



CENTRAL-PLACE FORAGING IN AN ARCTIC SEABIRD PROVIDES EVIDENCE FOR STORER-ASHMOLE'S HALO

KYLE H. ELLIOTT,^{1,6} KERRY J. WOO,² ANTHONY J. GASTON,³ SILVANO BENVENUTI,⁴
LUIGI DALL'ANTONIA,⁵ AND GAIL K. DAVOREN¹

¹Department of Biological Sciences, University of Manitoba, Winnipeg, Manitoba R3T 2N2, Canada;

²Department of Biology, University of Ottawa, Ottawa, Ontario K1N 6N5, Canada;

³Science and Technology Branch, Environment Canada, National Wildlife Research Centre, Ottawa, Ontario K1A 0H3, Canada;

⁴Dipartimento di Biologia, Ecologia ed Evoluzione, University of Pisa, Via volta 6, 56126 Pisa, Italy; and

⁵Istituto di Elaborazione dell'Informazione, C. N. R., Via S. Maria 46, 56126 Pisa, Italy

ABSTRACT.—Breeding seabirds are extreme central-place foragers, commuting long distances between colonies and feeding areas. Central-place foraging theory predicts that prey items close to the colony will be preferred over prey items distant from the colony, which can lead to prey depletion near the colony (“Storer-Ashmole’s halo”). To investigate the relevance of these ideas to a single-prey loader, we equipped chick-rearing Thick-billed Murres (*Uria lomvia*) with time–depth recorders (1999–2007) and monitored prey deliveries (1993–2008). Because feeding rates were constant for chicks 3–15 days old, we restricted analyses to that age group. Between-date relationships were examined within individuals to avoid confounding effects of specialization and parental quality. The mass of prey items increased with foraging distance^{0.5}, which suggests that large prey items were depleted by foraging pressure. Foraging distance for pelagic species increased through the season in years without spawning. After accounting for bathymetry, foraging effort decreased with distance from the colony for benthic fish and, in years without spawning, for pelagic fish. Within each season, Thick-billed Murres “fished down the food web”; they began by feeding on large fish, progressed to medium-sized prey (small fish), and finished feeding on small prey (invertebrates). We concluded that pelagic species responded to seabird foraging pressure by moving away from the colony, creating a three-dimensional halo. Benthic species, meanwhile, were depleted from a nearby shelf but remained abundant at a more distant offshore bench. We suggest that populations of central-place foragers are partially regulated by prey depletion. Received 5 December 2008, accepted 18 March 2009.

Key words: central-place foraging, food-web structure, Hudson Bay, resource depletion, Thick-billed Murre, top-down forcing, *Uria lomvia*.

L’approvisionnement à partir d’un nid central chez un oiseau de mer de l’Arctique fournit une preuve du halo de Storer-Ashmole

RÉSUMÉ.—Les oiseaux de mer nicheurs sont des cas extrêmes d’organismes s’approvisionnant à partir d’un nid central, faisant la navette sur de longues distances entre les colonies et les aires d’alimentation. La théorie de l’approvisionnement à partir d’un nid central prédit que les proies se trouvant à proximité de la colonie seront préférées à celles se trouvant loin de la colonie, ce qui peut mener à la diminution de la quantité de proies près de la colonie («halo de Storer-Ashmole»). Afin d’examiner si ces idées s’appliquent à un oiseau qui ne transporte qu’une proie à la fois au nid, nous avons muni d’enregistreurs de la durée et de la profondeur des *Uria lomvia* au cours de l’élevage des poussins (1999–2007) et suivi les livraisons de proies au nid (1993–2008). Les taux de nourrissage étant constants pour les poussins âgés de 3 à 15 jours, nous avons limité les analyses à ce groupe d’âge. Les relations entre les dates ont été examinées par individu pour éviter de confondre les effets de la spécialisation et de la qualité parentale. La masse des proies augmentait en fonction de la distance parcourue pour s’approvisionner, ce qui suggère que les grosses proies ont été épuisées par la pression de pêche. La distance parcourue pour s’approvisionner chez les espèces pélagiques augmentait avec l’avancement de la saison lors des années sans frai. En tenant compte de la bathymétrie, l’effort de pêche diminuait avec la distance de la colonie pour les poissons benthiques et, lors des années sans frai, pour les poissons pélagiques. À chaque saison, *U. lomvia* “ont pêché en descendant la chaîne alimentaire”; ils ont commencé à pêcher les gros poissons, puis les proies de moyenne taille (petits poissons), pour finir avec les petites proies (invertébrés). Nous avons conclu que les espèces pélagiques ont répondu à la pression de pêche des oiseaux de mer en s’éloignant de la colonie, créant de ce fait un halo tridimensionnel. Les espèces benthiques, pour leur part, ont été épuisées d’un plateau proche mais demeurent abondantes dans un banc plus éloigné au large. Nous suggérons que les populations de consommateurs retournant à un nid central sont partiellement contrôlées par la diminution des proies.

⁶E-mail: haliaeetus@gmail.com

MANY MARINE ANIMALS, including lactating seals and breeding seabirds, return to a central location after each foraging bout. For these central-place foragers, foraging time includes transit time to and from the central place, as well as searching and handling time (Orians and Pearson 1979, Ropert-Coudert et al. 2004, Wilson et al. 2005). To maximize foraging efficiency, central-place foragers are expected to minimize transit time by selecting nearby foraging patches and traveling along the most direct path to and from the central place (Baird 1991, Ydenberg et al. 1994, Saunders and Ydenberg 1995). Distant foraging patches will be used only if net energy gain (e.g., larger or more prey) is higher than at nearby patches (Houston and McNamara 1985, Cuthill and Kacelnik 1990, Waite and Ydenberg 1996). As predicted, the size of prey captured increases with the distance to the patch for many central-place foragers (colonial seabirds: Wanless et al. 1993b, Ainley et al. 1998; nesting songbirds: Carlson and Moreno 1981, Hegner 1982, Carlson 1983, Kacelnik 1984, Krebs and Avery 1985, Tamm 1989, Kacelnik and Cuthill 1990; rodents with central caches: Kramer and Nowell 1980, Elliott 1988, Fryxell and Doucet 1991, Bowers and Ellis 1993, Giraldeau et al. 1994, Jackson 2001, Gallant et al. 2004, Barrette and Giraldeau 2008; social insects: Martin and Vinson 2008). There are examples, however, where this trend was not observed (e.g., Jenkins 1980, Sodhi 1992, Alonso et al. 1994, Frey-Roos et al. 1995), and there is little information available on marine animals. Because of the three-dimensional nature of marine environments, other factors (e.g., bathymetry) may be more important than distance for determining the foraging efficiency of marine central-place foragers (Haney and Schauer 1994, Rodary et al. 2000, Sjöberg and Ball 2000).

Central-place foraging implies that net energy gain is higher at some distance from the central place than at the central place; if this were not so, there would be no reason to leave the central place. In the context of seabird colonies, foraging away from the immediate vicinity of the central place can occur for three reasons. First, there may be unsuitable habitat for nesting near prey patches. For example, foraging patches (fish spawning grounds) may be distant from the only location suitable for breeding (Davoren et al. 2003a, Hedd et al. 2009; see also Boersma et al. 2009). Second, intraspecific competition at prey patches close to the colony may decrease foraging efficiency at nearby patches (Davoren et al. 2003b). Lastly, prey may be initially distributed uniformly but may become depleted close to the colony as a result of preferential selection of prey items near the colony early in the breeding season. This can occur either through the removal of benthic species (Birt et al. 1987) or through movement away from the colony by mobile pelagic species (predator avoidance; Lewis et al. 2001, Litzow et al. 2004).

The last alternative implies that an annulus forms around the colony ("Storer-Ashmole's halo") where prey items become absent or in low abundance (Storer 1952, Ashmole 1963, Gaston 2004, Gaston et al. 2007). The size of Storer-Ashmole's halo is predicted to increase with colony size and seabird foraging success and, thus, reproductive success decreases with the size of the halo (Storer 1952, Cairns 1989, Gaston et al. 2007). This interaction leads to food-limited, density-dependent population regulation, which may be the ultimate cause for K-selected life-history strategies in seabirds, including delayed maturity, low fecundity, and high adult survival (Gaston 2004, Dobson and Jouventin 2007).

Despite the importance of Storer-Ashmole's hypothesis for understanding seabird population ecology, it has been directly tested only once. Fewer benthic fish were counted on SCUBA transects near a Double-crested Cormorant (*Phalacrocorax auritus*) colony than on those farther away (Birt et al. 1987). Indirect evidence of prey depletion, however, has been deduced from positive correlations between colony size and (1) reduced chick physiological condition (Tella et al. 2001, Davoren and Montevecchi 2003), growth (Gaston et al. 1983, Kitaysky et al. 2000), and meal size, quality, and regularity (Forero et al. 2002, Ainley et al. 2004, Hipfner et al. 2006); (2) reduced adult body condition (Gaston and Hipfner 2006) or increased adult metabolic rate (Kitaysky et al. 2000, Bal-lance et al. 2009); (3) reduced size of neighboring colonies (Furness and Birkhead 1984; Ainley et al. 1995, 2004; Lewis et al. 2001; Forero et al. 2002; Ford et al. 2007); and (4) increased trip duration (Lewis et al. 2001; Ainley et al. 2003, 2004; Davoren and Montevecchi 2003). Nonetheless, these correlations are not always observed (e.g., Falk et al. 2002, Frederiksen et al. 2005, Petersen et al. 2006) or are observed only in some years (Ainley et al. 2004). Cairns et al. (1990) showed that birds used shallower dive depths as they traveled farther from the colony. They suggested that this represents a three-dimensional halo, with prey being depleted at greater depth close to the colony than in more distant areas, which leads to a decrease in foraging effort with distance to the colony. However, all of the above indirect correlations may be attributable to interference rather than exploitative competition (Ainley et al. 2003, Davoren et al. 2003b).

Because most seabirds make relatively long foraging trips and return with many prey items, it is difficult to link specific dive bouts with particular prey (Simeone and Wilson 2003, Tremblay et al. 2005, Wilson et al. 2005). Thick-billed Murres (*Uria lomvia*; hereafter "murre") provide an opportunity for overcoming this difficulty because they are single-prey loaders, usually returning with a single, readily identifiable prey item, and are large enough to accommodate data-logging devices with little effect on behavior (Jones et al. 2002, Paredes et al. 2008, Takahashi et al. 2008). Here, we combine information on prey deliveries to chicks with at-sea foraging behavior from time-depth recorders (TDRs) attached to murre parents at an Arctic colony during chick rearing. We assume that the last dive represents the dive during which chick prey was captured and that individuals return directly to the colony after the last dive bout (Benvenuti et al. 1998; Falk et al. 2000, 2002). We predicted that (1) prey size would increase with distance to a foraging patch; (2) dive depth would be shallower as distance increased, because of the depletion of shallow-water prey in the vicinity of the colony resulting in birds foraging at more distant locations to capture prey at shallower depths; (3) distance to a foraging patch would increase with date during each breeding season, because of depletion of prey items in the vicinity of the colony; and (4) for similar reasons, the proportion of large prey items would decrease with date during each breeding season.

METHODS

At-sea behavior.—The study was conducted at the west colony on Coats Island (62°57'N, 82°00'W), Nunavut, Canada (Gaston et al. 2003, 2005), during 1993–2008. Murres were caught with a noose pole ($n = 24$ in 1999; $n = 23$ in 2004; $n = 33$ in 2005; $n = 80$ in 2006;

$n = 37$ in 2007). Handling time was always <10 min and usually <5 min. During 1999, we fitted “Benvenuti” TDRs (see Falk et al. 2000, 2002; Benvenuti et al. 1998, 2002; mass = 28 g; sampling interval = 4 s [pressure] or 8 s [flight]; maximum recordable depth = 76 m) to feathers along the midline of the lower back using tape to minimize drag. During 2004–2007, we secured Lotek 1100LTD TDRs (mass = 4.5 g; sampling interval = 3 s) with duct tape to plastic bands that were attached to the legs of murres. We used the temperature log from the TDR to determine whether the bird was on the water, in the air, or at the colony (Elliott et al. 2007, 2008d). Whereas back-mounted TDRs (e.g., Benvenuti TDRs) affect murre provisioning rates, trip duration, mass loss, dive depth, and time allocation during diving (Hamel et al. 2004; Paredes et al. 2004; Elliott et al. 2007, 2008a), our smaller, leg-mounted Lotek TDRs had no measurable effect on any of these parameters (Elliott et al. 2007, 2008d). Consequently, we completed separate analyses for each year. The TDR analyses followed Elliott et al. (2008d).

Because we also knew when the bird arrived at the colony from the feeding watches, we were able to determine flight time between the last dive and prey delivery to the chick. We converted flight time into distance assuming a flight speed of $75 \text{ km}\cdot\text{h}^{-1}$, ignoring variation in flight speed with wind speed, load, and other factors (Elliott and Gaston 2005). This calculation assumed that murres returned in a straight line from their foraging destination, as predicted from theoretical considerations for single-prey loaders (Orians and Pearson 1979, Houston and McNamara 1985, Chapman et al. 1989, Houston 2000) and as shown in other studies of murres (Benvenuti et al. 1998; Falk et al. 2000, 2002). We assumed that the maximum depth of the last dive before the individual returned to the colony represented the depth at which the prey item was caught. We ignored dives shallower than 3 m because of device uncertainty. Because few chick-provisioning dives occurred within the period when murres’ dive depth is reduced because of decreased light availability (2100–0400 hours; Croll et al. 1992; cf. Hedd et al. 2009), we ignored time of day as a factor in our analysis.

Prey observations.—During deployment of TDRs, continuous observational watches of 40–60 murre nest sites were conducted (“feeding watches”; Elliott et al. 2008a, b). All observations were made from blinds situated on the study plots, within 6 m of the birds. We also completed at least three continuous feeding watches at Q subcolony in years when TDRs were not deployed (1993–2008), with watches spaced approximately five to seven days apart, starting when ~50% of nestlings were hatched (Gaston et al. 2003). Fish length was estimated by reference to the white streak on the upper mandible of the adult’s bill (~5 cm). Length was then converted into energy content using known relationships derived as part of the same study (Elliott and Gaston 2008). When observer underestimation of tail length has been accounted for, this method is accurate at determining energy intake rates within $\pm 2\%$ (Elliott et al. 2008b). Because older chicks theoretically require more food and adults may fly farther or provision more or use different prey items in response to these changes, we examined the effect of chick age on feeding rates by recording the hatch date within 48 h for a subset of 10–40 feeding sites during 12 of 16 years. Because the number of feeds per hour and energy delivered per hour did not change for chicks 3–15 days old (see below), we used only chicks aged 3–15 days for all analyses, including the TDR deployments. Furthermore, because older, more experienced

birds tend to lay earlier, lower-quality parents are more likely to be represented later in the season (Hipfner 1997, Hipfner et al. 1999, Hipfner and Gaston 2002). Thus, it is possible that a reduction in foraging abilities later in the season is attributable to reduced parental quality. We completed all between-date comparisons pairwise within individuals to avoid the confounding effects of parental quality and individual specialization (Lewis et al. 2006, Woo et al. 2008). We excluded “sculpin” from the benthic fish category, because sculpins sometimes occur in the water column, because they have opercular spines that impede swallowing (which makes them lower-quality prey), and because different species of sculpin have very different ecology. For instance, large, shallow-water sculpins in the genus *Myoxocephalus* were captured by local Inuit immediately next to the colony, whereas the deeper-water sculpins in the genus *Triglops* that were identified during feeding watches were preceded by relatively long flights. Thus, murres appeared to treat sculpins differently from other benthic fish.

Statistical analyses.—All statistical analyses were performed in R, version 2.4.1 (R Foundation for Statistical Computing, Vienna). Before using parametric statistics, we tested for normality (Shapiro-Wilk test) and homogeneity of variance (Levine’s test). Prey energy content, distance from the colony, and dive depth were log-normally distributed and, therefore, we ln-transformed these data before analysis. Because the Benvenuti TDRs recorded a maximum depth of 76 m and depth, therefore, was not normally or log-normally distributed, we used a *t*-test on ln-transformed distance data to compare distance traveled for prey items collected above or below 76 m. We also used within-individual paired *t*-tests to determine whether the same prey items were collected farther from the colony during August than during July. We calculated the proportion of fish that were (1) benthic fish, (2) Arctic Cod (*Boreogadus saida*), and (3) Capelin (*Mallotus villosus*) during each feeding watch from 1994 to 2008 and the proportion of total deliveries that were (4) crustaceans during each feeding watch. We used paired *t*-tests (paired by year and individual) to determine whether the arcsine-transformed proportion of each of the four prey classes differed between August and July. We also used a Z-test to determine whether the slope of the least-squares regression (calculated for each year) on the arcsine-transformed proportion of each of the four prey classes against date (days since June 1) was significantly different from zero. Most of the variation in date reflects consistent seasonal progression (Gaston et al. 2003, 2005), because hatch is largely synchronous within the colony and median hatch date varied by less than a week during 1993–2008.

We used Akaike’s information criterion (AIC) to rank three potential models for describing the relationship between prey energy content and distance. The first model (“CPF”), based on standard central-place foraging theory and the ideal free distribution, predicts that energy expenditure is equal to energy gain and that prey energy content, E , increases linearly with distance, D ($E = aD + b$; Orians and Pearson 1979). The second model (“GYS”) assumes that adults maximize energy delivery, provided that they maintain a neutral energy budget, and that prey energy density is proportional to net feeding rate and increases as an accelerating function of distance (Gaston et al. 2007):

$$E = \frac{a + bD}{c - dD}$$

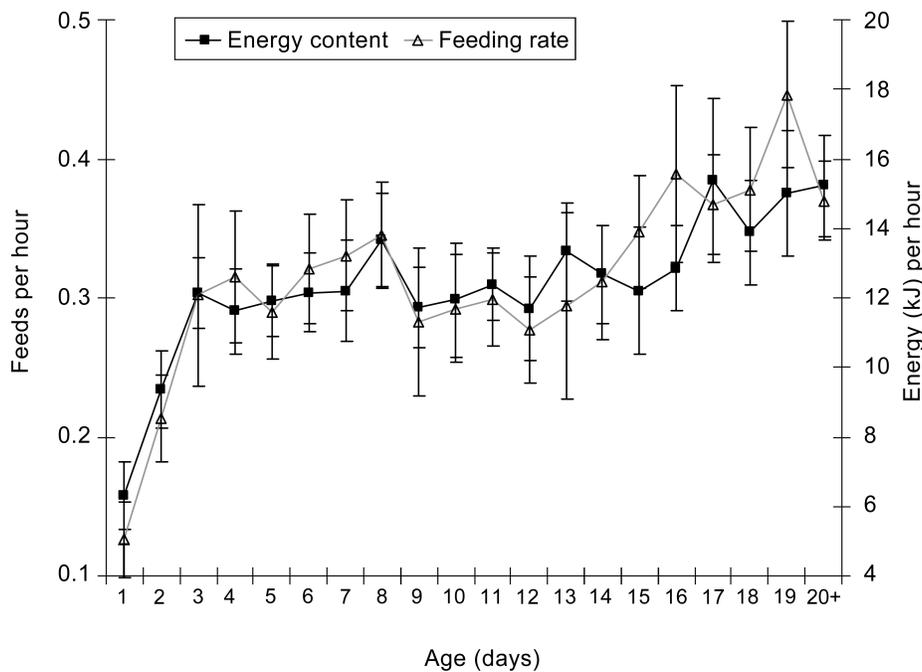


FIG. 1. Feeding and energy delivery rates per chick in relation to chick age in Thick-billed Murres at Coats Island, Nunavut, 1993-2008.

The third model (“Ashmole”) assumes that murres deplete large prey in a manner proportional to the available foraging area and that prey energy content increases as a decelerating function of distance, approximating distance^{0.5} ($E = aD^b$; Lewis et al. 2001). We completed AIC calculations on the least-squares nonlinear regression for each function, which determined parameters *a*, *b*, *c*, and *d* for each relationship; AIC values also are reported in relation to the null model (no relationship between energy content and distance).

To determine the role of bathymetry in determining the relationship between dive depth and flight distance, we estimated the locations of benthic prey captures assuming that (1) benthic prey items were captured at maximum dive depth, (2) birds returned via the shortest route possible that did not pass over land, (3) birds flew at 75 km·h⁻¹, and (4) all birds fed to the west (Elliott

and Gaston 2005, Elliott et al. 2008d). We then created a model that described the availability of different depths at different distances from the colony. We created a resource selection function to determine whether murres selected shallower depths (after considering the availability of different depths) farther from the colony (Elliott et al. 2008d).

RESULTS

Energy delivery rates increased for chicks that were <3 days old, remained constant for chicks that were 3–15 days old, and then increased for chicks that were >15 days old (Fig. 1). When all species were pooled, prey energy content increased with distance from the colony in all years, and this remained when invertebrates were excluded (Fig. 2 and Table 1). This pattern resulted from prey species

TABLE 1. Relationship between prey energy content delivered and return flight distance for prey items delivered by Thick-billed Murres at Coats Island, 1999–2007.^a

	Year	Capelin	Arctic Cod	Benthic	Sculpin	Total (fish) ^b	Total
Slope ^a	1999	0.38	0.17	-0.04	<i>3.41</i>	0.62	0.51
<i>r</i> ²		0.09	0.01	0.00	<i>0.80</i>	0.13	0.13
Slope	2004	0.24	1.89		0.24	0.41	0.41
<i>r</i> ²		0.01	0.00		0.01	0.09	0.09
Slope	2005	<i>0.37</i>	-0.03	0.22	0.37	0.21	0.31
<i>r</i> ²		<i>0.08</i>	0.00	0.09	0.15	0.10	0.10
Slope	2006	0.33	0.44	0.18	<i>0.33</i>	0.40	0.41
<i>r</i> ²		0.14	0.18	0.02	<i>0.18</i>	0.13	0.30
Slope	2007	0.14	0.24	0.06	0.14	0.32	0.40
<i>r</i> ²		0.00	0.04	0.03	0.07	0.14	0.23

^a All parameters refer to linear regressions on ln-transformed data, so slope represents the exponent for a prey mass–distance power law relationship. Only taxa with >5 observations in a given year are included. Values significant at *P* = 0.05 are shown in italics. Values significant at *P* = 0.01 are shown in bold.

^b Invertebrates excluded.

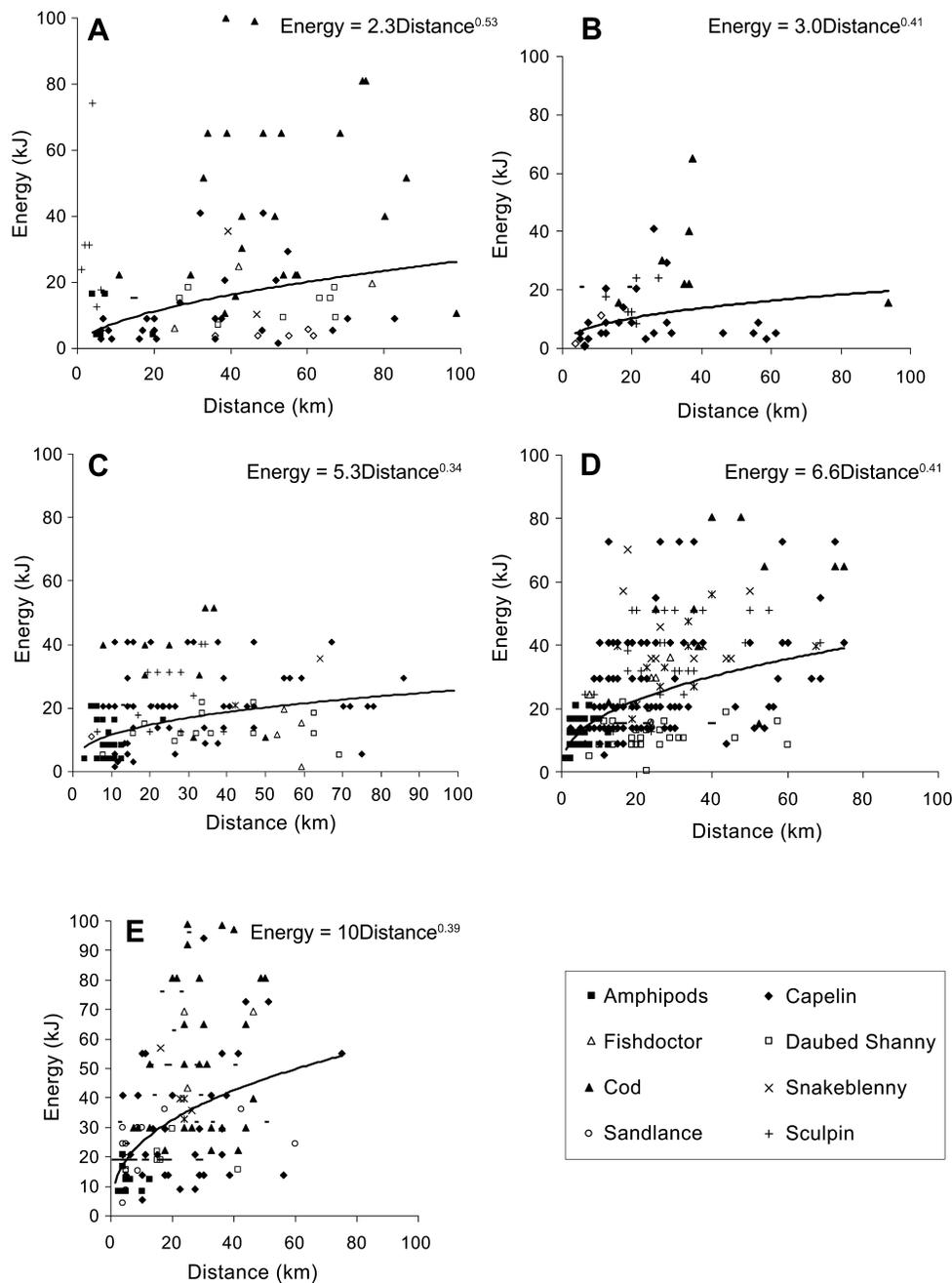


FIG. 2. Prey energy content increased with distance from the colony in Thick-billed Murres at Coats Island in (A) 1999, (B) 2004, (C) 2005, (D) 2006, and (E) 2007.

of different energetic value being collected at different distances from the colony, given that the pattern generally did not hold up within a given taxon (Table 1). The relationship was nonlinear, with the strongest increases in energy content with distance occurring within the first 20 km (Fig. 2). The “Ashmole” model was the most parsimonious model for explaining changes in prey energy content with distance across all years (Table 2). There was no relationship between depth and prey mass in any year (1999: $t = -0.30$, $df = 78$, $P = 0.76$, $r^2 = 0.00$; 2004: $t = -0.21$, $df = 45$, $P = 0.83$, $r^2 = 0.00$; 2005: $t = -0.57$, $df = 124$, $P = 0.52$, $r^2 = 0.00$; 2006:

TABLE 2. Akaike’s information criterion (AIC) values for models (see text) relating prey energy content delivered to return flight distance for prey items delivered by Thick-billed Murres at Coats Island, 1999–2007. Most-parsimonious models are shown in bold.

	1999	2004	2005	2006	2007
ΔAIC (null)	10.8	2.5	10.2	100.7	31.4
ΔAIC (CPF)	9.0	4.4	6.0	6.2	15.5
ΔAIC (GYS)	13.4	5.1	11.2	11.5	19.6
ΔAIC (Ashmole)	0.0	0.0	0.0	0.0	0.0

TABLE 3. Relationship between depth of last dive preceding delivery of a prey item and return flight distance for prey items delivered by Thick-billed Murres at Coats Island, 2004–2007.

	Year	Capelin	Arctic Cod	Benthic	Sculpin	Total (fish) ^a	Total ^b
Slope ^c	2004	-0.85	-1.48		-0.24	-0.72	-0.72
<i>r</i> ²		0.51	0.56		0.02	0.37	0.37
Slope	2005	-0.73	-0.04	-0.63	0.20	-0.32	-0.27
<i>r</i> ²		0.41	0.01	0.48	0.09	0.08	0.08
Slope	2006	-0.36	0.89	-0.49	0.51	-0.23	-0.22
<i>r</i> ²		<i>0.05</i>	0.29	0.49	0.25	<i>0.02</i>	0.05
Slope	2007 ^d	-0.07	-0.44	-0.41	0.15	-0.06	-0.01
<i>r</i> ²		<i>0.03</i>	0.10	0.30	0.02	<i>0.00</i>	0.00

^aInvertebrates excluded.

^bSignificance tests for “Total” were completed on the resource selection function that accounted for the availability of different depths at different distances from the colony.

^cAll parameters refer to linear regressions on ln-transformed data. Only taxa with >5 observations in a given year are included. Values significant at *P* = 0.05 are shown in italics. Values significant at *P* = 0.01 are shown in bold.

^dThis analysis was not completed for 1999 because TDRs did not measure depths >76 m in that year.

t = -0.39, *df* = 287, *P* = 0.81, *r*² = 0.00; 2007: *t* = -0.35, *df* = 129, *P* = 0.72, *r*² = 0.00).

Dive depth decreased with distance from the colony in 2004, 2005, and 2006 for all prey species combined (Fig. 2 and Table 3). This pattern was attributable to within-prey species patterns for Capelin and benthic fish. Depth decreased with distance for Capelin (2004–2005) and benthic fish (2005–2007). In 2006–2007, murres were observed delivering gravid Capelin to chicks. Because we could not identify whether a Capelin was gravid or not for most deliveries, we could not tell at what distance or depth gravid Capelin were collected. In 1999, parental murres returned with prey from significantly greater distances (*t* = 1.77, *df* = 22, *P* = 0.04) when they had final dives >76 m than when they had final dives <76 m. When all years were pooled, and in 2004 and

2005 for Capelin, murres collected prey at shallower depths farther from the colony (Fig. 3 and Table 3).

Individuals captured pelagic prey items farther from the colony in August than in July in years without spawning (Table 4). In 2006–2007, when spawning Capelin were observed at the colony in July, the reverse trend was true, presumably because birds were returning from Capelin spawning locations distant from the colony in July. At the same time, individuals collected a lower proportion of Arctic Cod and benthic fish in August than in July, whereas individuals collected a higher proportion of Capelin and crustaceans in August than in July (Table 5). Furthermore, individuals collected a declining proportion of Arctic Cod and benthic fish with date, whereas the proportion of Capelin and crustaceans increased with date (Table 5).

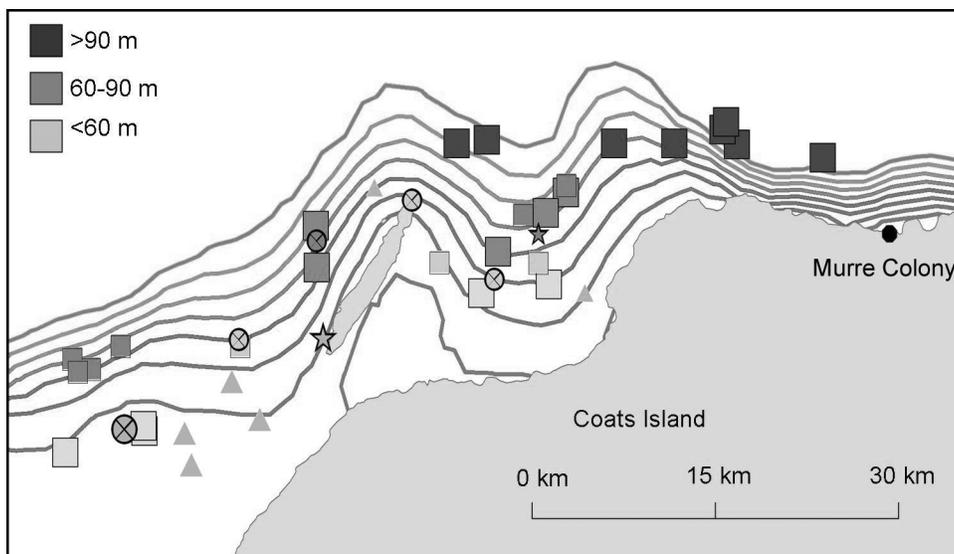


FIG. 3. Estimated locations where benthic fish were taken by Thick-billed Murres in the vicinity of the colony at Coats Island, Nunavut, in relation to depth. Depth contours are in 20-m intervals between 0 and 140 m. Squares represent Daubed Shanny (*Leptoclinius maculatus*), circles Snakeblenny (*Eumesogrammus praecisus*), stars Arctic Shanny (*Stichaeus punctatus*), and triangles Fish Doctor (*Gymnelus* sp.). Small symbols show values for 1999–2000, and large symbols show values for 2004–2007. Light gray represents prey items taken below 60 m, medium gray represents prey items taken between 60 and 90 m (including three values from 1999–2000 that read >76 m), and dark gray represents prey items taken below 90 m.

TABLE 4. Mean distance (km \pm SE) from the Coats Island colony that pelagic fish were collected by Thick-billed Murres during 1999–2007. Values and tests are for numerically dominant pelagic fish observed for equipped birds, which were Arctic Cod in 1999 and Capelin in the remaining years.

Year	July	August	<i>t</i>	df	<i>P</i>
1999	43 \pm 4	67 \pm 6	3.47	20	0.001
2004	16 \pm 2	27 \pm 4	2.22	25	0.02
2005	15 \pm 1	30 \pm 7	3.62	34	0.0006
2006 ^a	25 \pm 2	15 \pm 2	3.60	91	0.0005
2007 ^a	25 \pm 4	17 \pm 3	1.84	21	0.04

^aSpawning observed in July of these years.

DISCUSSION

All of our initial hypotheses for Storer-Ashmole's halo were supported. Specifically, prey energy content increased with distance^{0.5} and dive depth decreased with flight distance after accounting for bathymetry, pelagic prey items were obtained farther from the colony later in the season, and less-energetic items were collected later in the season. Our results suggest that Storer-Ashmole's halo operates at an Arctic seabird colony. The halo appeared to range ~20 km from the colony, given that the strongest increase in prey energy versus distance and in depth versus distance occurred within 20 km.

Provided that prey stores are finite and the ability of new prey to move into the area is finite, central-place foraging necessarily implies Storer-Ashmole's halo. If prey items close to the colony are selected over those far away, prey numbers near the colony will be lower; it is merely a question of whether predation is sufficient to create an observable difference or whether fish migrations or water flow occur rapidly enough to overwhelm any effect of predation. Individual adult murres at Coats Island need ~286 g·day⁻¹ (Croll 1990). Thus, 100,000 murres (35,000 breeding pairs + 30,000 non-breeders + their chicks feeding on 2 fish parent⁻¹ day⁻¹) feeding in a foraging radius of ~40 km (and excluding half of the radius, which is land) remove 25,000 fish·km⁻² over the entire 20-day chick-rearing season (fish mass = 10 g; Croll 1990). Assuming that half the fish are Arctic Cod, as indicated by prey deliveries to chicks at the start of our study (Gaston et al. 2003), this would translate into 12,500 Arctic Cod·km⁻² being removed per season. Given typical Arctic Cod densities in Arctic regions (2,200 cod·km⁻²; Welch et al. 1992, 1993; cf. Crawford and Jorgenson 1996), murres likely exert significant predation pressure on fish stocks surrounding the Coats Island colony. Furthermore, the relative scarcity of seals and belugas in the vicinity of the Coats, once the floe edge leaves (Gaston and Ouellet 1997), suggests that murres are a dominant predator of small fish (Ainley et al. 2006).

Energy delivery rates and feeding rates tracked one another very closely (Fig. 1), increasing over the first three days after hatching, then remaining stable until about day 16, before increasing slightly for the remaining period. Others have described similar patterns in murres (Gaston and Nettleship 1981, Harris and Wanless 1985, Burger and Piatt 1990, Hatchwell 1991, Barrett et al. 1997; *contra* Birkhead and Nettleship 1987, Hipfner et al. 2006), though in some cases feeding rates decrease after

TABLE 5. Mean (\pm SD) percentages of chick deliveries in Thick-billed Murres that were of each prey type at Coats Island in July and August, 1993–2008. ^a

	July	August	Slope (10 ⁻³) ^b
Benthic ^a	14 \pm 7	7 \pm 2	-6.6 \pm 1.4
Capelin	28 \pm 12	38 \pm 14	15.6 \pm 3.5
Arctic Cod	26 \pm 19	19 \pm 13	-9.4 \pm 2.7
Crustacea	0.4 \pm 0.4	7 \pm 10	7.5 \pm 3.2

^aValues that are significant at *P* = 0.01 are shown in italics. Values significant at *P* = 0.001 are shown in bold.

^bRate of change in proportions of total fish (benthic, Capelin, Arctic Cod) or total deliveries (crustaceans) per day (linear regression) averaged across years.

day 15 (Uttley et al. 1994, Paredes et al. 2006). We suggest that feeding rates may increase after day 15 at Coats Island because foraging conditions are generally good, allowing chicks from good-quality parents to stay at the colony for longer than they would otherwise. In some years, chick mass increases with departure date (Hipfner and Gaston 1999), and chicks from parents unable to feed at a high rate may leave the colony as early as possible, inflating mean feeding rates; perhaps this is why higher feeding rates occur just after the earliest time that chicks leave the colony (day 14).

Including only the period when feeding rates were constant (3–15 days), the relationship between distance and prey energy content was driven largely by differences in the composition of prey species rather than energy content within species, which is very different from findings in other ecosystems (Österblom et al. 2008). Murres brought back larger prey species (large fish) when foraging farther from the colony and smaller prey species (invertebrates) when foraging close to the colony (Fig. 2; cf. Baird 1991). The relationship was nonlinear, with most of the increase in prey mass occurring within ~20 km of the colony (Fig. 2; cf. Ainley et al. 1998). The best-fit relationship approximated energy distance^{0.5} (Table 1 and Fig. 2), which suggests that seabird foraging pressure may be directly responsible for prey size availability; randomly distributed foragers from a central place would distribute foraging pressure according to an inverse-square law (Lewis et al. 2001). If these foragers were depleting prey items in a manner proportional to the predators' abundance (Storer-Ashmole's halo), this would lead to prey distributions following an inverse-square law. Wanless et al. (1993a, b) also found that prey mass increased with flight time in European Shags (*Phalacrocorax aristotelis*) but found no relationship between prey mass and time spent diving (*contra* Tremblay et al. 2005—but their sample size was small).

The conclusion that some prey items were less abundant near the colony was supported by the tradeoff between distance and depth. Prey items collected at shallower depths were collected farther from the colony, after accounting for bathymetry (Figs. 3 and 4), which demonstrates that foraging effort decreased with distance traveled from the central place (Cairns et al. 1990, Ainley et al. 2004). This trend was much stronger within certain prey species than within the data set as a whole, which suggests that this relationship reflects prey distribution rather than predator behavior. Specifically, it appeared that in 2004–2005, Capelin were taken in deeper water close to the colony and in shallower

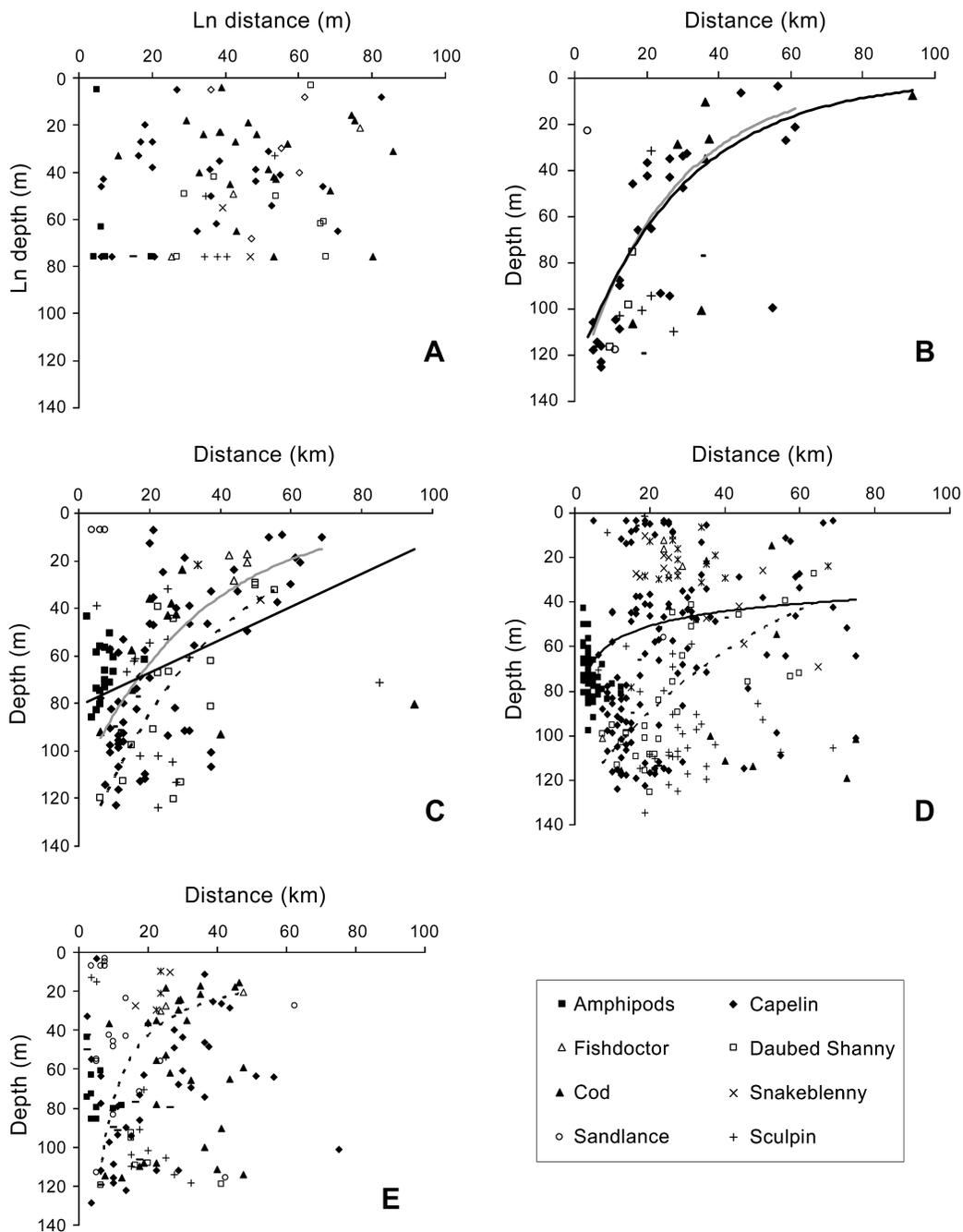


FIG. 4. Depth decreased with distance in Thick-billed Murres at Coats Island in (B) 2004, (C) 2005, (D) 2006, and (E) 2007, but not in (A) 1999. Trends are shown by black lines (combined), gray lines (Capelin), and dashed lines (benthic fish). Legend is the same as in Figure 2.

water farther from the colony, creating a three-dimensional zone around the colony where either Capelin were absent or sparse or murres chose not to obtain them. The relationship was relatively continuous (Fig. 2) and did not show abrupt changes that might reflect shallow benthic spawning grounds. By contrast, in years when murres were observed bringing back spawning Capelin (2006 and 2007), these relationships broke down, illustrating the importance of spawning grounds for murres' foraging behavior.

Capelin spawning grounds provide food sources that are so abundant that they are unlikely to be depleted (Davoren et al. 2003a, b). Furthermore, if most birds that specialize on Capelin (Woo et al. 2008) are merely commuting to one or two distant, shallow spawning grounds, this would break down the relationship between depth and distance.

Bathymetry may play an important role in determining dive depths of murres for benthic species. At distances <20 km, murres

captured benthic fish from depths below 90 m, whereas at greater distances, murres took benthic fish at shallower depths (20–40 m). It appeared that murres depleted benthic fish from the nearshore shelf during the early chick-rearing period; obtaining this prey item meant either traveling ≥ 20 km to a shallow bench or diving deep close to the colony (Fig. 4). The negative relationship between depth and distance likely did not reflect the distribution of suitable habitat for benthic fish because rocky substrate, the favored habitat for most benthic fish studied here, are present in the vicinity of the colony, though it is possible that benthic fish responded to finer-scale variation in habitat. For both Capelin and benthic fish, the depth–distance relationship was nonlinear, with depth decreasing sharply beyond 20 km (Fig. 4). Although the distance–depth tradeoff was significant for only two taxa, sample sizes were small and distances less variable for other taxa, which made it difficult to detect trends.

Further evidence of prey depletion was provided by the increase in flight distance for pelagic prey (Table 4; cf. Baird 1991) and the reduction in the proportion of large fish captured (Table 5) as the season progressed. Although it is possible that these changes represent migrations toward or from spawning grounds or other seasonal movements (Rose 2005, Davoren et al. 2006), they are also consistent with murre predation pressure causing local prey depletion (see Bonal and Arapicio 2008). Murres feed on amphipods during incubation, switching to fish during chick rearing (Woo et al. 2008). Presumably, mobile prey species may be able to respond to this switch by moving farther away from the colony, whereas benthic species that require specific habitat features may become reduced in number (Birt et al. 1987). As the chick-rearing period progressed, murres flew farther to capture prey. By the end of the chick-rearing period, profitable prey items appeared to have been depleted to such an extent that they were effectively no longer present within foraging ranges, and adults were left to exploit less-profitable prey items (amphipods, Capelin, or sculpins). Within each season—and especially within seasons without spawning Capelin (e.g., 2005)—murres brought back large fish (Arctic Cod) during the first set of prey observations (July), smaller fish (immature Capelin) during the second set of observations (early August), and tiny invertebrates during the final set of observations (mid-August). Thus, like humans, murres depleted fish stocks by “fishing down the food web” (Pauly et al. 1998).

Late breeders at our study site have low reproductive success and low rates of chick growth, though this is attributable to lower parental quality among late breeders, rather than deterioration in foraging conditions with date (Hipfner 1997, Hipfner et al. 1999, Hipfner and Gaston 2002). It is unlikely that depletion of fish stocks by intraspecific competition plays a role in the at-colony component of reproductive success at our study site, because most reproductive failure occurs at the egg stage (Hipfner et al. 1999) and adults do not start feeding primarily on fish until the chick stage (Woo et al. 2008). We suggest that chick growth rates, especially after 10 days of age, when chick metabolic demands are highest, are affected by Storer-Ashmole’s halo. Given that larger chicks have higher juvenile survival at our study site, we suggest that intraspecific competition regulates population size through juvenile survival. We propose that although at-colony reproductive success is primarily affected through carryover effects from adult condition upon arrival at the colony (Hipfner et al. 2003,

2005), food stocks regulate postcolony reproductive success (Gaston et al. 2007).

We have presented four pieces of evidence in support of the hypothesis that murres deplete prey abundance around Coats Island: (1) murres flew farther for a given prey item later in the breeding season; (2) murres “fished down the food web,” switching to lower-quality prey items later in the breeding season; (3) birds dove deep when near the colony and shallow when farther from the colony; and (4) prey mass increased with flight distance according to an inverse-square law. Taken together, this evidence suggests that large prey items are depleted from near the colony and from shallow depths as the breeding season progresses. Our results provide additional indirect evidence for Storer-Ashmole’s halo, adding to previous studies that have demonstrated (5) reduced prey abundance near the colony; (6) reduced physiological condition and growth of chicks and smaller or lower-quality chick provisions; (7) reduced adult body condition or increased adult metabolic rate; (8) reduced neighboring colony size; (9) increased trip duration; and (10) reduced ability of parents to regulate provisioning behavior to meet chicks’ needs. In each case, alternative explanations can be provided for the observed correlations, such as changing prey habitat availability with distance from the colony; to truly demonstrate that predator population size regulates prey abundance, it would be necessary to manipulate colony size and monitor changes in prey availability. In the absence of such manipulations, the abundance of indirect evidence from different taxa and locations supports Storer-Ashmole’s halo as an important determinant of variation in the breeding biology of a wide range of seabirds (Ainley et al. 2004, Gaston 2004, Ballance et al. 2009). Furthermore, we believe that it is irrelevant whether the number of individual fish (or any other index of prey abundance) changes with distance, depth, or time. What matters is the murres’ perception of prey availability with distance from the colony. In the hypothetical situation where there is an equal number of fish at all distances from the colony but they are dispersed or unobserved, or for any other reason (e.g., competition) not considered prey items near the colony, then, from the murres’ perspective, a Storer-Ashmole halo is still in effect. Thus, studying Storer-Ashmole’s halo from the predator’s perspective is warranted, provided that conclusions are made only with respect to the predator.

Our results add to the growing body of literature that shows that marine predators modulate their prey capture strategy for different prey types (Garthe et al. 2000; Wilson et al. 2002; Estes et al. 2003; Tremblay et al. 2005; Elliott et al. 2008c, d; Deagle et al. 2008; Paredes et al. 2008; Watanuki et al. 2008; but see Ropert-Coudert et al. 2002). Modulation occurs along three axes for murres at our study site (Elliott et al. 2008d): prey depth (dive depth, duration), foraging effort (flight time, number of dives), and benthic or pelagic prey lifestyle (dive shape, standard deviation). Here, we extend the understanding of the foraging-effort axis, showing that variation along this axis can be explained by prey energy content, with greater foraging effort expended when the predator captures prey with higher energy content (Fig. 2). We also provide a context for understanding tradeoffs between the depth and effort axes.

Evidence for the creation of Storer-Ashmole’s halo in the vicinity of Coats Island during the breeding season supports the hypothesis that the size of murre colonies in the Canadian Arctic is

partially regulated by prey availability. Indirect evidence for exploitative competition was deduced from increased foraging radius (Gaston 1985) and reduced adult and chick mass (Gaston et al. 1983, Gaston and Hipfner 2006) at larger colonies, though similar relationships among murre colonies in Newfoundland may be attributable to interference competition (Davoren and Montevecchi 2003). Our evidence that intraspecific competition in an Arctic seabird may be driven by prey distribution is yet another demonstration that Storer-Ashmole's hypothesis applies to a wide range of seabirds (Birt et al. 1987, Gaston 2004, Ballance et al. 2009) and confirms Storer's (1952) original ideas concerning population regulation in murre.

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