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Article

Prey capture and selection throughout the breeding season in a deep-diving generalist seabird, the thick-billed murre

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Generalist seabirds forage on a variety of prey items providing the opportunity to monitor diverse aquatic fauna simultaneously. For example, the coupling of prey consumption rates and movement patterns of generalist seabirds might be used to create three-dimensional prey distribution maps ('preyscapes') for multiple prey species in the same region. However, the complex interaction between generalist seabird foraging behaviour and the various prey types clouds the interpretation of such preyscapes, and the mechanisms underlying prey selection need to be understood before such an application can be realized. Central place foraging theory provides a theoretical model for understanding such selectivity by predicting that larger prey items should be 1) selected farther from the colony and 2) for chick-feeding compared with self-feeding, but these predictions remain untested on most seabird species. Furthermore, rarely do we know how foraging features such as handling time, capture methods or choice of foraging location varies among prey types. We used three types of animal-borne biologgers (camera loggers, GPS and depth-loggers) to examine how a generalist Arctic seabird, the thick-billed murre *Uria lomvia*, selects and captures their prey throughout the breeding season. Murres captured small prey at all phases of a dive, including while descending and ascending, but captured large fish mostly while ascending, with considerably longer handling times. Birds captured larger prey and dove deeper during chick-rearing. As central place foraging theory predicted, birds travelling further also brought bigger prey items for their chick. The location of a dive (distance from colony and distance to shore) best explained which prey type was the most likely to get caught in a dive, and we created a preyscape surrounding our study colony. We discuss how these findings might aid the use of generalist seabirds as bioindicators.

Keywords: center place foraging, foraging behaviour, preyscape, prey selection, thick-billed murre

Introduction

Recent advancements in biologging have revealed the behaviour of many otherwise hard-to-study animals (Boyd et al. 2004, Ropert-Coudert and Wilson 2005). In particular, diving seabirds are challenging to study, as they often feed far offshore and spend a considerable amount of time underwater, and miniature biologgers are



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sometimes the only way to obtain precise information on their behaviour. For example, biologgers, like accelerometers, GPS or depth loggers, have given insights on the foraging behaviour of penguins diving to great depths or the foraging routes of albatrosses across entire oceans (Wilson et al. 1993, Tuck et al. 1999).

Specialist seabirds have been a significant focus of the studies using biologgers to monitor foraging behaviour (Garthe et al. 1999, Weimerskirch et al. 2006, Kokubun et al. 2015). The relationship between foraging behaviour and prey selection in specialist predators is often straightforward, with birds having stereotypic behaviours that maximize the capture of a given prey. Common murre *Uria aalge*, for example, use a narrow range of deep depths to increase the chance of capturing their preferred prey, capelin *Mallotus villosus* (Barrett and Furness 1990). The well understood predator–prey relationships in specialist seabirds have even led to direct applications, like their use as indicator species for marine food supply (Cairns 1988, Brisson-Curadeau et al. 2017). For instance, time spent diving can be used to estimate fish abundance in pigeon guillemots *Cepphus columba* that specialize on nearshore fish (Litzow and Piatt 2003), while foraging trip length can be used as a proxy of prey availability in common murre and Cape gannets *Morus capensis* (Monaghan et al. 1994, Cohen et al. 2014). In contrast, while generalist seabirds' diverse diet is typically associated with more flexible behaviours (Barrett and Furness 1990), prey selection choices are often unclear. Optimal foraging theory provides a theoretical model for understanding such choices (MacArthur and Pianka 1966, Orians and Pearson 1979, Houston and Carbone 1992) but rarely do we know how foraging features such as handling time, capture methods or choice of foraging location varies among prey types. Consequently, it is often more difficult to use generalist seabirds as indicators. Yet, generalists should in theory provide more information on the aquatic ecosystem than specialists, as they feed on a wider array of prey type.

In the Arctic, the widely-distributed thick-billed murre *Uria lomvia* is a generalist predator that forages up to 150 m deep (Elliott et al. 2008a), and so is in contact with several species of aquatic fauna. The coupling of GPS-depth loggers with observations of prey captures to determine where fish are captured could in theory provide information on how fish species are distributed in the Arctic ('preyscape'). However, to accurately create a preyscape from the foraging behaviour of predators, we first need to understand prey selectivity by the predator. Central place foraging theory (Orians and Pearson 1979) provides a hypothesis that explains some aspects of prey selection. For example, central place foraging theory predicts that birds should select larger prey when central place foraging (chick-rearing) than self-feeding (incubation; Ito et al. 2010), and that prey size should increase with distance from the central place (colony; Elliott et al. 2009). If murre do indeed follow those rules, then we can use such models to determine prey availability from apparent preyscapes. Handling and searching times are also important parameters

in foraging theory (MacArthur and Pianka 1966) and can consequently influence prey selectivity and the interpretation of preyscapes (Watanabe and Takahashi 2013). These aspects are seldom known in diving seabirds; for instance, it is often assumed that murre capture their prey while at the bottom phase of a dive (Mori et al. 2002, Elliott et al. 2008a), and that the ascent and descent phase are 'transit time' rather than 'searching time', but that assumption has not been directly tested. Finally, a related issue is the existence of individual specialists within the generalist population (Vader et al. 1990, Woo et al. 2008). If individual murre are using stereotyped behaviour, then their diet might be biased towards certain prey types due to memory of previous encounters rather than being influenced solely by prey availability. Yet, it is still unclear whether individuals select their prey by choosing specific foraging locations ideal for a given prey type, or by adopting a particular underwater behaviour which will maximize the capture of a prey type (Regular et al. 2013, Wakefield et al. 2015).

Here, we use several types of biologgers on thick-billed murre to gain insights on how prey selection and capture occurs throughout the breeding period. We test the assumptions of central place foraging theory that 1) prey size increases with distance from the colony and 2) prey size and foraging effort increases during chick-provisioning. We used camera loggers to obtain the first bird-borne footage of Atlantic thick-billed murre *U. lomvia lomvia* and gain information on how murre capture their prey (ascent/descent, handling time), in which context (benthic/pelagic dives), and how that varies with prey type. Next, we tested whether diving behaviour or foraging location best explain which prey types a given bird specializes upon. Finally, we create a preyscape for thick-billed murre and discuss how the above results may allow us to interpret the preyscape.

Material and methods

We collected all data at the Coats Island west murre colony (62°56'52.20"N, 82°01'03.70"W) in Hudson Bay, Nunavut, Canada in July 2017. The murre colony, situated on cliffs, hosts ~15 000 breeding pairs (Gaston 2002). We conducted all analysis using R (R Development Core Team) and ArcGIS for desktop (ESRI 2011).

Biologger deployment and feeding watches

We equipped 14 birds with camera-loggers (DVL400M, Little Leonardo, Tokyo, Japan, 15 g) attached on back feathers. Out of those birds, 4 were incubating, 9 were chick-rearing and one was equipped during both periods (see Supplementary material Appendix 1 for individual deployments). The cameras recorded for ~1–2 h, and all birds were recaptured within 24 h. We also attached a Technosmart depth-logger (AxyDepth, 6.5 g, Technosmart, Rome Italy, depth = 1 Hz) on the tail. As the lightest equipped birds weighed 850 g,

the two devices (with attachment gear) did not exceed the recommended 3% of the bird's mass (Phillips et al. 2003). The individuals equipped with cameras and accelerometers were not the same individuals as those used for feeding watches (see next section).

We deployed GPS loggers (AxyTrek, 18 g, Technosmart, Rome, Italy, depth and temperature = 1 Hz; GPS locations recorded every 5 min) on 52 birds captured with a noose pole. Only one member of the pair was equipped at a given moment, except on one occasion where overlapping of the members of two pairs occurred due to time constraints. We retrieved the GPS after 2–8 days via recapture of the individual. All birds captured originated from a plot containing around 30 breeding sites ('Q Plot'). All GPS-equipped birds were rearing chicks. Equipped birds that did not forage extensively during the GPS-recording were re-equipped later in the season.

We conducted feeding watches while GPS units were recording. Feeding watches consisted of observing the plot for 12–19 h a day (between 03:00 and 22:00) over several days, during the chick-rearing period (Hipfner et al. 2006). Observations were made from a blind located 2–10 m away from focal birds, and involved noting when an adult returned to its nest with prey and what prey type was caught. Prey length was also visually estimated relative to the length of the white stripe on the bill (~5 cm, Elliott and Gaston 2008). We separated *Triglops* sp. from other sculpins, as *Triglops* are easily identifiable in the field and likely have a different life history than *Myoxocephalus scorpius* and *Gymnocanthus tricuspis*, which comprised most of the remaining sculpins (Elliott and Gaston 2008).

Data analysis

We watched the videos using VLC (VideoLAN, France). We recorded the behaviour of individuals during dives: prey catching events, prey handling time and dive shape (U-shaped or bottom dives vs V-shaped or pelagic dive). The prey type was noted for each capture. We compared the diving behaviour of camera-equipped birds that were incubating versus those that were rearing chicks using a Welch two-sample t-test (for depth) and Fisher's exact test (for dive shape). We also used the camera loggers as a training set to develop an algorithm that could discriminate benthic dives (U-shape dives) from pelagic dives (V-shape, Elliott et al. 2008a) using solely depth profiles, which was useful for analyzing the habitat use of birds only equipped with GPS-depth recorders. We recorded dive shape from the camera logger based on whether the ocean bottom was observed on the video. We used a linear discriminant function analysis with 1) the ratio of the dive spent near maximum depth and 2) maximum depth, as input variables to discriminate between bottom (ocean bottom visible) and pelagic (ocean bottom not visible) dives.

We linked the prey type brought to the chick by a GPS-equipped bird with the information recorded during the previous dive bout. A bout is defined as a series of dives

with a difference of less than 37.4 m and less than 63.4 s of surface time between sequential dives (criteria developed for our study site; Elliott et al. 2008a). Only dives deeper than 2 m were considered. The variables used to describe prey type were: maximum depth, distance from the colony, dive shape and distance from shore. Distance from shore was calculated using a high resolution polygon of the nearby shoreline (Wessel and Smith 1996). We used a principal component analysis to determine relationships among the variables and qualitatively assess the associations between foraging behaviour and prey type.

Murres at our study site show strong individual diet specialization when provisioning their chicks (Woo et al. 2008). However, capelin comprises 50–60% of the diet, and so a 'generalist' individual might still have a high proportion of capelin (Woo et al. 2008). Considering this, diet specialization of an individual was categorized into three groups: 1) if a prey type other than capelin constituted more than 25% of the diet of a bird, the individual was considered a specialist for this prey type, 2) if no prey type other than capelin constituted more than 25% of the diet and if capelin consisted of more than 50% of the diet, the bird was considered a capelin specialist and 3) if no prey type other than capelin constituted more than 25% of the diet, but capelin consisted of less than 50% of the diet, the bird was considered generalist. Only birds for which we observed five feeds or more were classified as having a diet specialization. Feeds for a given bird were sometimes observed during the feeding watch when the individual was no longer equipped with a GPS, or had not been equipped with a GPS yet. These feeds were nonetheless used to establish the specialization of a bird.

Data deposition

Data available from Movebank Digital Repository: <doi:10.5441/001/1.8b3k178b> (Brisson-Curadeau and Elliott 2019).

Results

Diving behaviour

The camera loggers recorded a total of 278 dives from the 14 equipped birds. In total, 65 h of video were recorded, of which 7.5 h involved birds diving underwater. While benthic and pelagic dives occurred at similar depths, benthic dives were – unsurprisingly – longer than pelagic dives on average (Table 1). Most prey captures (> 99%) were very small invertebrates, likely the amphipod *Parathemisto libellula*, averaging one capture per 3.75 s when diving. Only 21 fish large enough to be distinguished were observed (all capelin *Mallotus villosus*, except three: one sculpin sp. and two *Triglops* sp.), leading to a capture rate of 2.8 fish per hour. The handling time for all small prey was instantaneous (< 0.5 s), but was variable for larger prey (13 ± 16 s, Fig. 1). More than half (57.1%) of the 21 large fish were brought back to the

Table 1. Dive characteristics for thick-billed murres.

	n	Dive time (s)	Depth (m)	% containing captures while descending	% containing captures while at bottom	% containing captures while ascending
Benthic dives	64	133 ± 43	43 ± 28	26.3%	100%	57.9%
Pelagic Dives	215	74 ± 50	58 ± 31	72.1%	Not applicable	95.6%

surface before being eaten, although some were swallowed almost instantly underwater. Capture events were most common in the ascent phase, occurring in 57.9% and 95.6% of the benthic and pelagic dives respectively (Table 1). Prey captures also occurred in the descent phase for 26.3% of the benthic dives and 72.1% of the pelagic dives. All benthic dives contained captures at the ocean floor. Prey type at the bottom phase could not be identified due to camera position as the birds tilted their head downwards during such captures. However, in two occasions a bird went straight to the surface after capturing a prey at the bottom and prey type could be identified (one capelin and one sculpin sp.) as the fish was dangling in the bird's beak in range of the camera while the bird was sitting on the surface. In total, 18 of 21 large fish were captured in the ascent phase, with five of them (four capelin and one *Triglops* sp.) being caught less than a meter below the surface. Only one large fish (a capelin) was captured while descending. Of all the dives containing a large fish capture, 52.4% were benthic dives (while only 22.9% of total dives were benthic). Two prey captures intended to feed the chick were witnessed through the camera loggers. In one of them, the adult caught a capelin, and kept diving at shallow depth (< 2 m) with the fish in its beak, with some consecutive dives being separated by short flights. The bird kept doing so for at least 20 min before the video ended. In the other, the bird directly flew back to the colony after capturing the fish.

The best algorithm to discern benthic dives from pelagic dives using depth profile did so with an accuracy of 95% (kappa index of 0.88). The algorithm used the percentage of the dives that occurred within 6% of the maximum depth, adjusted according to maximum depth as follows:

$$S = -0.01837d + 10.0249r$$

where S is the scaling value used to separate benthic dives from pelagic dives, d is the scaled maximum depth (negative value) and r is the scaled percentage of a dive occurring at 6% or more of the dive's maximum depth. Negative values of S were classified as pelagic dives.

Foraging behaviour according to breeding stage

Dives during the chick-rearing period were deeper (47 ± 30 m) than dives during incubation (27 ± 15 m, $t_{132} = 5.28$, $p < 0.001$). There was no difference between periods in the percentages of bottom dives (incubation 19%, chick-rearing 21%; Fisher's exact test $p = 0.84$). While smaller prey items (invertebrates) were captured abundantly by self-feeding adults throughout the breeding season, the rate of larger fish

captures during the chick-rearing period (3.0 capture h^{-1}) was much greater than during the incubating period (0.6 capture h^{-1}).

Prey type as described by dive characteristics

We observed 189 feeds by GPS-equipped birds, with an average of 2.4 feeds per bird per day (average foraging trip length: 1.7 h \pm 4.54, median = 2.4 h). We randomly removed 86 pseudo-replicates (68% of which were capelin), which were defined as all feeds of the same prey type from the same bird. We also removed another 16 feeds which consisted of rare prey items ($n < 5$), leaving 89 feeds for the analysis. The remaining 87 feeds included 9 feeds of invertebrates (shrimps and amphipods), 45 feeds of capelin, 11 feeds of arctic cod *Boreogadus saida*, 7 feeds of daubed shanny *Leptoclinius maculatus*, 9 feeds of *Triglops* sp. and 6 feeds of non-*Triglops* sculpin.

The three first axes of the PCA explained 39, 29 and 25% of the variation, respectively (see Supplementary material Appendix 1 for full output). The second axis was only useful to differentiate variation within prey types (Supplementary material Appendix 1) and so only the first and third axis were considered (Fig. 2). The first axis was almost exclusively composed of geographical variables (distance from the colony and distance from shore). The third axis, while also influenced

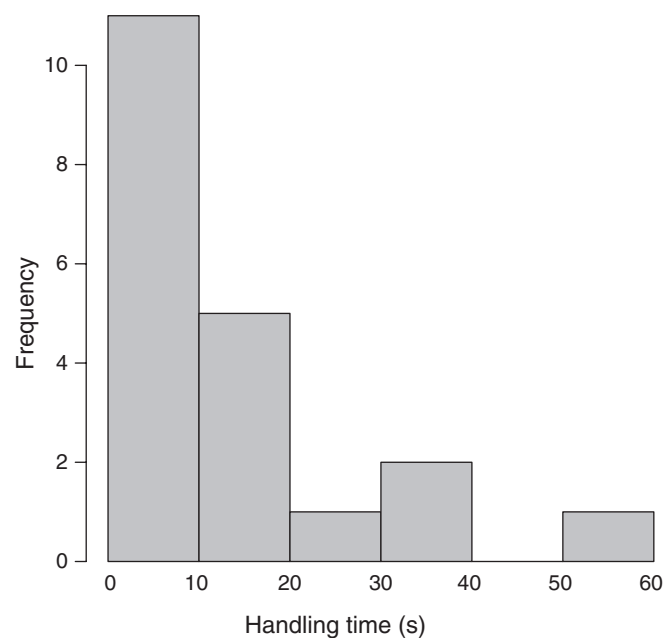


Figure 1. Histogram of underwater handling time for large fish captures.

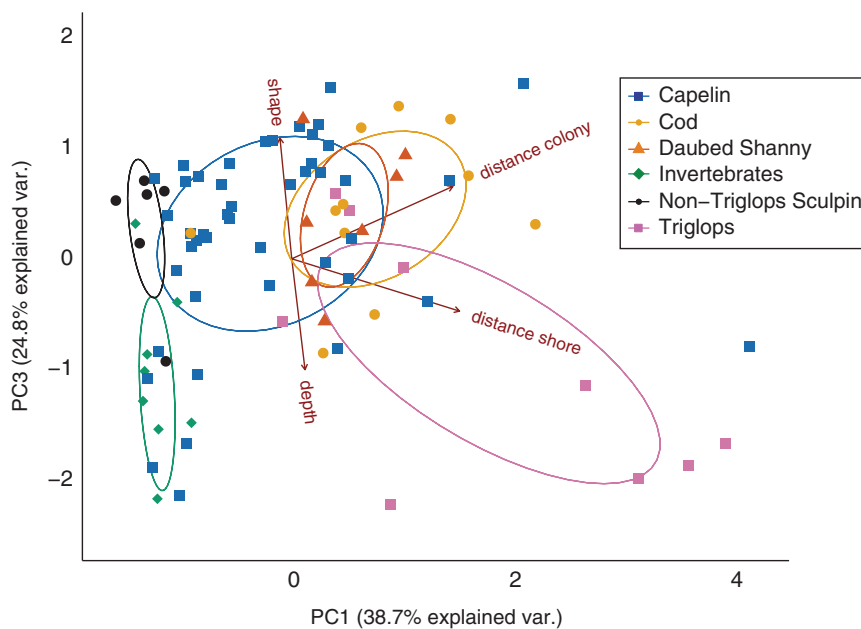


Figure 2. Principal components analysis of dive characteristics for thick-billed murres at Coats Island, including maximum depth (depth), percentage of benthic dives in a dive bout (shape), distance from the colony (distance colony) and distance to shore (distance shore). Colour represents the prey type recorded at the colony following each dive bout, with the assumption that the prey was caught in the final dive bout prior to the bird returning to the colony.

by geographical variables, consisted mostly of underwater variables (depth and dive shape). Geographical variables created a first dichotomy: colony-adjacent prey (invertebrate and non-*Triglops* sculpin) compared with larger, remote prey (*Triglops*, arctic cod and daubed shanny, Fig. 3). Capelin was near the centroid, being present both near and far from the colony. Among the remote prey, cod and shanny were found

closer to coastal waters (but not as close as colony-adjacent prey), while *Triglops* were found far off-shore. The third axis primarily discriminated sculpin from invertebrates, with sculpin being captured in shallower waters near the sea floor and invertebrates being caught in deeper water and in the middle of the water column. When all species were considered, distance from the colony had an asymptotic positive

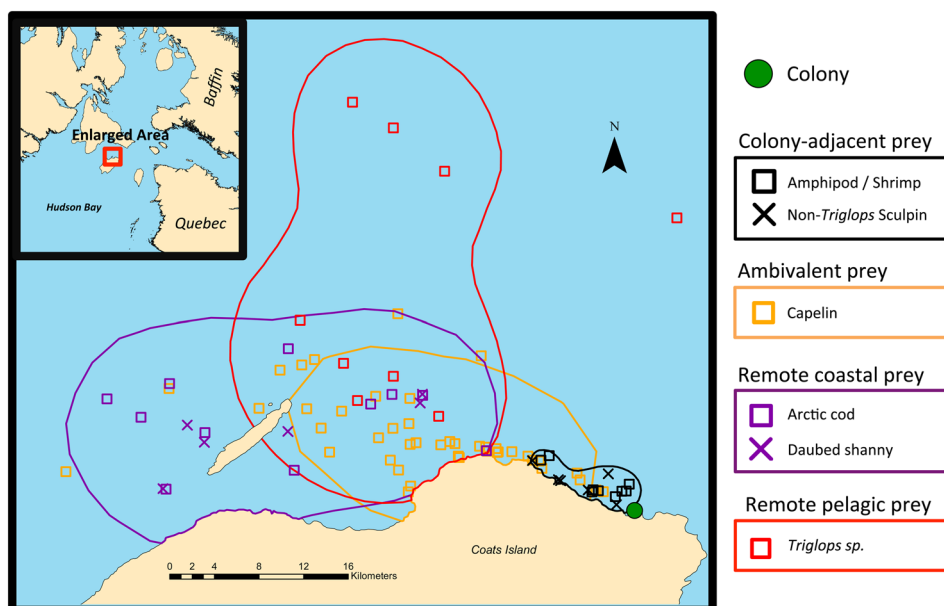


Figure 3. Map of prey capture locations for thick-billed murres feeding near the Coats Island colony. Each point represents the location of the final dive bout prior to the return of an individual to the colony with a particular prey item, and assumes the prey item was caught in the final dive bout. Two prey capture events (one capelin and one daubed shanny) occurred well outside the area shown.

relation with prey size ($t_{34} = 5.96$, $p < 0.001$; Fig. 4). *Triglops* were also typically caught in the middle of the water column, while cod and daubed shanny were caught during a mixture of dive shape (Table 2).

Diet specialization

In the surveyed plot, 31 birds were observed feeding their chicks at least five times. Four birds specialized on invertebrates, 15 on capelin, five on cod, one on daubed shanny, three on non-*Triglops* sculpin, two on *Triglops* and one was a generalist. To obtain sufficient statistical power, we clumped colony-adjacent specialists (invertebrate or sculpin) and remote prey specialists (cod, shanny or *Triglops*). The sole generalist was removed from analysis. Capelin was the most common prey and was brought back by all individuals (48.5% of all feeds). As capelin was also caught in various geographic conditions, near the centroid of Fig. 2, we investigated if capelin could have been an opportunistic prey sometimes caught by specialists. We tested if capelin caught by colony-adjacent prey specialists were captured in different locations than those caught by remote prey specialists or capelin specialists. Indeed, capelin caught by colony-adjacent specialists were caught closer to the colony and closer to shore than the ones caught by remote prey specialists, which follows the same tendency as the prey for which these birds specialised on (Fig. 5). Capelin caught by capelin specialists overlapped with both groups.

Discussion

Based on locations where murres captured their prey, we created a preyscape surrounding the Coats Island colony (Fig. 3). Arctic cod and non-*Triglops* sculpins were caught

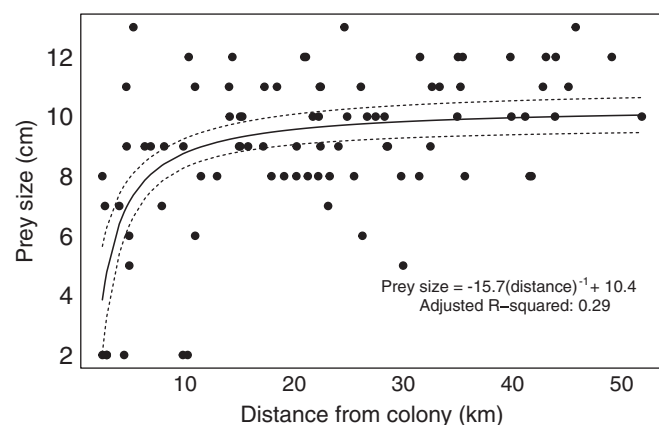


Figure 4. Prey size (all species) increases with return distance to the colony for thick-billed murres foraging near Coats Island in 2017. The full line is a fitted linear model, while the dashed lines represent the 95% confidence interval. Distance from the colony represents the distance between the colony and the final dive bout prior to the return of each murre to the colony, under the assumption that the prey item was caught in the final dive bout.

primarily in the region surrounding Bencas Island, a thin island about 30 km west of the colony, while capelin were caught closer to the colony, *Triglops* sculpins were caught offshore of Bencas Island and invertebrates were caught primarily close to the colony. As predicted by central place foraging theory, chick-provisioning birds fed more on large prey and dove deeper than incubating birds, as has been found in other studies of auks (Benvenuti et al. 1998, Davoren and Burger 1999, Elliott et al. 2008b, Ito et al. 2010), but surprisingly there was no switch to benthic diving. Amphipods dominated adult diet throughout the season (> 99% of prey capture), although there was a slight increase in large fish captures during chick-rearing. In contrast, chick diet was dominated by large fish and only few feeds (< 5%) were consisting of amphipods. Adult stomach contents are generally dominated with amphipods compared with chick diet (Gaston and Nobel 1985, Gaston and Bradstreet 1993, Provencher et al. 2013), a result supported by isotopic analyses (Hobson 1993). These results imply that our preyscapes are unreliable for invertebrates, which appeared to be abundant (based on adult diet) throughout the region, but were only selected for chick-provisioning when close to the colony. However, as prey size reached a plateau quickly with distance from the colony (Fig. 4), the preyscapes are likely unaffected by distance selectivity once the plateau is reached.

Prey capture and handling

Prey capture method depended on the size of the prey type. While small invertebrates were captured instantaneously throughout the dive, larger fish were caught mostly at the bottom or ascending phase of the dive, and often (but not always) required extensive handling preventing any further capture from occurring in the dive. Buoyancy during the descent phase reduces the ability of murres to capture rapid prey (Lovvorn et al. 1999, Lovvorn 2004, Elliott et al. 2007). Fish may also be more visible from below, therefore easier to capture during the ascent. Similarly, 73% of fish caught by rhinoceros auklets showed bite marks from below, implying they were caught from below (Burger et al. 1993). While the ascent phase was especially productive, the non-negligible number of small prey captures during the descent phase is quite surprising. Indeed, many foraging theories consider that prey capture occurs exclusively at the bottom phase, with the descent and ascent counting solely as 'travel time' (Kramer 1988, Houston and Carbone 1992, Mori et al. 2002).

Prey selection and specialisation

Elliott et al. (2008a) found that the behaviour of a bird while diving can be useful to determine what prey type is likely to be caught. In contrast, our results suggest that, even before a murre starts diving, the location where the bird is foraging provides a better estimate and narrows down the possible prey type caught to one or two (but up to four in small high diversity pockets, see Fig. 3). Two factors can explain the difference between our results and those

Table 2. Average characteristics of final dive bouts prior to the arrival of thick-billed murres to the colony with each prey type.

Prey type	n	Distance to colony (km)	Distance to shore (km)	Depth (m)	Percentage of bottom dives
Invertebrates	9	5.0±3.0	1.3±0.5	-75±29	22
Capelin	45	21.4±10.4	3.4±5.2	-44±27	51
Arctic Cod	11	34.2±11.1	5.7±3.1	-49±31	55
Daubed Shanny	7	32.2±9.4	4.1±2.0	-65±37	71
Non- <i>Triglops</i> Sculpin	6	6.5±3.0	0.8±0.9	-45±9	83
<i>Triglops</i> sp.	9	31.9±8.0	15.1±10.4	-75±29	22

from Elliott et al. (2008a). Firstly, their study did not have access to GPS technology, so that foraging location was coarsely estimated using dive depth, flight time and a bathymetry map. This can of course underestimate the effect of foraging location on prey selection. Secondly, their differences in dive behaviour were primarily associated with prey items such as squid or fish doctor *Gymnelus viridis*, that were too rare during our study to be analyzed; the species present on both studies, like cod and sculpin, were considered to be caught in similar foraging conditions by Elliott et al. (2008a), while we showed that foraging location can easily be used to separate those prey items. Indeed, fish habitat preference might drive most of the variation in prey scapes (Takahashi et al. 2008, Watanuki et al. 2008). *Triglops* is found in deeper water than young cod and daubed shanny, which prefer coastal areas (Andriyashev 1954, Craig et al. 1982, Pietsch 1993, Mecklenburg and Sheiko 2004). Similarly, small invertebrates are more abundant in the middle of the water column (Iken et al. 2005), and sculpin near the bottom and closer to shore (Vanier 1996). Furthermore, more energetic prey (e.g. shanny and cod) are likely depleted around the colony and only captured further off, while the less energetic invertebrates and small sculpins are only fed to the chick if caught close to the colony (Elliott et al. 2009).

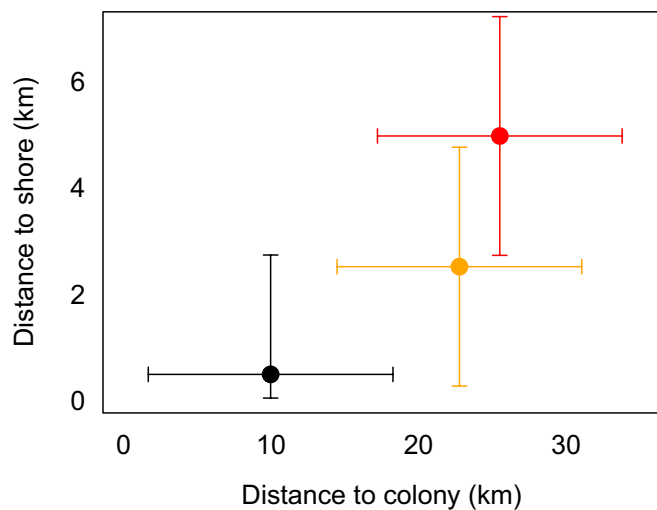


Figure 5. Distance to shore and distance to colony is larger for capelin caught by remote-prey specialists (red) compared with those caught by colony-adjacent prey specialists (black) and capelin specialists (orange). The arrows represent the standard deviation.

Woo et al. (2008) showed a high level of dietary specialisation among individuals at our study site, with some individuals coming back to their nest with otherwise rare prey types year after year. Apparently, birds specialize by having preferences for particular locations when foraging, while underwater behaviour has little effect on the bird's diet. For example, even capelin, the most widespread prey, was caught farther from the colony by remote-prey specialists than by colony-adjacent specialists. This highlights the fact that individuals have stereotyped foraging location preference, which will then have an effect on which prey type they will likely capture.

Applications for indicator species and research needs

The proposed preyscapes could provide insight into the distribution of the marine fauna in the Arctic. Thick-billed murres can travel hundreds of kilometers from the colony to forage for their chick (Benvenuti et al. 1998). A boat survey by icebreaker of the same Arctic area would cost hundreds of thousands of dollars, and only provide a snapshot in time. As already noted, such preyscapes could be biased towards the energetically-profitable prey (e.g. amphipods are clearly present far from the colony). The different handling and capture methods depending on the prey type could also be exploited to remotely detect large fish captures using accelerometers (Watanabe and Takahashi 2013, Chimienti et al. 2016). Our results are less promising for the ability to develop such preyscapes that include maximum depth, as maximum depth and dive shape were only weakly related to prey type. Moreover, we clearly cannot assume that prey delivered to the chick were caught at the deepest point of the dive (Elliott et al. 2008a) as fish captures occurred even in the ascent phase centimeters below the surface. Rather than using that assumption, we recommend using acceleration to identify where the last prey capture event occurred, using algorithms similar to the ones proposed by recent research (Watanabe and Takahashi 2013, Chimienti et al. 2016). Similarly, we cannot assume that the prey were caught on the final dive, as is usually assumed (Elliott et al. 2008a); we observed one bird that kept diving after it caught a fish for its chick. Possibly, the individual was assessing the possibility of catching a larger prey. The use of accelerometers could again provide a solution to the problem, as considering the last catching event before the prey delivery to the chick would eliminate all the capture-less dives. However, a

good validation of the algorithm determining prey capture using acceleration needs to be realized on thick-billed murres before this methodology is implemented.

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Conflicts of interest – There is no conflict of interest among the authors.

Author contributions – ÉBC and KE both designed the experiment and collected data in the field. ÉBC conducted the analysis, while both authors took part in the writing.

Permits – Wildlife Research permit no. 2016-036 from the Dept of Environment was acquired for the experiments.

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Supplementary material (available online as Appendix jav-01930 at <www.avianbiology.org/appendix/jav-01930>). Appendix 1.