & BONESS, D.J. 2005. Reduced parental care, compensatory behaviour and reproductive costs of thick-billed murres equipped with data loggers. *Animal Behaviour* 69: 197–208. doi:10.1016/j.anbehav.2003.12.029

PARSONS, M., MITCHELL, I., BUTLER, A. ET AL. 2008. Seabirds as indicators of the marine environment. *ICES Journal of Marine Science* 65: 1520–1526. doi:10.1093/icesjms/fsn155

PERSHING, A.J, ALEXANDER, M.A., HERNANDEZ, C.M. ET AL. 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science* 350: 809–812.

PETERSON, B.J. & FRY, B. 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* 18: 293–320.

PHILLIPS, R.A., BEARHOP, S., MCGILL, R.A.R. & DAWSON, D.A. 2009. Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabirds during the non-breeding period. *Oecologia* 160: 795–806. doi:10.1007/s00442-009-1342-9

PHILLIPS, R.A., LEWIS, S., GONZÁLEZ-SOLÍS, J. & DAUNT, F. 2017. Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. *Marine Ecology Progress Series* 578: 117–150. doi:10.3354/meps12217

PHILLIPS, R.A., MCGILL, R.A.R., DAWSON, D.A. & BEARHOP, S. 2011. Sexual segregation in distribution, diet and trophic level of seabirds: insights from stable isotope analysis. *Marine Biology* 158: 2199–2208. doi:10.1007/s00227-011-1725-4

PHILLIPS, R.A., SILK, J.R.D., CROXALL, J.P., AFANASYEV, V. & BRIGGS, D.R. 2004. Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series* 266: 265–272. doi:10.3354/meps266265

PHILLIPS, R.A., XAVIER, J.C. & CROXALL, J.P. 2003. Effects of satellite transmitters on albatrosses and petrels. *The Auk* 120: 1082–1090. doi:10.1093/auk/120.4.1082

POPPICK, L. 2018. Why is the Gulf of Maine warming faster than 99% of the ocean? *Eos* 99: doi:10.1029/2018EO109467. Published online on 12 November 2018.

PRACH, R.W. & SMITH, A.R. 1992. Breeding distribution and numbers of Black Guillemots in Jones Sound, N.W.T. *Arctic* 45: 111–114. doi:10.14430/arctic1380

PYLE, P. 2008. *Identification Guide to North American Birds.* Point Reyes Station, USA: Slate Creek Press.

QUILLFELDT, P., MCGILL, R.A.R. & FURNESS, R.W. 2005. Diet and foraging areas of Southern Ocean seabirds and their prey inferred from stable isotopes: review and case study of Wilson's storm-petrel. *Marine Ecology Progress Series* 295: 295–304. doi:10.3354/meps295295

R DEVELOPMENT CORE TEAM 2017. R: *A language and environment for statistical computing.* Vienna, Austria: The R Foundation for Statistical Computing.

RABINER, L.R. 1989. A tutorial on hidden Markov models and selected applications in speech recognition. *Proceedings of the IEEE* 77: 257–286.

RATCLIFFE, N., CROFTS, S., BROWN, R. ET AL. 2014. Love thy neighbour or opposites attract? Patterns of spatial segregation and association among crested penguin populations during winter. *Journal of Biogeography* 41: 1183–1192. doi:10.1111/jbi.12279

ROBINSON, J.L. & JONES, I.L. 2014. An experimental study measuring the effects of a tarsus-mounted tracking device on the behaviour of a small pursuit-diving seabird. *Behaviour* 151: 1799–1826.

RONCONI, R.A. & ST. CLAIR, C.C. 2002. Management options to reduce boat disturbance on foraging black guillemots (*Cepphus grylle*) in the Bay of Fundy. *Biological Conservation* 108: 265–271. doi:10.1016/S0006-3207(02)00126-X

RONCONI, R.A. & WONG, S.N.P. 2003. Estimates of changes in seabird numbers in the Grand Manan Archipelago, New Brunswick, Canada. *Waterbirds* 26: 462–472.

SCHACTER, C.R. & JONES, I.L. 2017. Effects of geolocation tracking devices on behavior, reproductive success, and return rate of *Aethia* auklets: An evaluation of tag mass guidelines. *The Wilson Journal of Ornithology* 129: 459–468.

SCOPEL, L., DIAMOND, A., KRESS, S. & SHANNON, P. 2019. Varied breeding response of seabirds to a regime shift in prey base in the Gulf of Maine. *Marine Ecology Progress Series* 626: 177–196.

SCOTT, J.S. 1980. Occurrence of pollock, *Pollachius virens*, and sand lance, *Ammodytes* sp., larvae in the Bay of Fundy. *Journal of Northwest Atlantic Fishery Science* 1: 45–48.

SHACKELL, N.L., FRANK, K.T., PETRIE, B., BRICKMAN, D. & SHORE, J. 1999. Dispersal of early life stage haddock (*Melanogrammus aeglefinus*) as inferred from the spatial distribution and variability in length-at-age of juveniles. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 2350–2361.

SHAFFER, S.A., TREMBLAY, Y., AWKERMAN, J.A. ET AL. 2005. Comparison of light- and SST-based geolocation with satellite telemetry in free-ranging albatrosses. *Marine Biology* 147: 833–843. doi:10.1007/s00227-005-1631-8

SORENSEN, M.C., HIPFNER, J.M., KYSER, T.K. & NORRIS, D.R. 2009. Carry-over effects in a Pacific seabird: stable isotope evidence that pre-breeding diet quality influences reproductive success. *Journal of Animal Ecology* 78: 460–467. doi:10.1111/j.1365-2656.2008.01492.x

ST. JOHN GLEW, K., WANLESS, S., HARRIS, M.P. ET AL. 2018. Moult location and diet of auks in the North Sea inferred from coupled light-based and isotope-based geolocation. *Marine Ecology Progress Series* 599: 239–251. doi:10.3354/meps12624

TAKAHASHI, A., ITO, M., SUZUKI, Y. ET AL. 2015. Migratory movements of rhinoceros auklets in the northwestern Pacific: connecting seasonal productivities. *Marine Ecology Progress Series* 525: 229–243. doi:10.3354/meps11179

TIBBO, S.N., LEGARÉ, J.E.H., SCATTERGOOD, L.W. & TEMPLE, R.F. 1958. On the occurrence and distribution of larval herring (*Clupea harengus* L.) in the Bay of Fundy and the Gulf of Maine. *Journal of the Fisheries Research Board of Canada* 15: 1451–1469. doi:10.1139/f58-078

TROTTIER-PAQUET, M. & ROCK, J. 2018. *Country Island Seabird Monitoring and Tern Restoration Program: Annual Report 2018 (Year 21).* Unpublished report. Nova Scotia, Canada: Canadian Wildlife Service, Environment and Climate Change Canada.

VANDENABEELE, S., WILSON, R.P. & GROGAN, A. 2011. Tags on seabirds: How seriously are instrument-induced behaviours considered? *Animal Welfare* 20: 559–571.

WAGGITT, J.J., CAZENAVE, P.W., TORRES, R., WILLIAMSON, B.J. & SCOTT, B.E. 2016. Quantifying pursuit-diving seabirds' associations with fine-scale physical features in tidal stream environments. *Journal of Applied Ecology* 53: 1653–1666. doi:10.1111/1365-2664.12646

WHIDDEN, S.E., WILLIAMS, C.T., BRETON, A.R. & BUCK, C.L. 2007. Effects of transmitters on the reproductive success of Tufted Puffins. *Journal of Field Ornithology* 78: 206–212. doi:10.1111/j.1557-9263.2007.00103.x

WINN, H.E. 1950. The Black Guillemots of Kent Island, Bay of Fundy. *The Auk* 67: 477–485. doi:10.2307/4081088

WONG, S.N.P., RONCONI, R.A. & GJERDRUM, C. 2018. Autumn at-sea distribution and abundance of phalaropes *Phalaropus* and other seabirds in the lower Bay of Fundy, Canada. *Marine Ornithology* 46: 1–10.

WOTHERSPOON, S., SUMNER, M., & LISOVSKI, S. 2016. *TwGeos: Basic data processing for light-level geolocation archival tags.* Version 0.0.1. San Francisco, USA: GitHub.

YODER, J.A., ATKINSON, L.P., BISHOP, S.S., HOFMANN, E.E. & LEE, T.N. 1983. Effect of upwelling on phytoplankton productivity of the outer southeastern United States continental shelf. *Continental Shelf Research* 1: 385–404. doi:10.1016/0278-4343(83)90004-3