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Body size affects individual winter foraging strategies of thick-billed murres in the Bering Sea

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Summary

1. Foraging and migration often require different energetic and movement strategies. Though not readily apparent, constraints during one phase might influence the foraging strategies observed in another. For marine birds that fly and dive, body size constraints likely present a trade-off between foraging ability and migration as smaller bodies reduce flight costs, whereas larger bodies are advantageous for diving deeper.

2. This study examines individual wintering strategies of deep diving thick-billed murres (*Uria lomvia*) breeding at three colonies in the south-eastern Bering Sea: St Paul, St George and Bogoslof. These colonies, arranged north to south, are located such that breeding birds forage in a gradient from shelf to deep-water habitats.

3. We used geolocation time-depth recorders and stable isotopes from feathers to determine differences in foraging behaviour and diet of murres during three non-breeding periods, 2008–2011. Body size was quantified by a principal component analysis (wing, culmen, head + bill and tarsus length). A hierarchical cluster analysis identified winter foraging strategies based on individual movement, diving behaviour and diet (inferred from stable isotopes).

4. Structural body size differed by breeding island. Larger birds from St Paul had higher wing loading than smaller birds from St George. Larger birds, mainly from St Paul, dove to deeper depths, spent more time in the Bering Sea, and likely consumed higher trophic-level prey in late winter. Three winter foraging strategies were identified. The main strategy, employed by small birds from all three breeding colonies in the first 2 years, was characterized by high residency areas in the North Pacific south of the Aleutians and nocturnal diving. In contrast, 31% of birds from St Paul remained in the Bering Sea and foraged mainly during the day, apparently feeding on higher trophic-level prey. Throat feather stable isotopes indicated that individuals exhibited flexibility in the use of this colony-specific foraging strategy. The third strategy only occurred in 2010/2011, when birds dove more and deeper, suggesting limited prey resources.

5. Foraging strategies partitioned with respect to annual differences, presumably in response to shifts in distribution of prey, and were linked to body size. The presence of a colony-specific wintering strategy suggests the potential for overwinter survival differences between these populations.

Key-words: Bering Sea, body size, foraging strategies, geolocation, local adaptation, marine habitats, stable isotopes, *Uria lomvia*, winter migration

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Introduction

Both migration and niche specialization can evolve in response to resource limitation (Chase & Leibold 2003; Milner-Gulland, Fryxell & Sinclair 2011). Within populations, individual foraging strategies can reduce competition; however, changing environmental conditions and subsequent responses of prey resources can seasonally alter the relative efficiency of particular foraging strategies. The use of individual foraging strategies, though widespread across taxa (Bolnick *et al.* 2003), appears to be especially common in diving marine predators (Hoelzel, Dorsey & Stern 1989; Kato *et al.* 2000; Tremblay & Cherel 2000; Tinker *et al.* 2007; Woo *et al.* 2008; Weise, Harvey & Costa 2010; Kim *et al.* 2012). Many of these predators also make extended seasonal migrations (Bost *et al.* 2009; Block *et al.* 2011; Gaston *et al.* 2011). The temporal scale of studies investigating individual foraging strategies varies widely (breeding season, migration, multiple years) and influences both the types of strategies observed and how they are quantified. Seasonal changes in available prey resources, particularly shifts in prey depth as well as resource utilization in a new habitat, may alter how individuals forage (Sims *et al.* 2005; Harding *et al.* 2013). Long time frames are necessary to understand how individuals are able to adjust foraging behaviour to changing conditions while fulfilling life-history needs, especially in species that appear to employ specialized predatory strategies.

Body size is a fundamental characteristic that influences life-history traits including animal movements, reproduction, energy requirements and longevity (Peters 1983; Schmidt-Nielsen 1984). In marine predators, body size constrains behaviours as the physiology of diving and flying are strongly related to allometric relationships (Costa 1991; Costa & Shaffer 2012). In particular, diving–flying seabirds face body size constraints in two modes of movement. Larger body sizes generally equate to enhanced diving performance, where durations are longer and depths are deeper (Burger 1991; Boyd & Croxall 1996). Additionally, wings with reduced surface area are better for propulsion underwater (Pennycuik 2008). Large bodies and small wings are not, however, efficient for flying and result in high wing loading, high flight speeds and greater flapping rates to stay aloft (Pennycuik 2008). Within species, body size differences arise through a number of mechanisms, including ontogeny, sexual selection, nutrition and local adaptations (Bolnick & Doebeli 2003; Millien *et al.* 2006; Fairbairn 2010). Within flying–diving birds, differences in body size can facilitate niche partitioning and diet specialization between size classes (Wanless & Harris 1991; Paredes *et al.* 2008; Ratcliffe *et al.* 2013) or result from local adaptations to environmental conditions around breeding colonies (e.g. Hilton *et al.* 2000; Cook *et al.* 2013).

For flying–diving seabirds, the dual use of specialized locomotion through two mediums has required functional

compromises that may vary in importance during breeding and migration. Migration necessitates relatively large-scale movements outside of home ranges and appears to be important in flying–diving seabird life histories (e.g. Gaston *et al.* 2011; Guilford *et al.* 2011); therefore, body size also influences migratory ability and strategies, both through mode of locomotion and through how animals fuel migrations (Milner-Gulland, Fryxell & Sinclair 2011). Thick-billed murres (*Uria lomvia*) are at the extreme of this trade-off, physiologically adapted to dive to extreme depths for their body size (up to 207 m; see Results), with lower than predicted costs, but with flight costs that are the highest yet recorded (0.83 J N m^{-1} ; Elliott *et al.* 2013). Regardless, some birds make foraging trips of up to 70 km during breeding (Harding *et al.* 2013) and migrate from High Arctic colonies to lower latitudes for winter (Gaston *et al.* 2011; Fort *et al.* 2013; McFarlane Tranquilla *et al.* 2013). Murres are adaptable predators and adjust their diving behaviour relative to ocean stratification, prey species, and prey patch depth and density (Elliott *et al.* 2008; Takahashi *et al.* 2008; Benoit-Bird *et al.* 2011). Individual learning and experience are likely important for successful predatory strategies, as these long-lived birds employ extended parental care and can specialize on prey species over many breeding seasons (Woo *et al.* 2008).

In this study, we tracked birds during the non-breeding period belonging to the largest bodied subspecies of thick-billed murre (*U. l. arra*, Pallas, 1811), breeding at three colonies along a north–south transect in the south-eastern Bering Sea. Metrics of spatial distributions, diving behaviour and diet data inferred from stable isotopes of feathers were used to identify migratory foraging strategies and investigated in relation to body size. We hypothesized that body size differences, between sexes and colonies, constrain individual wintering strategies of thick-billed murres.

Materials and methods

The Pribilof Islands, with St Paul ($57^{\circ}10'N$ $170^{\circ}17'W$) to the north and St George ($56^{\circ}34'N$ $169^{\circ}36'W$) ~ 80 km to the south, are situated on the edge of the shallow continental shelf in the south-eastern Bering Sea at the limit of winter sea ice extent, while ~ 315 km to the south, Bogoslof Island ($53^{\circ}55'N$ $168^{\circ}02'W$) is surrounded by deep waters that remain ice free. At these three colonies, chick-rearing thick-billed murres (hereafter murres) were captured off ledges using a telescoping noose pole; at recapture, some failed breeders were caught with foot snares. A combined geolocation and time-depth logger (LAT2500, 3.6 g; Lotek Wireless Inc., Newmarket, ON, Canada), weighing 0.3% of average murre body mass ($n = 148$, $1058 \pm \text{SD } 112$ g), was deployed attached to leg bands during July of 2008–2010, at St Paul ($n = 13/25/19$ per year, respectively), St George ($n = 15/16/15$, respectively) and at Bogoslof ($n = 15$ in 2008 only). Additional birds used in overwinter survival estimates and for isotope analysis were deployed with a time-depth logger in 2010/11 (LAT1500, 3.4 g, St Paul $n = 10$, St George $n = 12$). Blood samples were col-

lected from each bird for molecular sexing (Fridolfsson & Ellegren 1999). To examine for logger effects, (i) body mass at recapture of individual murres deployed with loggers was compared to mass at deployment and (ii) body mass was compared between chick-rearing birds retrieved with loggers (2009 and 2010) and birds without using ANOVA and including sex, colony and interaction terms in the model.

A principal component analysis (PCA) integrated scaled body size metrics measured at deployment (head+bill, culmen, tarsus and natural wing chord). The first principal component (PC1), representing 51.4% of the variance, was retained for comparison with foraging strategies as the other principal components had eigenvalues <1 (Table S1.1, Supporting Information); PC1 was significantly positively correlated with body mass ($r^2 = 0.441$, $P < 0.001$). In 2011 only, we measured wing area using wing tracings to calculate wing loading (mass/wing area) (Shaffer, Weimerskirch & Costa 2001; Pennycuik 2008). To investigate the association of body size with foraging behaviour, PC1 was regressed against the metrics of foraging used to determine migratory strategies (sex was included as a fixed effect; however, colony was not).

MIGRATORY STRATEGIES

To process locations calculated by the geolocation loggers (Ekstrom 2004), we used a generalized additive model (GAM) with thin plate regression splines to separately smooth both latitude and longitude over time (Mosbech *et al.* 2011). This allowed for both short and rapid long distance changes in location and provided tentative estimations of location during the equinox periods. Full tracks are presented; however, residency and associated behaviour analysis was limited to October through February. We decided that the GAM approach was warranted, as there was a high degree of error in the tag-derived geolocations, likely due to periods when the sensor was obscured. For longitude, we allowed gamma to remain at the default 1 to prevent over-smoothing, while the gamma for latitude was adjusted to 1.4 (Mosbech *et al.* 2011). Daily locations were then predicted using the GAM output.

The cumulative amount of time an individual animal spent within a circle of constant radius around each location, or residency time (Barraquand & Benhamou 2011), was calculated along each track. Ideally, this radius would be based on a biologically relevant characteristic, such as sensory perception, but in our case, we chose a radius (60 km) roughly equivalent to the standard error of the GAM models for latitude ($\pm 0.66^\circ$) and longitude ($\pm 0.53^\circ$). Because murres spent long periods of time in localized areas, we used a temporal step length of 1 day. Areas of high residency were identified as the upper quartile of each individual's residency times (Torres *et al.* 2011); the percentage of these locations in the Bering Sea versus south of the Aleutians for each individual was then calculated as a metric of habitat use. The minimum convex hull area and maximum distance from the colony of high residency locations were used to determine individual spatial patterns and area use.

Loggers recorded pressure conditionally every minute below 5 dBar, equivalent to 5 m. Average dive durations during the breeding season range from 89 to 120 s (Paredes *et al.* 2008), suggesting our sampling rate likely provided 1–2 samples per dive; however, short shallow dives could have been missed. Loggers independently recorded daily maximum dive depth. Sunrise and sunset times were determined from geolocations and

matched to dive records to identify dives as day or night ('suncycle', air-sea toolbox 2.0). Dive bout end criteria were calculated for each individual dive record using maximum-likelihood estimates from a mixture of a fast (successive dives) and a slow (successive bouts) random Poisson processes (DIVEMOVE 1.3.4; Luque & Guinet 2007). For the resolution of this data set, dive bouts concluded when 25.7 ± 3.1 min (\pm SD, $n = 80$) transpired without a dive.

For $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope analysis, we sampled breast feathers grown in the autumn and throat feathers from breeding plumage grown between February and March (Gaston & Jones 1998). Feathers were analysed using a Carbo-Elba elemental analyser interfaced with a Finnigan Delta Plus XP mass spectrometer (Light Stable Isotope Lab, UCSC). Measurement precision (standard deviation), based on within-run replicates of the laboratory standard (pugel), was 0.13% for $\delta^{13}\text{C}$ and 0.14% for $\delta^{15}\text{N}$.

Migration foraging strategies were identified on the basis of individual spatial distributions, diving behaviour and feather stable isotope values. Standard deviations of diving parameters were included to account for temporal variation. A PCA was run on the correlation matrix of scaled parameters (Lé, Josse & Husson 2008). Eight PCs, accounting for 78% of the variance (Table S1.2, Supporting Information), were loaded into a hierarchical clustering algorithm using Ward's method and Euclidean distances to build the tree. Clusters were determined by minimizing inertia gain between potential clusters (Lé, Josse & Husson 2008). *Post hoc*, cluster composition was tested in relationship to body size (PC1) using ANOVA, and colony, sex, year and breeding status at recapture (attending egg or chick vs. failed) using chi-squares. To look at temporal variability in foraging effort within clusters, per cent time diving at night was regressed against the fraction of the moon illuminated (<http://aa.usno.navy.mil/data/docs/MoonFraction.php>). Likewise, stable isotope values from the two feather tracks and seasonal changes in diving behaviour were tested for differences within strategies using paired *t*-tests.

All data processing and spatial analysis were conducted using MATLAB (The Mathworks, Natick, MA, USA). All statistical tests were done in R 3.0.0 (R Development Core Team, 2013). Significance was set to $P < 0.05$. Means are \pm standard error except where indicated.

Results

Overall, 84% of logger-tagged birds were resighted each year (St George: 2009 = 80%, 2010 = 65%, 2011 = 85%; St Paul: 2009 = 92%, 2010 = 80%, 2011 = 84%; Bogoslof: 2009 = 93%). Logger recovery rates were 68% on the Pribilofs and 93% on Bogoslof. Logger failures were common; however, 74 tracks and 83 dive records of various lengths were obtained, resulting in full data sets for 49 individuals (St Paul = 29, St George = 14, Bogoslof = 6). There was no significant difference in body mass between deployment and recapture for all birds that carried a logger (paired *t*-test = -0.584 , $P = 0.561$, $n = 105$), but in 2010, birds retrieved with loggers, attending chicks, were significantly lighter than control birds ($F_{1,100} = 7.73$, $P = 0.007$; Logger = 1043 ± 24 g, $n = 14$; Control = 1068 ± 12 g, $n = 94$); interaction terms were not significant ($P > 0.05$).

BODY SIZE

Murres from St Paul had higher body mass and wing loading than murres from St George, whereas measurements of murres from Bogoslof overlapped with both colonies, but St Paul murres were still heavier (Table 1, Table S1.3, Supporting Information). Significant sexual size dimorphism was apparent, as males were heavier and with larger structural size (Table 1). Body size (PC1) differed by colony ($F_{2,49} = 10.30$, $P < 0.001$; Table 1) and sex ($F_{1,49} = 10.03$, $P = 0.003$; Table 1). Using linear models with body size and sex as factors, body size had a significant negative relationship to daytime dive depth ($F_{1,51} = 9.49$, $r^2 = 0.140$, $P = 0.003$; Fig. 1a) and bout depth ($F_{1,51} = 12.77$, $r^2 = 0.185$, $P < 0.001$), and a positive relationship to throat feather $\delta^{15}\text{N}$ ($F_{1,51} = 7.04$, $r^2 = 0.104$, $P = 0.011$) and $\delta^{13}\text{C}$ ($F_{1,51} = 15.11$, $r^2 = 0.213$, $P < 0.001$; Fig. 1b). Larger birds were more likely to have high residency locations in the Bering Sea than south of the Aleutian Islands ($F_{1,63} = -2.135$, $P = 0.037$, $n = 64$; Fig. 1c). Sex differences were found in breast feather $\delta^{15}\text{N}$ ($\sigma = 16.07 \pm 0.22\%$, $\varphi = 16.74 \pm 0.11\%$, $F_{1,51} = 7.33$, $P = 0.009$), maximum distance of high residency locations ($\sigma = 184 \pm 6.86$ km, $\varphi = 205 \pm 7.12$ km, $F_{1,51} = 4.55$, $P = 0.038$) and per cent time diving at night ($\sigma = 6.7 \pm 0.69\%$, $\varphi = 10 \pm 1.21\%$, $F_{1,51} = 6.03$, $P = 0.018$).

COLONY DIFFERENCES IN WINTER DISTRIBUTIONS

Murres predominantly wintered in the southeastern Bering Sea and areas in the North Pacific south of the Aleutian Islands (Fig. 2). A few birds travelled away from common wintering areas; three birds from St Paul moved into the western Bering Sea, while seven birds from Bogoslof and St George travelled eastward into the Gulf of Alaska (Fig. 2). Murres from St George and Bogoslof largely left the Bering Sea from November through January, while 88% of birds from St Paul spent some of this time in the Bering Sea.

MIGRATION STRATEGIES

Overall, 19 variables contributed significantly to the cluster analysis and three migration foraging strategies were identified (Table 2, Table S1.4, Supporting Information). The first cluster was characterized by low throat feather $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ and birds dove to shallow dive depths more often at night; these birds spent the least amount of time in the Bering Sea (Fig. 3a). This cluster was termed ‘shallow night divers’ (Cluster SN). Individuals in the second cluster had the highest values for throat feather $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Table 2). These birds spent the majority of their time in the Bering Sea (Fig. 3a). They dove the least at night, diving deeper, mainly during daytime; therefore, this cluster was termed ‘deep day divers’ (Cluster DD). Individuals in the third cluster had low $\delta^{15}\text{N}$ values from throat feathers, spent the most time diving, particularly at

Table 1. Morphometric comparison of thick-billed murres (*Uria lomvia algae*) from colonies in the southeastern Bering Sea

	St Paul (P)		St George (G)		Bogoslof (B)		Colony comparison
	σ (39)	φ (36)	σ (53)	φ (29)	σ (17)	φ (15)	
Body Mass (g)	1184 ± 16	1106 ± 16	998 ± 8.4	960 ± 12.1	1038 ± 17.7	1003 ± 13.9	P>B=G
Culmen (mm)	42.8 ± 0.4	41.6 ± 0.3	41.1 ± 0.3	39.8 ± 0.4	42.1 ± 0.5	40.1 ± 0.5	P>G, P=B, G=B
Head+bill (mm)	117.1 ± 0.5	113.7 ± 0.4	112.0 ± 0.5	109.9 ± 0.5	114.9 ± 0.7	111.1 ± 0.9	P>G, P=B, G=B
Tarsus (mm)	40.7 ± 0.3	39.0 ± 0.3	38.9 ± 0.2	37.8 ± 0.2	40.1 ± 0.3	38.9 ± 0.65	P>G, P=B, G=B
Wing (mm)	227 ± 1.0	226 ± 0.8	223 ± 0.8	222 ± 0.7	223 ± 1.7	224 ± 1.3	P>G, P=B, G=B
Wing Area (cm ²) ^a	719.4 ± 9.9	708.1 ± 17.7	679.5 ± 10.1	647.6 ± 20.5	—	—	P>G
Wing Loading (Nm ²) ^a	163.6 ± 2.8	165.2 ± 5.2	147.1 ± 2.3	140.7 ± 2.7	—	—	P>G
Body Size (PC1) ^b	1.17 ± 0.33	0.22 ± 0.25	-0.66 ± 0.37	-1.85 ± 0.36	-0.166 ± 0.76	-1.79 ± 0.63	P>G
					SDD	SDD	
					4.27	4.27	3.39
					2.88	3.27	5.00
					3.09	1.91	3.42
					4.35	2.91	3.08
					0.44	0.45	-0.45
					1.60	4.93	—
					-0.96	4.57	—
					—	—	—

Bolded sexual size dimorphism (SSD) values indicate sexes are significantly different (SSD = (male-female)/female × 100). Three-way colony comparisons are results of *t*-tests. Sample sizes are indicated in parentheses. Means ± SE.

^aSt Paul σ (7), φ (8); St George σ (12), φ (5).

^bSt Paul σ (12), φ (21); St George σ (11), φ (3); Bogoslof σ (3), φ (3).

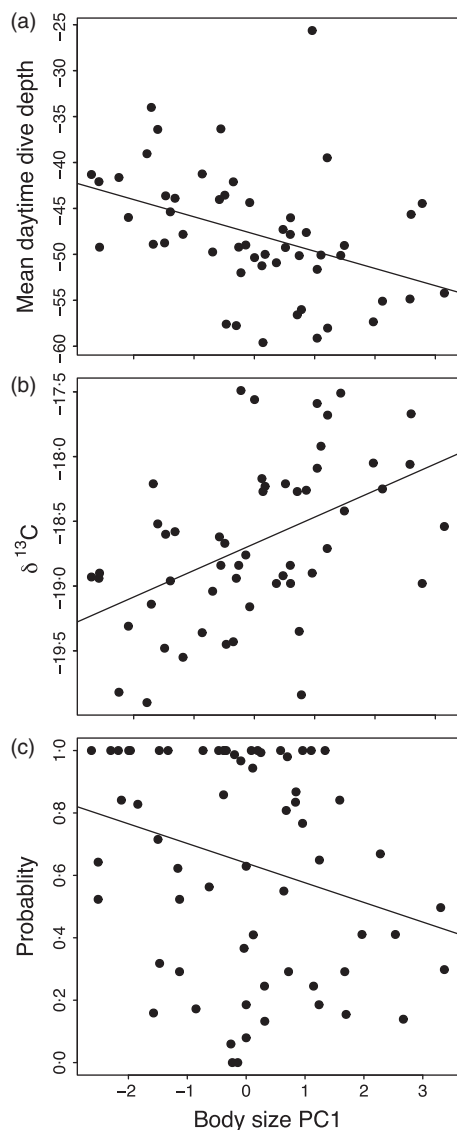


Fig. 1. Relationship between body size of thick-billed murres (PC1 of culmen, head+bill, tarsus and wing length) and (a) mean daytime diving depth, (b) throat feather $\delta^{13}\text{C}$ (%) and (c) logistic regression of proportion of occurrence in the Bering Sea (0) versus in the North Pacific south of the Aleutians (1).

night, similar to Cluster HF but had longer and more variable dive bouts (Table 2); therefore, this cluster was termed 'high-frequency divers' (Cluster HF). Like Cluster SN, spatial distributions of Cluster HF were largely outside of the Bering Sea along the southern side of the Aleutian Islands (Fig. 3a). Maximum dive depth did not contribute to the three clusters, but the deepest dive recorded was 207 m.

The assignment of individuals to the three clusters related significantly to year ($\chi^2_4 = 41.93$, $P < 0.001$) and colony ($\chi^2_4 = 12.03$, $P = 0.017$), but not sex ($\chi^2_2 = 1.09$, $P = 0.579$) or breeding status at recapture ($\chi^2_2 = 3.77$, $P = 0.152$). Cluster SN included birds from all three colonies and the majority of birds from 2008/2009 (75%) to 2009/2010 (81%). Cluster HF was composed of both St

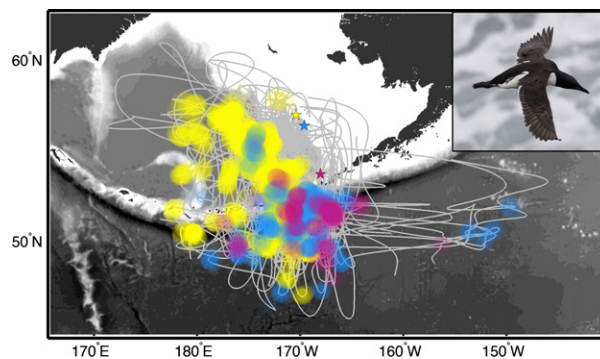


Fig. 2. Winter distributions of thick-billed murres in the Bering Sea and North Pacific. High residency locations of birds from St Paul (yellow, $n = 40$), St George (blue, $n = 23$) and Bogoslof (pink, $n = 11$) are shown from October through February, with complete tracks in grey; the radius of the circles is scaled to the search area of residency time (60 km). Stars of corresponding colours label the breeding colonies. Inset: A thick-billed murre in flight at St Paul Island, Alaska (photo: D. Cushing).

Paul and St George birds from only 2010 to 2011, constituting 87% of birds from this year; the other birds were contained in Cluster DD. Cluster DD was composed entirely of birds from St Paul from all three study years, 31% of all birds from St Paul (Table 2). Body size, represented by PC1, was significantly related to Cluster DD ($v = 2.74$, $P = 0.006$) and SN ($v = -2.12$, $P = 0.034$), with larger bodied birds comprising Cluster DD and smaller birds in Cluster SN (Table 2); however, body size of birds in Cluster DD was not significantly different from that of St Paul birds in other clusters ($F_{2,26} = 1.38$, $P = 0.27$).

Birds in all three clusters showed shifts in diving behaviour throughout the non-breeding period, along with shifts in isotopic values (Table 2, Fig. 3b). For all three clusters, depth utilization was at a minimum in November and then rapidly increased, with the deepest dive depths occurring from January through February (Fig. 3b). Depth utilization showed strong monthly cycles in shallow dive depths for Cluster HF (Fig. 3b). A significant positive relationship was found between per cent time diving at night and the fraction of the moon illuminated for Cluster HF ($F_{1,82} = 9.74$, $P = 0.002$, slope = 0.16, intercept = 0.05), but not for the other two clusters (Cluster DD: $F_{1,93} = 0.06$, $P = 0.81$; Cluster SN: $F_{1,97} = 0.55$, $P = 0.462$). Overall, time spent diving was lower for birds in Clusters DD ($6.3 \pm \text{SD } 2.4\%$) and SN ($6.9 \pm \text{SD } 2.1\%$), whereas birds in Cluster HF increased time spent diving from $8.0 \pm \text{SD } 2.3\%$ in the autumn (Oct and Nov) to $17.3 \pm \text{SD } 4.0\%$ in late winter (Feb and Mar; Fig. 4). Breast feathers (autumn) were not a significant contributor in determining foraging clusters; however, throat feathers were (late winter, Table 2). Seasonal shifts in feather $\delta^{15}\text{N}$ were evident, as breast feather $\delta^{15}\text{N}$ was significantly higher than throat feather $\delta^{15}\text{N}$ for Cluster HF (paired t -test = 3.73, $P = 0.002$) and Cluster SN (paired t -test = 5.71, $P < 0.001$); however, $\delta^{15}\text{N}$ was not different for Cluster DD (paired t -test = -1.04 , $P = 0.328$).

Table 2. Numbers of individual birds and means (\pm SE) of each of the behavioural and dietary parameters used to determine wintering foraging clusters of thick-billed murres

	η^2	Shallow night	Deep day	High frequency
<i>n</i>		27	9	13
Sex (σ/φ)	–	13/14	6/3	6/7
Colony (P/G/B)	–	13/8/6	9/0/0	7/6/0
Year (2008/2009/2010)	–	9/18/0	3/4/2	0/0/13
Body Size PC1	–	-0.42 \pm 0.17	1.20 \pm 0.18	-0.02 \pm 0.42
Diet				
Throat $\delta^{15}\text{N}$ (%)	0.41	14.78 \pm 0.17	17.05 \pm 0.15	14.82 \pm 0.42
Throat $\delta^{13}\text{C}$ (‰)	0.41	-18.96 \pm 0.09	-17.89 \pm 0.06	-18.63 \pm 0.09
Breast $\delta^{15}\text{N}$ (%)	0.10	16.09 \pm 0.18	16.69 \pm 0.13	16.71 \pm 0.29
Breast $\delta^{13}\text{C}$ (‰)	0.12	-18.60 \pm 0.13	-18.60 \pm 0.12	-18.11 \pm 0.13
Spatial				
% HR in Bering Sea	0.28	23 \pm 6.7	82 \pm 6.2	27 \pm 13.9
Convex hull area (Mm ²)	0.00	50.4 \pm 12.0	52.3 \pm 14.4	43.2 \pm 12.7
Max. distance (km)	0.032	190 \pm 8.3	207 \pm 6	189 \pm 7.5
Temporal				
Date of maximum depth	0.08	Jan 31 \pm 5.6	Jan 13 \pm 8.5	Jan 20 \pm 7.2
Date at maximum distance	0.21	Jan 1 \pm 8.7	Nov 11 \pm 8.3	Nov 18 \pm 11.6
Dive				
Maximum dive depth (m)	0.13	152.3 \pm 2.6	143.6 \pm 2.7	161.8 \pm 6.3
% 24-h day diving	0.37	5.7 \pm 0.4	7.4 \pm 0.5	10.2 \pm 1.0
Day mean depth (m)	0.35	44.1 \pm 1.2	54.1 \pm 0.7	50.5 \pm 1.7
SD % 24 h day diving	0.56	3.6 \pm 0.2	4.6 \pm 0.4	7.1 \pm 0.3
SD day depth (m)	0.65	13.1 \pm 0.5	11.1 \pm 0.4	20.5 \pm 0.8
% 24 h night diving	0.31	7.9 \pm 0.7	4.5 \pm 0.4	13.0 \pm 1.9
Night mean depth (m)	0.02	31.4 \pm 1.3	33.6 \pm 1.4	32.3 \pm 1.1
SD % 24 h night diving	0.47	7.2 \pm 0.7	4.1 \pm 0.3	15.1 \pm 1.9
SD night depth (m)	0.16	11.2 \pm 0.5	12.9 \pm 0.6	13.9 \pm 0.9
Dive Bouts				
Bout duration (min)	0.13	67.9 \pm 2.4	65.4 \pm 2.0	80.5 \pm 6.5
Bout depth (m)	0.39	39.6 \pm 1.0	47.0 \pm 0.8	40.0 \pm 1.1
% of bout diving	0.64	39.0 \pm 1.1	41.4 \pm 2.3	59.1 \pm 1.0
Post bout interval (min)	0.12	310 \pm 37.3	622 \pm 125	333 \pm 62
No. of bouts/day	0.020	4.1 \pm 0.1	3.9 \pm 0.1	4.0 \pm 0.14
SD bout duration (min)	0.42	68.1 \pm 3.5	68.0 \pm 2.6	105.4 \pm 7.3
SD bout depth	0.39	16.9 \pm 0.4	16.8 \pm 0.3	21.4 \pm 1.0
SD % of bout diving	0.31	23.9 \pm 1.0	20.9 \pm 1.0	30.1 \pm 1.2
SD # bouts/day	0.21	1.48 \pm 0.05	1.34 \pm 0.05	1.72 \pm 0.1

The importance of each variable in the overall model was tested via a *F*-test. η^2 is presented as an index of the proportion of variance explained by each of the factors; bold η^2 indicates a significant contribution to the overall model. The variables that significantly contribute to each cluster, determined via *t*-tests, are shown in bold ($P < 0.05$). Sex, colony, year, and body size PC1 were not included as variables in the cluster analysis.

(Table 2). Significant shifts in feather $\delta^{13}\text{C}$ also occurred from autumn to winter, decreasing for Cluster HF (paired *t*-test = 2.32, $P = 0.039$) and Cluster SN (paired *t* = 2.17, $P = 0.040$), while increasing for Cluster DD (paired *t*-test = -3.44, $P = 0.009$) (Table 2).

Because isotope values in throat feathers were a significant factor defining foraging clusters, we analysed these values ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$) from all birds sampled throughout the study ($n = 211$ winter trips) in a hierarchical cluster analysis (using Ward's method and Euclidean distances) to test association of foraging clusters with solely isotopic-based clusters (identified by inertia gain, L  , Josse & Husson 2008). Murre isotope values clustered into three groups, significantly related to colony ($\chi^2_2 = 52.69$, $P < 0.001$) and year ($\chi^2_2 = 27.63$, $P < 0.001$), but not sex ($\chi^2_1 = 0.04$, $P = 0.978$; Fig. 5). Birds from St Paul dominated isotopic

Cluster C (94%), characterized by high $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. All of the tracked birds from foraging Cluster DD were included in this elevated $\delta^{15}\text{N}$ group, along with two birds from St George and two birds from foraging Cluster HF, suggesting that this solely isotopically based cluster related strongly to the St Paul foraging strategy of deep day diving. We then assessed the prevalence of elevated $\delta^{15}\text{N}$ (isotopic Cluster C) and tested fidelity to this strategy between years ($n = 28$ birds). The proportion of birds in isotopic Cluster C differed by year (2008/09 = 57.7%, 2009/10 = 31.7%, 2010/11 = 46.4%), with 60% of individuals from St Paul using this foraging strategy in at least 1 year. Individuals were not always faithful to this strategy, however, as 64% of birds changed their isotopic cluster. The other two isotopic clusters did not separate according to foraging cluster (Fig. 5).

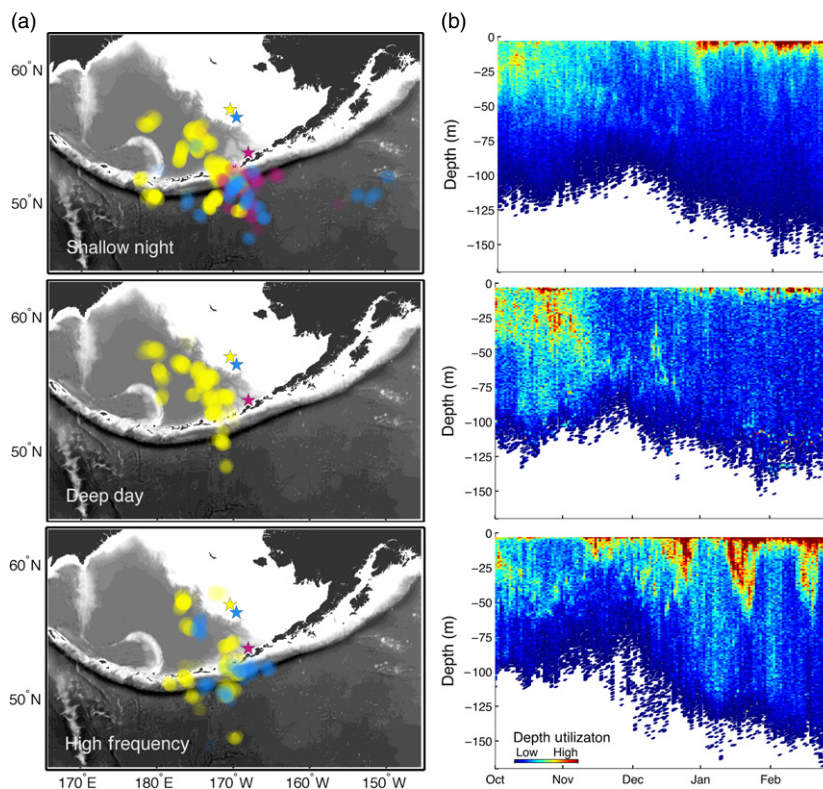


Fig. 3. Winter distributions and depth utilization of thick-billed murres, October through February, by foraging cluster, with a) spatial extent, (high residency locations; St Paul [yellow], St George [blue] and Bogoslof [pink]) and b) depth utilization of the three foraging clusters. Depth utilization is normalized by the number of birds tracked daily.

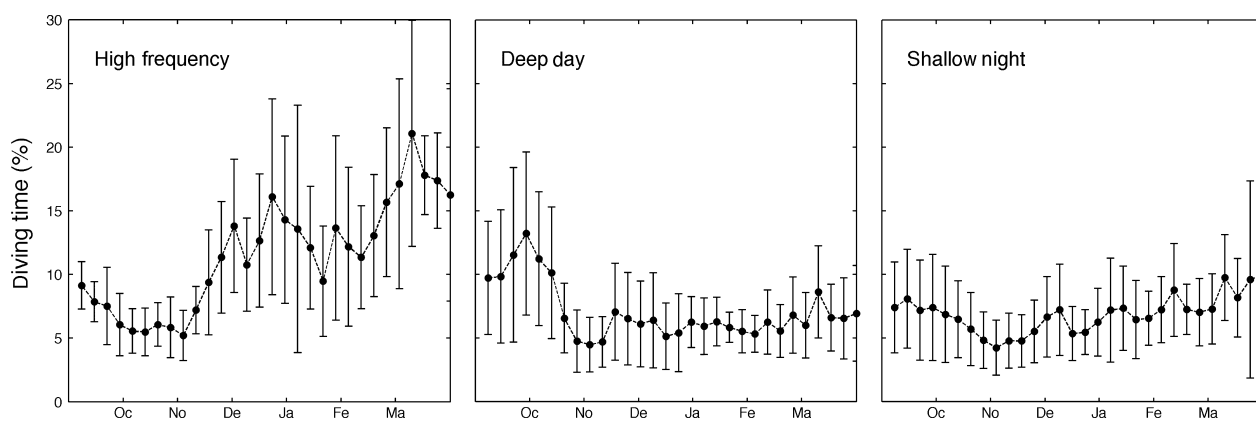


Fig. 4. Weekly proportion of time (24 h) spent diving \pm standard deviation for thick-billed murres from the three winter foraging clusters.

Discussion

Wintering murres maintained a relatively large degree of spatial structure in both horizontal (surface) and vertical (depth) distributions relative to their breeding colony, which was associated with body size differences. We found that metrics of foraging behaviour, specifically dive depth, late winter isotopic values and residency in the Bering Sea, correlated significantly with body size and predicted to a significant extent the winter foraging strategies of individual thick-billed murres. A portion of the birds from the colony with the largest average body

size, St Paul, utilized a unique foraging strategy that was more resident in the Bering Sea and involved deeper dives during the day. Nonetheless, these birds were capable of switching foraging strategies between years. The majority of the birds in our study migrated to the North Pacific south of the Aleutian Islands and employed a foraging strategy of primarily shallow dives at night. Birds' seasonally adjusted foraging behaviour indicating considerable flexibility in response to environmental changes. Overall, winter foraging strategies appear to relate to body size and annual changes in foraging conditions, rather than a random assortment of individual foraging strategies.

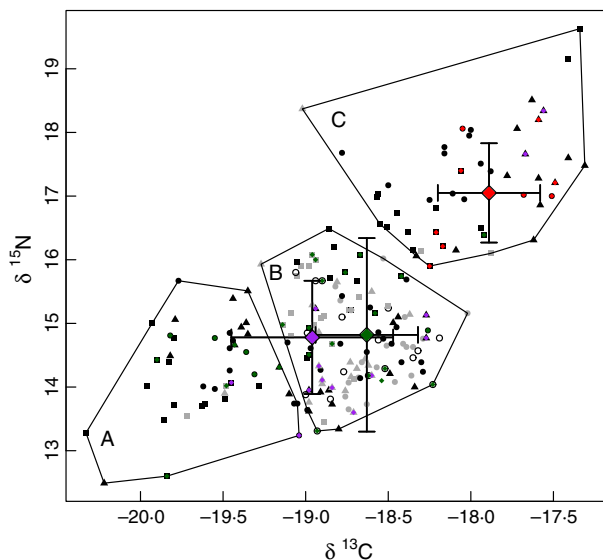


Fig. 5. Isotopic Clusters A, B and C of throat feathers from thick-billed murres ($n = 211$), overlaid with isotopic values from foraging clusters HF, DD and SN (cross plot # standard deviation). Sampling years (summer) are indicated by circles (2009), squares (2010) and triangles (2011), while colonies are shown by black (St Paul), grey (St George) and white (Bogoslof). Points corresponding to individuals included in the foraging cluster analysis are overlaid with a circle, coloured according to cluster (HF = green, DD = red, and SN = purple).

LOGGER EFFECTS

Attaching instruments to a small flying-diving seabird is challenging because buoyancy, size and weight of instruments and attachment location can all have measurable negative effects (Paredes, Jones & Boness 2005; Elliott *et al.* 2012; Vandenabeele *et al.* 2012). In our study, the majority of logger-tagged birds returned to breed and mass at recapture was not significantly different than at tag deployment; however, following the winter of 2009/2010 birds carrying geolocators (and raising chicks) were lighter than control birds. Birds from 2009 to 2010 nevertheless clustered with the previous year, indicating that behavioural differences were minimal. Throat feathers from both instrumented and control birds originating from St. Paul had elevated $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, suggesting that this is not an artefact of logger effects.

BODY SIZE AND FORAGING STRATEGIES

Allometry predicts that divers of larger body size are capable of diving deeper and longer due to lower mass-specific metabolic rates and increased O_2 stores (Kleiber 1975; Boyd & Croxall 1996; Schreer & Kovacs 1997; Halsey, Butler & Blackburn 2006). This prediction may apply to wintering murres, as individual body size correlated with mean daytime dive depth, regardless of cluster, with larger individuals diving deeper. Larger murres from Cluster DD spent the most time at deeper depths and the

least amount of time diving, suggesting they were able to meet daily energetic requirements with only a relatively few deep dives, despite the higher absolute energy requirements of their larger bodies (Peters 1983). Thick-billed murres wintering in the northeast Atlantic dove more frequently (Fort *et al.* 2013) than the comparatively larger and more resident Cluster DD birds, further suggesting that fewer deeper dives allowed these larger birds to reduce foraging time. Conversely, smaller birds used a foraging strategy (Clusters SD and HF) characterized by more time spent at shallow depths, where it is more energetically costly to forage due to higher buoyancy (Wilson *et al.* 1992); however, the quality (lipid content) and predictability of shallow prey could outweigh this cost.

Flying is the most expensive foraging activity for murres, while dive costs are comparatively small (Elliott *et al.* 2013). Wintering murres do not make repeated foraging trips, and, overall, our study birds did not migrate substantial distances, especially when compared to murres in the North Atlantic (Gaston *et al.* 2011; Fort *et al.* 2013). Regardless, the higher wing loading of murres from St Paul, relative to those breeding at St George, may favour birds that fly less often, thereby limiting distributions to the Bering Sea, as reflected in distributions of St Paul birds regardless of cluster. Although the majority of larger birds clustered with that of smaller birds from St George in all 3 years, smaller birds did not adopt the foraging strategy deep diving as residents. Being small may preclude birds from accessing deeper prey resources in the Bering Sea, while larger birds appear to have a choice. The relative profitability of these strategies is probably dependent on yearly conditions and the individual, as prey availability/quality and murre body size likely play a role. On a broad scale, body size variation between colonies of thick-billed murres and the similarly sized common murre (*U. aalge*) could be used to test this trade-off during migrations between flight and diving, as common murre are more residential during the winter (McFarlane Tranquilla *et al.* 2015).

Differences in body size of birds from our three study colonies could have evolved due to foraging conditions during the breeding season, similar to blue-eyed shags (*Phalacrocorax verrucosus*) breeding in the Kerguelen Archipelago, where there are colony-based differences in diets, foraging habitats and distances to foraging areas (Cook *et al.* 2013). Together, long-term differences in summer diets and foraging distributions (Sinclair *et al.* 2008; Renner *et al.* 2012; Harding *et al.* 2013) suggest that St Paul birds are constrained to forage in shelf habitats and may have specialized to feed locally on benthic prey, while murres from St George and Bogoslof are able to forage over the deeper basin. Birds nesting on St George commute long distances on over-night trips that likely favour smaller body size, whereas Bogoslof birds can access deep waters adjacent to the colony (Harding *et al.* 2013; Paredes *et al.* 2015). Regardless of the mechanistic explanation for colony differences in body size, there

appear to be similarities between summer foraging behaviour and behaviours employed during winter.

Murre fathers accompany their flightless chicks out to sea and associated differential distributions between the sexes are known to occur in Alaskan populations during the autumn (Hatch *et al.* 2000), while males tracked from the Canadian High Arctic tend to remain farther north than females (Gaston *et al.* 2011). Despite these sex-specific behaviours and the sexual size dimorphism of our study populations, we did not find differences in foraging strategies related to sex. We did find differences in breast feather $\delta^{15}\text{N}$, per cent time diving at night and maximum distance from the breeding colony, but these differences did not drive the results from the cluster analysis. In particular, sex differences indicated by isotopic differences in breast feathers reflect autumn diets, but during winter (October–February) foraging behaviours grouped birds primarily by colony, body size and year.

DIETS, FORAGING AND DISTRIBUTIONS

In addition to forage fishes and squid, thick-billed murres consume euphausiids and amphipods, both during breeding and winter (Falk & Durinck 1996; Renner *et al.* 2012). Elevated $\delta^{15}\text{N}$ values generally reflect foraging at higher trophic levels, spatial changes in the baseline of the food web and fasting (Post 2002). In the Bering Sea, there is a strong baseline gradient of $\delta^{15}\text{N}$, with lower values occurring in the basin and increasing onto the shelf (Schell, Barnett & Vinette 1998; Jones *et al.* 2014); however, euphausiids in the Alaska Stream ($\delta^{15}\text{N} = 8.16$, $\delta^{13}\text{C} = -18.7$) are more similar to those in the Bering Sea slope region ($\delta^{15}\text{N} = 8.64$, $\delta^{13}\text{C} = -17.72$) than the Gulf of Alaska (Pomerleau *et al.* 2014; Pomerleau, pers. comm.). Thus, given the location data, the $\delta^{15}\text{N}$ values of throat feathers indicate that murres in foraging Cluster DD are likely foraging on a higher trophic-level diet than the majority of wintering murres. For Cluster DD, $\delta^{15}\text{N}$ increased from autumn to winter while most birds maintained residency in the Bering Sea. This increase suggests that these birds were consuming more fish and squid during later winter than during autumn, while those in the other foraging clusters reduced their intake of fish and squid. Thick-billed murres wintering off the southwest coast of Greenland also appeared to increase reliance on fish during late winter (Linnebjerg *et al.* 2013), while birds from the High Arctic showed little seasonal variability in diets (Karnovsky *et al.* 2008).

Murres in both foraging Cluster SN and Cluster HF dove to shallow depths at night, a behaviour associated with foraging on diel-vertically migrating prey (Benoit-Bird *et al.* 2011, 2013). Birds using these strategies wintered predominately in oceanic waters south of the Aleutians and along the continental slope. This offshore area is influenced by the Alaska Stream and characterized by an oceanic zooplankton community, including the large euphausiid *Euphausia pacifica* (Coyle 2005). This oceanic euphausiid may be a predictable prey source for

fishes, squids and murres, as they are omnivorous, can produce multiple broods in a year, have continuous growth rates and showed little annual variation in abundance over 5 years in the Gulf of Alaska (Pinchuk, Coyle & Hopcroft 2008). Despite this evidence of a predictable prey source, foraging behaviour changed in 2010/2011.

One of the strongest La Niña years on record occurred during 2010/2011, following closely upon El Niño conditions in the central Pacific (Hu *et al.* 2014). Concomitantly, zooplankton biomass, survival estimates for age-1 pollock (*Theragra chalcogramma*), and catch rates of juvenile pink salmon (*Oncorhynchus gorbuscha*) in the Gulf of Alaska were all low (Orsi *et al.* 2013; Zador 2013). During the winter of 2010/2011, murres increased their foraging effort, notably through longer bout durations, moonlight foraging, and a ~2 fold increase in time spent foraging, particularly during the latter half of the winter. Murres from Bogoslof were not tracked during 2010/2011; however, the high degree of spatial overlap between St George and Bogoslof birds in 2008/2009 suggests that Bogoslof murres likely responded similarly to apparent low prey availability.

Within each foraging cluster murres exhibited the capacity to adjust foraging behaviour in response to environmental changes. At the daily and monthly scales, foraging strategies related to preferences for foraging during the day or night. Like murres wintering in the North Atlantic, dives shoaled in late autumn and then deepened in mid-winter, probably in response to seasonally driven shifts in prey availability within the water column (Fort *et al.* 2013). The HF cluster birds dove more with increasing moonlight, a behaviour observed in common murres, which increased diving efficiency during periods of moonlight versus starlight (Regular, Hedd & Montevecchi 2011). Within the foraging clusters, standard deviations indicate a substantial amount of individual variation in behaviour (Table S1.5, Supporting Information). Spatially, thick-billed murres in this study displayed individual tracks that were dispersive through the wintering area; similarly, murres wintering in the northwest Atlantic displayed a diversity of core wintering areas (McFarlane Tranquilla *et al.* 2014). Likewise, diets during winter were geographically and seasonally flexible. In combination, the temporal plasticity in foraging behaviour and diversity of behaviour among individuals demonstrates an impressive capacity to adjust behaviours in response to local conditions. Nevertheless, because the breeding colony of thick-billed murres on St Paul continues to decline (Byrd, Schmutz & Renner 2008), the behavioural flexibility exhibited by murres, as constrained by body size, may not be enough to adapt to changing conditions in the Bering Sea.

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Data accessibility

Data are available from the North Pacific Research Board (Orben 2012a, b,c,d,e).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Table S1.1–S1.5.