Modeling foraging range for breeding colonies of thick-billed murres *Uria lomvia* in the Eastern Canadian Arctic and potential overlap with industrial development

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ABSTRACT

Mapping areas of conservation concern for wildlife in the Arctic is urgently required to evaluate the impact of accelerating development in northern regions. There is substantial evidence that large seabird colonies reduce the availability of food in adjacent waters, creating a zone known as "Ashmole's Halo". Given the existence of the halo, Central Place Foraging theory (CPF) allows us to make predictions about the distribution of food and birds at different distances from the colony. Using a time-budget approach and a CPF framework, we modeled the relationships between foraging range and colony size for thick-billed murre colonies in Eastern Canada and calibrated these predictions against foraging trip distances recorded by GPS loggers attached to incubating birds at two colonies differing in population size by an order of magnitude. Our results support the general predictions of CPF and allow us to predict maximum foraging ranges for Canadian Eastern Arctic colonies, enabling us to map likely zones of overlap between the foraging of breeding birds and future development activities in Canadian Arctic marine waters. A similar approach could be used for many seabird species where the majority of breeding birds occupy a small number of discrete colonies.

1. Introduction

"*The most significant threat from ships to the Arctic marine environment is the release of oil through accidental or illegal discharge.*" (Arctic Council, 2009).

Global requirements for oil and minerals and the increasing duration of the open water period created by climate change are encouraging industrial developments in the Arctic. These include many that are likely to have an impact on marine environments: the opening up of new mines, with attendant shipping (Ho, 2010); exploration for offshore hydrocarbons (Borgerson, 2008; Gautier et al., 2009); and exploitation of new fishing grounds (Zeller et al., 2011). Given the very low level of human interference

that many of these waters have experienced to date, the environmental consequences of these developments need to be carefully assessed (Huntington, 2009).

Seabirds are among those marine organisms most likely to be affected by developments in the marine Arctic. They are particularly vulnerable to oil pollution at sea (Clark, 1984; Wiese et al., 2004) and mass mortality of seabirds occurs periodically as a result of marine oil spills (Piatt et al., 1990; Crawford et al., 2000). Feeding may also be disrupted by vessel traffic (Schwemmer et al., 2011; Agness et al., 2013). As many seabirds feed high in marine food chains, they are sensitive indicators of changes in ecosystem states (Burger, 2006; Parsons et al., 2008). During the summer, many species gather to breed in large colonies situated on the coast. These localities are mostly well known and have persisted over long periods of time (Gaston and Donaldson, 1996; Moss, 2007). The localisation and fixity of these breeding sites confers an advantage in making decisions on the sensitivity of different marine areas and it is customary to consider the waters immediately adjacent to large colonies as being highly sensitive

(Wilcox and Chaundy, 2001). However, the colonies simply form the operational base for birds commuting to distant foraging grounds. To better evaluate the potential for disturbance to foraging breeders and pollution of feeding areas, we need to know where they are going to feed and how much time they are spending there (Camphuysen et al., 2012). The at-sea distribution of breeding birds is being gradually mapped through the deployment of various position-logging devices (Benvenuti et al., 1998; Ropert-Coudert and Wilson, 2005; Ford et al., 2013; Tranquilla et al., 2013). However, many breeding sites are very remote and it may be many years before basic tracking information is available for all of them, placing a premium on our ability to make general predictions about likely foraging ranges.

In this context, the Central-Place Foraging (CPF) theory, a special case of Optimal Foraging theory, provides an ideal framework for predicting the area within which disturbance at sea on seabirds might occur. CPF deals with animals which commute from a central site, whether a roost, a nest, or a breeding colony, to feed at distant feeding areas (Hamilton and Watt, 1970; Charnov et al., 1976; Andersson, 1978, 1981; Orians and Pearson, 1979). One of the applications of the CPF to seabirds has been to explore the potential effects on prey stocks of large numbers of birds commuting from a breeding colony. These aggregations can create a zone of food depletion around the site, commonly known as Ashmole's Halo, after the idea originally proposed by R.W. Storer (1952) and N.P. Ashmole (1963) (see Birt et al., 1987; Lewis et al., 2001; Gaston et al., 2007). One prediction of CPF is that foraging will become more efficient, in terms of food acquisition rate, as animals move away from the central place (Charnov et al., 1976; Kacelnik, 1984) and this has been demonstrated for some seabirds (Birt et al., 1987; Gaston et al., 2007; Ballance et al., 2009; Elliott et al., 2009a), but not all (Grémillet, 1997; Ford et al., 2013).

Using the framework of CPF theory we can make useful predictions about the behaviour of colonial seabirds (Satterthwaite and Mangel, 2012). If the CPF prediction of increasing feeding efficiency as animals travel farther from the central place holds true then we should not expect to find the highest densities of seabirds close to their breeding site – in fact the reverse should be true (Gaston et al., 2007). At the same time, breeding imposes constraints on seabirds, which force them to return to the colony periodically, either to take their share of incubation, or to provision their nestlings. The duration of the at-sea period is imposed by many factors relating to their life-history characteristics (Gaston, 2004; Shoji et al., 2011) and forces an upper limit to their foraging range, as commuting time approaches the entire time available for foraging. An interaction between the limits imposed by life history constraints and the depletion of local food supplies is to be expected and will influence the distribution and density of birds feeding around a colony.

We investigated travel distances and at-sea feeding areas for thick-billed murres (*Uria lomvia*) during incubation at two colonies in the Eastern Canadian Arctic, which differ in population size by an order of magnitude. The thick-billed murre is the most numerous seabird in the Canadian Arctic (Gaston et al., 2012a) and in the region of the two study colonies the species outnumbers all other auks by more than 10:1 (Gaston et al., 2012a). In addition, species of the genus *Uria* are very susceptible to oil pollution (Seip et al., 1991; Wiese et al., 2004) and therefore are most likely to be affected by increased shipping and offshore oil and gas developments in the future.

During the incubation period, birds do not need to deliver food to their chicks and therefore are only constrained in returning to the colony by their partner's capacity to fast. This should allow them to feed farther away from their colony during incubation than during the chick-rearing period (Gaston, 1985). Hence, we compare observed maximum foraging range and distributions at sea with predictions from CPF and use this information to predict the likely maximum foraging range for Canadian Arctic colonies – at least during the incubation phase – to provide a scientific background to the creation of more realistic maps of marine sensitivity than could be achieved by assuming a fixed foraging radius for all colonies.

CPF predictions were modeled using the technique presented by Gaston et al. (2007), based on a time budget estimate of energy expenditure but updated with recent information on activity-specific energy costs for thick-billed murres (Elliott et al., 2012) and on realised travel speeds measured by bird-borne data loggers (this paper). The earlier model (Gaston et al., 2007) was developed to compare birds rearing chicks and therefore incorporated the food needed by the nestlings. In this paper we deal with the simpler situation during incubation, when the birds are foraging only for themselves. The paper is intended to illustrate the use of foraging theory to make useful predictions about potential conflicts with development activities and, as such, we do not attempt to describe the foraging of the murres in detail. Consequently we use our field data only to derive two statistics for model input: the maximum foraging radius of the colonies and the mean flight speed of the birds.

2. Methods

2.1. GPS deployment and analysis

Fieldwork was carried out at Coats Island, Nunavut, Canada (62°57′N, 82°00′W; Gaston et al., 1994) in 2010 and 2011 and at Digges Island (62°33′N, 77°43′W; Gaston et al., 1985) in July 2012. The Coats Island colony is estimated at 30,000 breeding pairs and the Digges Sound colony, of which the Digges Island birds form a part, at 400,000 pairs (Gaston et al., 2012a,b). We attached GPS tags (CatTraQ™1, Catnip Technologies, http://www.mr-lee-cat-cam.de/pe_cc_i9.htm; modified at the Institut Pluridisciplinaire Hubert Curien, CNRS, France, with additional waterproofing) weighing 30 g (3% body mass), external dimensions $5 \times 3 \times 1.5$ cm, to the dorsal feathers of adult birds incubating eggs, using marine adhesive tape (Tesa©). Birds were captured by noosing around the neck, a procedure that has been used on many thousands of murres without injury to the birds. Birds were weighed (±10 g on a spring balance) before the device was attached. The deployment of the devices took less than 5 min and birds were released immediately. They were recaptured within 72 h, the devices removed and the data downloaded in the field. The times of deployments and retrievals were recorded to within 1 min. All procedures were approved under Environment Canada Animal care permits 1000-AG01a, 11-AG02, EC-PN-12-0, Migratory Bird Research Permits NUN-MBS-09-01, NUN-SCI-11-07 and NUN-SCI-12-01 and Nunavut and Nunavik Wildlife Research permits (WL-2010-038; WL-2011-019, WL-2012-04-06).

The GPS loggers provide data on location, as well as speed, heading (bearing in degrees) and distance from last location. GPS locations were recorded every 5 min for devices deployed at Digges Island. For those used at Coats Island, GPS locations were recorded every 2 min if the speed was below 10 km h^{-1} and every 13 s at higher speeds. For analysis the following data were extracted from the GPS records: duration of trip (T); location of the furthest point on each trip away from the colony; distance to furthest point (D_{max}, km); and the position of Presumed Feeding Areas (PFA). The position of PFA was defined as locations >2 km from the colony where the birds spent >10 min traveling at <5 km/h (at Coats Island >5 consecutive 2-min periods or at Digges Island >1 consecutive 5 min periods). Areas within 2 km of the colony were frequently used by birds engaged in social behaviour and little active feeding

was observed in these aggregations (AJG pers. obs.). The distance between the mid-point of each PFA and the colony by the shortest over-water route was measured (D_{feed}, km), as was the time spent at each PFA (T_{feed}). Where more than one PFA was identified on a trip, we calculated the mean of D_{feed}, weighted by the length of time (T_{feed}):

$$\text{Mean } D_{feed} = \Sigma(D_{feed} * T_{feed})/\Sigma(T_{feed})$$

An index of foraging range as a function of D_{max} was calculated as:

$$\text{Foraging Range Index (FRI)} = \text{Mean } D_{feed}/D_{max}$$
$$= \Sigma(D_{feed} * T_{feed})/\Sigma(T_{feed}) * D_{max}$$

The FRI provides a simplified index of how the area where birds feed relates to their maximum distance from the colony. If birds feed more or less randomly throughout their trip then the value should approach 0.5.

Mean values are given ±1 SD, unless otherwise stated. Data were tested for normality using the Shapiro–Wilk's W-test. All statistics were computed using Statistica 7.1 (Statsoft, 2005). One incomplete trip (logger ceased to operate on the return journey) from Coats Island was included in estimates of D_{max}, but not for total trip duration or FRI.

2.2. CPF modeling

Our model, based on the framework given by Ydenberg (2007), assumes that all adult murres balance their energy budget over a foraging cycle (from the start of one trip to the start of the next) and that they forage "optimally" with respect to the distance they travel, that is, that on average, all travel distances result in a similar energy gain. We divide the time budgets of incubating murres into three segments: incubation at the colony, t_r (assumed to be 50% of the time, as the sexes share incubation duties equally: Gaston and Hipfner, 2000), flight time, t_t, estimated from travel distance (D_{max}), number of foraging trips per day (assumed to be 1 for incubating murres: Gaston and Hipfner, 2000) and flight speed, S km/h, (63 km/h, derived from GPS data, see results) so that $t_t = (D_{max} * 2)/S$; and time on the sea (including diving) t_f (all the remaining time). For details of input constants, see Table 1.

Given the above, Daily Energy Expenditure (DEE) for a given D_{max} can be estimated from (1):

$$\text{DEE} = (((D_{max} * 2)/S) * e_t) + (t_r * e_r) + (t_f * e_f)$$

As birds travel farther away from the colony to feed they spend more time flying, increasing their energy expenditure, as murres burn energy very rapidly in flight, compared with other activities (Elliott et al., 2012), and decreasing the time available for feeding. Our assumption of balanced energy budgets therefore requires that rate of energy acquisition in feeding increases with D, a general assumption of CPF (Andersson, 1981; Kacelnik, 1984). The model enables the estimation of a required feeding rate (F) in relation to D_{max} ($F = \text{DEE}/(0.78*t_f)$), where 0.78 represents the efficiency of assimilation (Brekke and Gabrielsen, 1994; Hilton et al., 2000).

Table 1
Constants used in CPF model. Energy expenditure values are from Elliott et al. (2012), based on the best-fit model not invoking diving depth (unknown for the Digges Island colony).

Input constants	Unit	Value
Flight speed	(km/h)	63
Trip frequency	Trips/day	1
Time at the colony	(h)	12
Energy expenditure at the colony	(kJ/h)	32
Energy expenditure in flight	(kJ/h)	533
Energy exp. on other activities away from the colony	(kJ/h)	99

To model the relationship between colony size and foraging radius, Gaston et al. (2007) assigned the intensity of foraging activity that a given density of prey could sustain throughout the breeding season. They defined the relationship between feeding rate and travel distance as $F_{(d)}$. In reality this is a complex interaction between functional response (Anderson, 2001; Weitz and Levin, 2006), regeneration (growth and reproduction) of the prey base, and the degree to which prey availability can be allowably reduced in the course of a breeding season. All of this ecological context was compressed into an assumed linear relationship between the sustainable density of feeding birds and $F_{(d)}$, where the relationship was labelled α.

To find the colony size that could be sustained within a given foraging range, we computed the area of ocean in successive rings of 5 km, assuming that sea extended for 360° around the colony (A_d), and calculated the sustainable density of feeding birds in each. The number of birds feeding in a given ring (N_d) is the product of the sustainable density and area (A_d):

$$N_d = A_d * F * \alpha$$

In addition to the birds feeding in each ring at any one time, there are birds in transit between that ring and the colony. The number of birds in transit is related to the number feeding as the ratio of transit time to feeding time. The sum of the number of birds traveling and those feeding gives the number exploiting that particular ring. The colony size for a given foraging range can then be calculated from:

$$\text{Colony size} = \Sigma N_d(1 + 2D/(S * t_f))$$

The relationship between colony size and foraging range is approximately logarithmic over the mid-range of observed colony size (Gaston et al., 2007). The shape of the relationship is not dependent on α and should be robust. Note that the assumption of sea for 360° around the colony could be adjusted to accommodate differences in geography, but for colonies with similar geographical settings, which is true for the Coats and Digges island colonies, both having approximately 270° of sea around them, the outcome will be the same, being compensated for by an equivalent adjustment in α.

For the calculations used here we set α to a value (0.003) which gave a relationship of foraging range to colony size that corresponded roughly to what we have observed previously (Gaston et al., 2007), then compared the predicted values of D_{max} to those obtained from our GPS data for the Coats and Digges island colonies. We used the upper 95% confidence bounds on the means of D_{max} for each colony as our values for incorporation into the model, based on the longest trip for each individual (where more than one trip was measured). Colony sizes (breeding individuals) were taken from Gaston et al. (2012a). We then made progressive iterations, varying the value of α by 0.0001, to find the value which minimized the sum of squares for the deviations of the two colony points from the predicted relationship of D_{max} on colony size (α_{fit}, see results). This value was used to predict foraging ranges for all colonies in Eastern Canada. The general form of the results is relatively insensitive to the value of α (Gaston et al., 2007). The model was written as an Excel spreadsheet program.

3. Results

3.1. GPS observations

3.1.1. Coats Island

Data were obtained from 10 birds in 2010 and nine birds in 2011 (Fig. 1a and b). The mean maximum foraging range did not differ significantly between 2010 (19.7 ± 12.2 km) and 2011

(27 ± 14.3 km, t_{17} = −1.17, P = 0.26) nor did the duration of those foraging trips (9.3 ± 4.4 h and 10.6 ± 4.6 h, respectively; t_{17} = −0.59, P = 0.56). Consequently, the data were combined for model input. The duration of foraging trips for the combined sample was 10.0 ± 3.6 h (N = 18, range 3–17 h). Mean D_{max} for the combined sample was 23.3 ± 13.5 km (range 7–50 km, 95% upper bound 50.0 km). Modal foraging range was 16–32 km and only one bird travelled less than 8 km. Mean FRI for longest trips only in 2010 was 0.80 ± 0.07 and in 2011, 0.79 ± 0.10. The corresponding mean PFAs for all trips were 0.78 ± 0.09 (2010) and 0.82 ± 0.09 (2011).

3.1.2. Digges Island

We obtained information on foraging trips from 15 birds at Digges Island (Fig. 1c). The duration of foraging trips averaged 17.9 ± 8.6 h (range 7–30 h) and D_{max} averaged 96.1 ± 37.3 km (range 34–150 km, 95% upper bound 168.8 km). All but three birds travelled more than 64 km from the colony and modal foraging range was 64–128 km (Fig. 2). Mean FRI at Digges was 0.85 ± 0.09 both for all trips and for longest trips only (Fig. 1c).

3.1.3. Inter-colony comparisons

D_{max} for Digges Island birds was significantly higher than for those at Coats Island (t_{31} for unequal variance = −7.17, P < 0.0001) and trips averaged longer than those at Coats Island (t_{31} for unequal variance = 3.30, P = 0.004). Variance in trip duration was higher among Digges Island birds than among those from Coats Island (variance:mean ratios 4.13 and 1.29, respectively, F-ratio variances 5.64, P = 0.001). At both colonies D_{max} was correlated with the total duration of the foraging trip (R^2: Digges 0.74, Coats 0.47) but the slope of the two relationships differed (Fig. 3), with distance increasing more rapidly with duration of foraging trip at Digges than at Coats. At Coats Island the proportion of time spent feeding at different distances from the colony diminished with distance, but at Digges Island the proportion remained fairly uniform out to at least 120 km from the colony (Fig. 4). There was no significant difference in mean FRI between the two colonies (t_{47} = −1.89, P = 0.07; 2010 and 2011 pooled for Coats Island). The median FRI for both colonies combined was 0.86.

Speeds recorded by the devices were highly bimodal, with peaks at 0 and 65 km/h (Fig. 5). We assumed that the second peak corresponded to the flight. Mean of speeds >35 km/h averaged 60 ± 9 km/h for Coats Island and 63.1 ± 10.0 km/h for Digges Island. No significant variation was observed among individuals for flight speeds >35 km/h, after Bonferroni correction. We used the mean of speeds >35 km/h recorded for Digges Island birds (63 km/h) as our model input, as birds there undertook longer sustained flights than at Coats Island.

3.2. Model outputs

Iteration of the model for different values of α gave a minimum sum of squares at α_{fit} = 0.001 for the estimated D_{max} for the two colonies (Coats Island 50.0 km, Digges Island 168.8 km). The resulting model derived relationship of D_{max} to colony size fits the cubic relationship $y = 0.98x^3 − 2.85x^2 + 6.71x − 1.16$ very closely (R^2 > 0.99). This model estimates that a colony supporting 10,000 breeding murres should forage up to 43 km from the colony, with a mean foraging distance of 37 km, a mean rate of energy acquisition during feeding of 258 kJ/h and an ADEE of 2186 kJ (Fig. 6). A colony of 1 million birds – the maximum size currently existing (Gaston and Jones, 1998) would – given similar constraints – forage up to 149 km from the colony, have a mean foraging range of 124 km, acquire energy at that distance at 609 kJ/h (2.4 × the rate necessary at the foraging limit of the 10,000-bird colony) and have an ADEE of 3588 kJ. Both values for ADEE are well within individual

variation measured at Coats Island (Croll et al., 1992; KHE unpubl. data).

Based on currently known population sizes, the fitted relationship predicts foraging ranges for Eastern Canadian Arctic (Nunavut) thick-billed murre colonies ranging from 65 km (Cape Graham Moore, 40,000 birds) to 142 km (Digges Sound and Akpatok Island North, 800,000 birds; Fig. 7).

4. Discussion

Our GPS results are broadly consistent with previous information on thick-billed murre foraging range, although most previous information relates to birds rearing chicks rather than to incubating birds (Mehlum et al., 1998; Benvenuti et al., 1998; Falk et al., 2000, 2002; Takahashi et al., 2008; Elliott et al., 2009a,b), The maximum foraging range reported elsewhere, at 168 km (Benvenuti et al., 1998), is the same as our 95% upper bound for the Digges Island colony. The colony involved in the earlier study (Latrabjorg, Iceland) supported fewer thick-billed murres than Digges (360,000 individuals), but mixed with more than a million common murres *Uria aalge* and razorbills *Alca torda*, potentially causing inter-specific competition around the colony. This may be the biggest colony of large auks anywhere (Gaston and Jones, 1998), so foraging ranges should be near the limits for the species involved.

Because our data for the two colonies was obtained in different years it is possible that some of the difference we observed between the two colonies might be accounted for by inter-year variation. However, data on the duration of return trips to the colony for birds from Coats Island derived from temperature loggers suggested maximum foraging ranges of <60 km for Coats Island birds in several earlier years (Elliott et al., 2008, 2009b). Conversely, observations of birds at sea in earlier years suggest foraging typically extends to >100 km from the colony around Digges Island (Gaston et al., 1985). Consequently the inter-colony variation we observed was probably colony-specific, rather than year-specific. Mean foraging distances observed were smaller than predicted by the model (Coats Island 23 km instead of 37 km, Digges Island 96 km instead of 124 km), but model predictions fell within 1 standard deviation in both cases. The upper confidence bound for Digges Island birds exceeded the predicted maximum foraging range.

At both Coats and Digges islands the number of birds traveling a given distance increased initially with distance from the colony, as predicted by CPF. Most birds from Coats Island foraged beyond 16 km and at Digges Island most foraged beyond 64 km. This result appears to contradict the assumption of Grecian et al. (2012) that the density of foraging seabirds falls exponentially with increasing distance from the colony. However, their assumption involved use of all marine areas, including flying over in transit, whereas our model refers only to time spent on the water, presumably feeding. Moreover, northern gannets *Morus bassanus*, on which Grecian et al. (2012) based their model, search for ephemeral patches of food, spending most of their time in flight (Garthe et al., 2011; Pettex et al., 2012) and create interference competition through prey disturbance (Lewis et al., 2001; Camphuysen, 2011), whereas thick-billed murres spend less time flying and more time on or under the water while foraging (Elliott et al., 2009b) and feed mainly close to their most distant point from the colony, as suggested by Benvenuti et al. (1998) and as demonstrated by our FRI indices (mean feeding distance 86% of D_{max}).

The distribution of feeding time in relation to distance from the colony for Digges Sound birds suggests the presence of Ashmole's Halo during incubation, with birds concentrating their feeding far from the colony (Fig. 4). However, this was not evident for Coats Island, where more time was spent close to the colony. Several
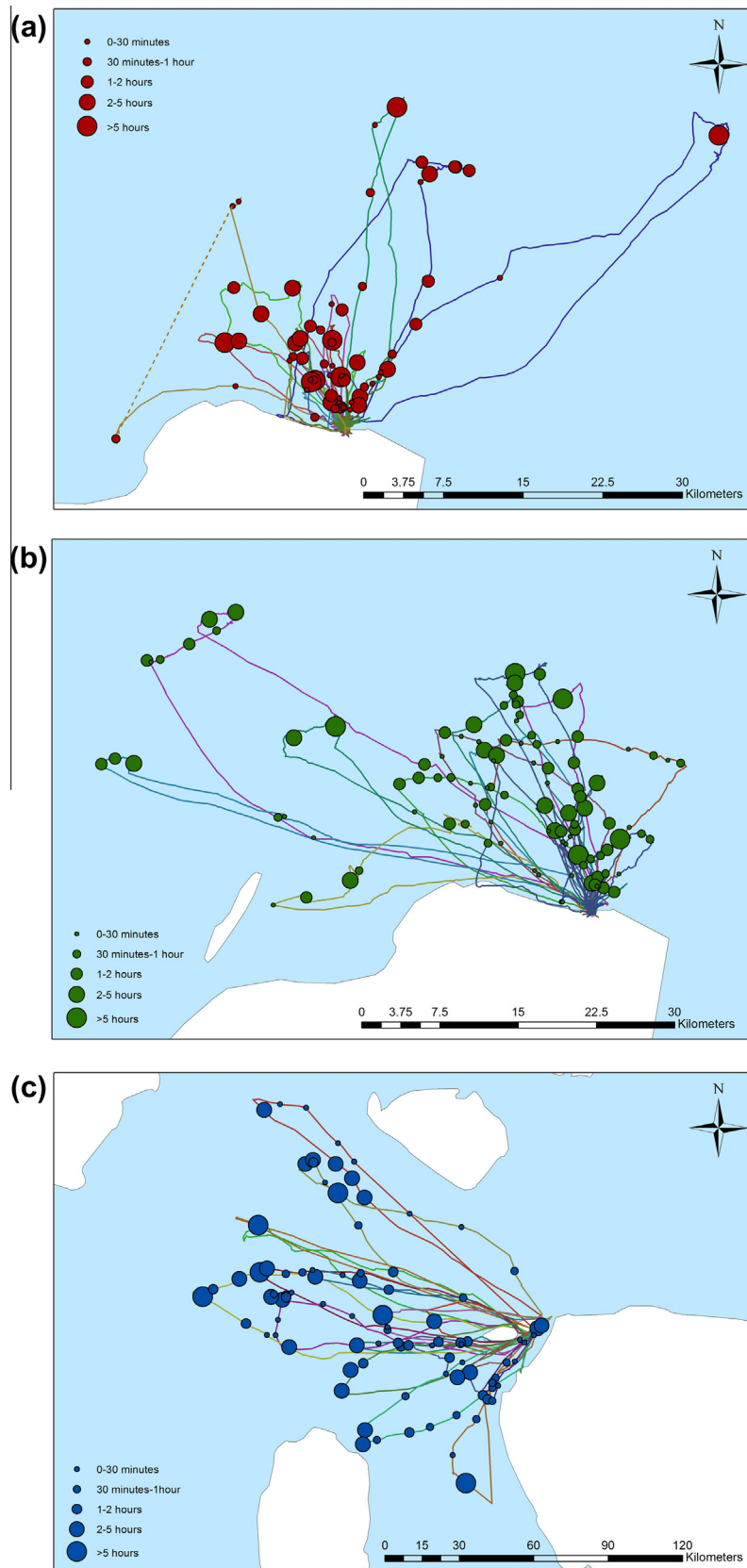
Fig. 1. GPS tracks of incubating thick-billed murres from Coats Island (a) in 2010; and (b) in 2011 and from Digges Island (c) in 2012, showing the position of Presumed Feeding Areas (PFA), the duration of PFA-activity and the direction of travel.

other aspects of breeding biology suggest that breeders at Coats Island find food more easily than those at Digges Sound, at least in recent decades (Gaston and Hipfner, 2006), perhaps delaying the formation of the halo. Nevertheless, information from the chick-rearing period strongly suggests the creation of a halo around the Coats Island colony by that stage of breeding (Elliott et al., 2009a).
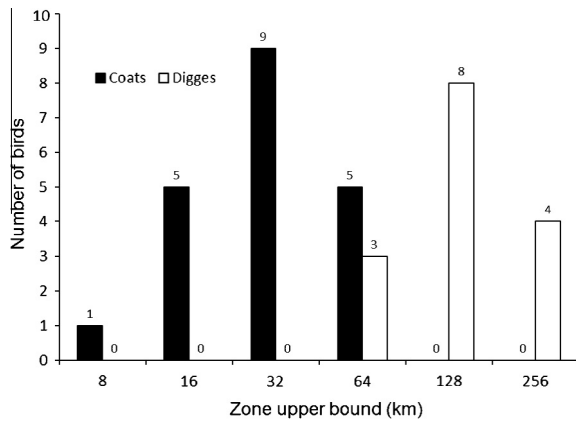
Fig. 2. Distribution of D_{max} for incubating adult thick-billed murres from Coats (2010 and 2011) and Digges (2012) islands.
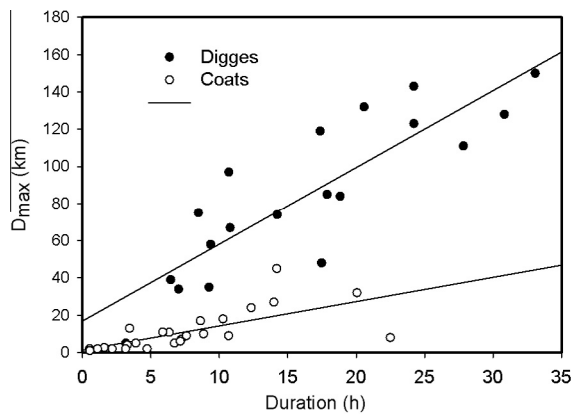

Fig. 3. The relationship of D_{max} to the duration of foraging trips for Coats (open symbols) and Digges (closed symbols) islands. Dotted lines represent 95% confidence intervals on the linear regression lines.
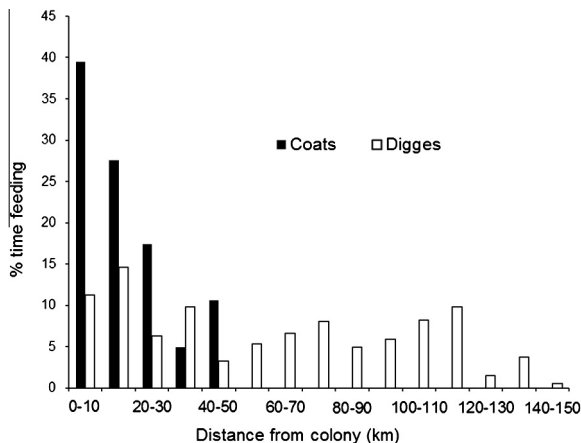

Fig. 4. Proportion (%) of time spent feeding at different distances from the colony by murres from the Coats and Digges island colonies.

The mean duration of foraging trips at Coats Island (10 h) was similar to that expected on the basis of the model assumption of one trip per day (maximum 12 h). However, those at Digges Island were significantly longer (17.9 h, $t_{14} = 2.66$, $P = 0.02$), which suggests that the birds were visiting the colony less than once daily on average. This could be a behavioural adaptation to breeding in such a large colony. If there is a general tendency to make fewer incubation change overs at larger colonies then the model could
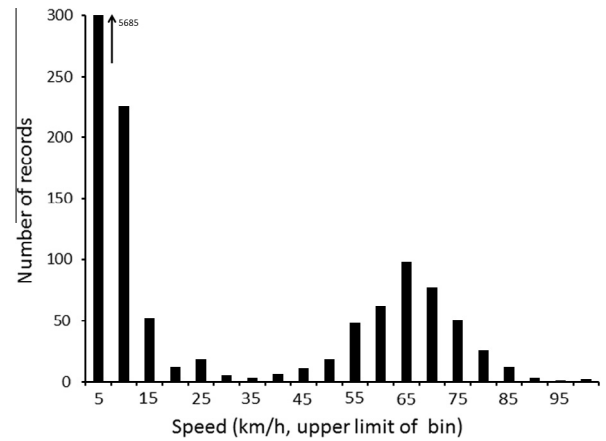
Fig. 5. Distribution of movement speeds recorded for thick-billed murres foraging from the Digges Island colony in 2012.
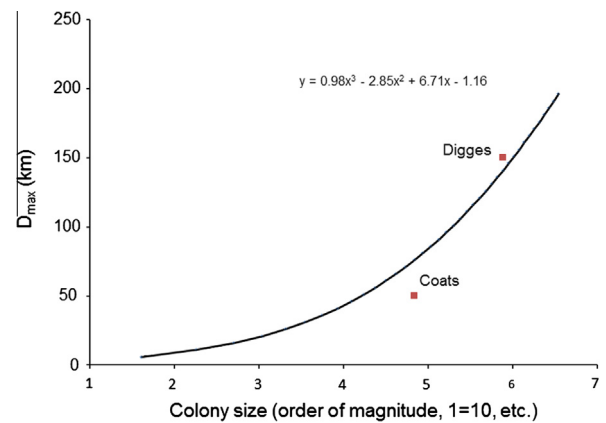

Fig. 6. Model output: maximum foraging range (D_{max}) in relation to colony size (number of breeding birds).

be adjusted to take this into account but, at present, data are insufficient to allow incorporation of varying incubation shift lengths. Information from one high Arctic colony at Prince Leopold Island (74°N) suggests an approximately 12 h shift duration (Gaston and Nettleship, 1981, AJG unpubl. data).

The distributions of outbound headings at both colonies were heavily skewed towards the west (Fig. 1), a feature already noted at Coats Island for birds rearing chicks (Elliott et al., 2008). At both Coats and Digges islands the GPS loggers were deployed on birds breeding at the westernmost of two sub-colonies (see insets in Fig. 1a and c). Waters to the east of these colonies are exploited by birds from the Eastern sub-colonies (the authors' unpubl. data obtained in 2013). Similar segregation in foraging areas between birds from different parts of a single island was observed for three species of penguins by Masello et al. (2010). Such observations support the idea of strong intraspecific competition around colonies, as proposed by Ashmole (1963) and required by CPF theory.

Superimposing estimated foraging ranges on the geography of Canada's Eastern Arctic shows little overlap among colonies (Fig. 7). Only the North and South colonies at Akpatok Island overlap by more than 3% of their combined range. This result is similar to the findings of Furness and Birkhead (1984) for four species of seabirds and of Grecian et al. (2012) for northern gannets and, like the restricted foraging areas of the selected subcolonies, supports the general hypothesis that intra-specific competition is important in determining food availability for breeding murres. The total foraging area estimated for the 10 major thick-billed murre colonies
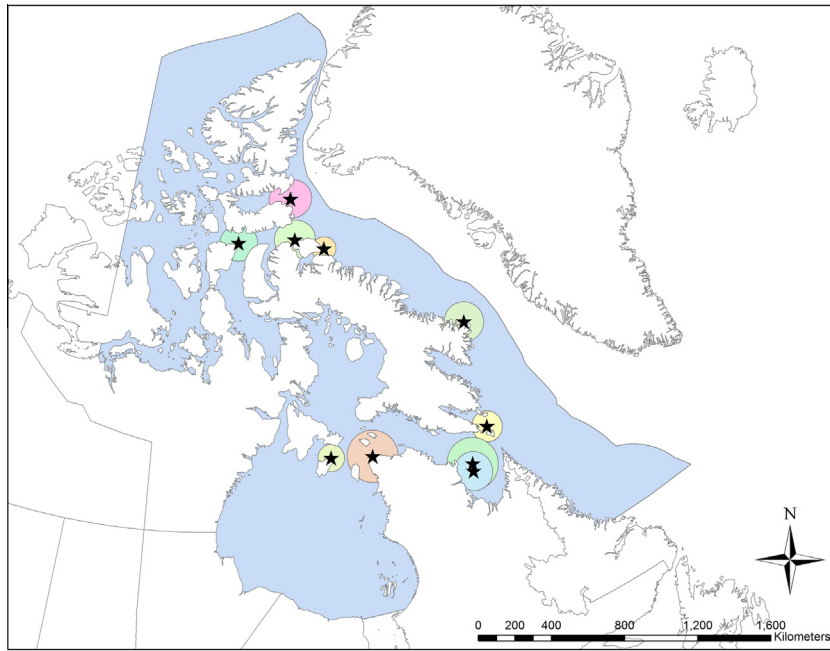
Fig. 7. Model projections for the foraging areas of thick-billed murre colonies in the Eastern Canadian Arctic, based on the most recent estimates of population size (Gaston et al., 2011).

in the Eastern Canadian Arctic amounts to 221,746 km², 8% of Arctic marine waters (north of 55°N, east of 110°W and within Canadian jurisdiction). Individual regions are much more heavily used, with 42% of Hudson Strait and 60% of Lancaster Sound and Barrow Strait (Eastern Parry Channel) within the foraging range of murre colonies. Overlap of the Akpatok colonies is almost total ($\sim$90%). If they are treated as one colony, with a breeding population of 1,004,000, D_{max} is estimated at 149 km and the predicted foraging area is very similar to that shown in Fig. 7, hence treating them separately or together has little influence on the outcome.

Although the foraging range of incubating thick-billed murres covers only a small proportion of Arctic waters, the distribution of colonies is such that shipping cannot enter Hudson Strait, Lancaster Sound or Jones Sound without passing through part of a projected colony feeding area (Fig. 8). To assess the potential disturbance to different colonies from current shipping patterns, we counted the total number of ship routes passing through the model-predicted foraging ranges of each colony in 2010 (Fig. 8); a year when ice conditions were relatively open in the Eastern Canadian Arctic. We used these counts to develop an index of

High Potential for Oil Development
★ TBMU Colonies
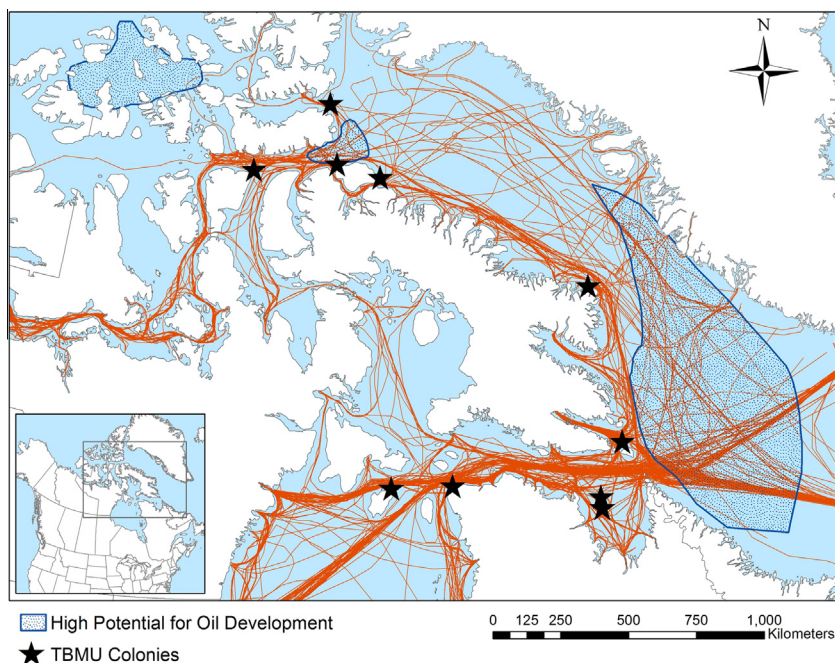
Fig. 8. The position of shipping tracks during 2010 (Transport Canada, 2011) and known or anticipated offshore oil and gas deposits (Beauregard-Tellier, 2008) in waters of the Canadian Eastern Arctic.

Table 2
Location and model-derived maximum foraging radius for the ten thick-billed murre colonies in Nunavut and calculations for the disturbance index (ship tracks passing through the zone defined by a circle of radius D_{max} around the center of the colony, divided by the sea area within this foraging zone).

Colony	Location	Estimated population (breeding birds)	Estimated D_{max} (km)	Actual sea area within D_{max} (km²) ('A')	Ship tracks intersecting foraging zone ('B')	Disturbance index ($B*10,000/A$)
Coburg Island	75°48′N, 79°25′W	300,000	111.8	26,388	17	6
Prince Leopold I.	74°02′N, 90°00′W	200,000	100.9	20,541	59	29
Cape Hay, Bylot I.	73°46′N, 80°23′W	280,000	109.9	21,682	57	26
Cape Graham Moore	72°56′N, 76°02′W	40,000	65.2	8377	25	30
The Minarets	66°56′N, 61°46′W	260,000	107.8	25,932	44	17
Hantzsch Island	61°55′N, 65°00′W	100,000	84.1	18,621	115	62
Akpatok N1	60°34′N, 68°00′W	800,000	141.5	55,976	222	40
Akpatok S	60°15′N, 68°15′W	240,000	105.7	31,577	61	19
Digges Sound	62°33′N, 77°36′W	800,000	141.5	42,266	150	35
Coats Island	62°57′N, 82°00′W	60,000	73.2	13,481	48	36

disturbance (tracks*10,000/foraging area; Table 2). The index ranged from 6 for the large, remote colony on Coburg Island to 62 for the smaller Hantzsch Island colony, situated at the mouth of Frobisher Bay. With exception of the south colony at Akpatok Island, the low Arctic colonies show a greater likelihood of disturbance (indices 35–62) than the high Arctic colonies (indices 6–30). Although crude, the index does illustrate how disturbance from shipping is likely to differ widely among colonies, depending on size and geography.

It is noteworthy that Hudson Strait, currently the busiest shipping route in the Eastern Canadian Arctic and home to the largest thick-billed murre colonies, is one of the regions in Canada where ice conditions are changing most rapidly (Derksen et al., 2012). Moreover, current plans for shipping in Hudson Strait include year-round ice-breaking that will see ships passing the Strait every 48 h (Fisheries and Oceans Canada, 2012). The consequences for marine ecosystems of this ice-breaking, on top of the rapid ongoing changes in ice conditions, are unknown. However, it seems almost certain that trends already identified in the diets of thick-billed murres towards a lower intake of ice-associated Arctic cod *Boreogadus saida* and a high intake of capelin *Mallotus villosus* and invertebrates (Provencher et al., 2012; Gaston et al., 2012b) will continue, irrespective. Likewise, ship traffic through Baffin Bay into Lancaster Sound is likely to increase soon, as a result of increases in tourism, military activity and mining (Arctic Council, 2009), as well as inter-continental trade (Smith and Stephenson, 2013). In addition, prospects for offshore oil and gas extraction include areas either within the projected foraging range of murre colonies, or in localities that would require marine transport of oil to pass through such foraging zones.

Advances in miniature tracking technologies (e.g. Elliott et al., 2009a,b) have allowed us to reliably measure the foraging ranges for part of the season at two thick-billed murre colonies in the Canadian Arctic. This represents a very small sample so extrapolations must be performed with caution. However, given that the results fitted well with expectations from CPF theory, we felt justified in using these results to model foraging ranges around other murre colonies in the Eastern Canadian Arctic. What are now required are: (a) data on foraging ranges during different stages of the breeding season, to look for seasonal shifts in range; (b) data from other murre colonies, to improve our predictions; and (c) data on foraging ranges of other Arctic marine bird species

(e.g., black-legged kittiwakes *Rissa tridactyla*, black guillemot *Cepphus grylle*, Arctic tern *Sterna paradisaea*), so that we can identify important areas to conserve as part of marine spatial planning (e.g., Agardy, 2000; Douvere and Ehler, 2011; Camphuysen et al., 2012). Nonetheless, our preliminary results suggest strongly that increased development activities in Canada's Arctic will inevitably overlap with important feeding areas for murres (and probably other seabirds). Consequently, we need to study how shipping and other human activities will influence murre distribution and foraging at sea and, by extension, influence the marine ecosystems of which they form a part. This issue is especially important at a time when threats of disturbance and potential pollution come on top of stresses already affecting these populations from climate change (Provencher et al., 2012; Gaston and Elliott, 2013).

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.09.018. These data include Google maps of the most important areas described in this article.

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