

COMPARISON OF CAPELIN *MALLOTUS VILLOSUS* IN THE PREY LOADS OF COMMON MURRES *URIA AALGE* AND NORTHERN GANNETS *MORUS BASSANUS* FORAGING FROM THE SAME BREEDING SITE IN THE NORTHWEST ATLANTIC

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Forage fishes often play key roles in the food web dynamics of top predators (Cury *et al.* 2012), especially in marine systems in which a diversity of large predators prey on focal forage species (Bakun 2006). In such circumstances, different seabird predators often focus on different age classes, sexes or densities of prey (Piatt 1990, Davoren & Montevecchi 2003, Frederiksen *et al.* 2006).

During the energy-demanding chick-rearing period, seabird parents are constrained by foraging from, and returning to, the breeding site — a situation referred to as Central Place Foraging (CPF; Orians & Pearson 1979). Under the constraints of CPF, parents are assumed to select prey that provide the most nutrients for offspring with the greatest efficiency (Kamil *et al.* 1987, Burke & Montevecchi, 2009). The pressure for prey selectivity and efficient parental foraging is considered to be most intense among single-prey-loaders, i.e. species that deliver an individual prey item to offspring following a foraging trip (Orians & Pearson 1979). By contrast, species in which parents capture and carry multi-prey loads to chicks are expected to experience less stringent pressure for selecting individual prey when rearing offspring (Burke & Montevecchi, 2008).

In the Northwest Atlantic, capelin (*Mallotus villosus*) is a focal forage species, which provides a major food base for piscivorous fishes, birds and mammals (Lavigne 1996). Among the breeding seabirds, Common Murres (*Uria aalge*) are the primary seabird consumer of capelin (Montevecchi 2000); they are also single-prey-loaders during chick-rearing (Davoren & Montevecchi 2003). Northern Gannets (*Morus bassanus*) also often prey extensively on capelin and deliver multi-prey loads, often of tens of fishes, to their chicks (Montevecchi 2007). Murres deliver mostly female capelin to chicks, with high proportions in gravid condition (Davoren & Montevecchi 2003). Gravid capelin provide the richest energy density of any of the capelin condition classes (gravid, spent, immature) and of the sexes (Montevecchi & Piatt 1984), and are considered a preferred prey for chicks.

Common Murres and Northern Gannets foraging sympatrically from large colonies such as Funk Island (~413 000 pairs of murres, ~15 000 pairs of gannets; Chardine *et al.* 2003, 2013) in the northwest Atlantic exhibit considerable spatial overlap at sea (Davoren *et al.* 2003, 2010). While both murres and gannets exploit capelin, they have different access to them in the water column: foraging murres at times reach depths in excess of 100 m (Hedd *et al.* 2009; Regular *et al.* 2011), whereas gannets are limited to foraging in the upper 20 m of the water column (Garthe *et al.* 2000).

Species differences in diving capabilities can result in differential availability of capelin (i.e. capelin below 20 m are inaccessible to gannets), while all capelin available to gannets are presumably also available to murres.

To gain insight into the prey selectivity and foraging behavior of common murres, we compared simultaneous collections of murre parental prey-loads with the prey-loads of non-breeding, roosting gannets, which are not constrained by parental demands and are less likely to selectively target prey. Owing to their foraging capabilities and CPF constraints, we expected less diversity in the prey deliveries of murre parents compared with the prey-loads of non-breeding gannets and predicted that parental murres would take more gravid females than non-breeding gannets.

STUDY AREA AND METHODS

The research was carried out at Funk Island Seabird Ecological Reserve (49°45'N, 53°11'W) over a 23-year period from 1990 through 2012. Diet information was collected in late July and early August. Fish were collected from adult murres captured in the air by pole-net as they were delivering fish to their chicks (Davoren & Montevecchi 2003). Diet samples were collected from non-breeding gannets that regurgitated as researchers approached them at the island's main roosting site (Montevecchi 2007). Prey samples were identified to species, counted and measured to the nearest millimetre (Davoren & Montevecchi 2003). Capelin sex (male, female, unknown) and spawning condition (female gravid or spent, unknown, immature, or male) were recorded.

Data were expressed as percent frequency of occurrence (% FO): that is, the percentage of prey-loads containing a prey species (capelin or otherwise) out of the total number (N) of prey-loads ($N_{\text{COMU}} = 2952$, $N_{\text{NOGA}} = 5581$). For comparisons involving the sex of capelin, data were expressed as percent number (% N) of all individual capelin; for single prey-loading murres, % N is the same as % FO, while for gannets the relative numbers of capelin of different sexes and spawning conditions were compared in all regurgitations combined across years. Individual capelin were grouped into five categories: 1) female gravid, 2) female spent, 3) male, 4) immature and 5) unknown. The number of fish in each category was divided by the total number of capelin to determine % N. Unsexed capelin were more common in the gannet dataset, as prey are transported internally, resulting in partially digested prey-loads that are often difficult to identify as to sex and condition class. The proportionate frequencies of different

categories of capelin in the murre and gannet prey-loads were compared with χ^2 tests.

Length frequency distributions of capelin in murre and gannet prey-loads were generated for all measured capelin, as well as separately for males and females (including both gravid and spent). All capelin collected from murrees were measured, but it was possible to measure only a small subsample of the less digested capelin from gannet prey-loads. Independent sample *t*-tests were used to assess differences in size of capelin preyed upon by murrees and gannets.

RESULTS

The proportions of capelin differed in the prey-loads of murrees and gannets ($\chi^2 = 386.4$; $P < 0.001$). Capelin %FO was 92.7% for murrees (n = 2952) and 75.0% for gannets (n = 4962). The next most common fish in murre diets was sand lance (*Ammodytes* spp.; 5.7% FO). Other fishes occurring in $\geq 2\%$ of gannet prey-loads included Atlantic saury (*Scorpaenopsis scorpaenoides*; 8.0% FO), Atlantic herring (*Clupea harengus*; 5.1% FO), Atlantic salmon (*Salmo salar*; 5.1% FO), Atlantic mackerel (*Scomber scombrus*; 3.0% FO), and sand lance (2.3% FO).

The classes of capelin in the prey-loads of murrees and gannets were very different ($\chi^2 = 2905.6$; $P < 0.001$). Females constituted 84.5 % of capelin in the murre prey-loads (44% were gravid, 40.5% spent), 5.5% were male, and 4.0% were immature (n = 2736; Table 1; sex not determined for 6%). By comparison, in gannet prey-loads only 39% of capelin were female (n = 26585; 10% gravid, 29% spent), 48.5% were male and 2% were immature (sex could not be determined for 10.5%) (Fig. 1).

The overall mean length of capelin delivered by murrees (144.2 \pm 0.3 mm, n = 2429) was significantly shorter than those in gannet prey-loads (157.5 \pm 0.5 mm, n = 555; $t = 21.8$, $P < 0.001$). Male capelin in murre prey-loads averaged 7.6 \pm 1.5 mm shorter (154.7 \pm 1.0 mm, n = 150) than those in gannet prey-loads (162.3 \pm 0.5 mm, n = 412; $t = 6.95$, $P < 0.001$). There was no significant difference in the mean length of female capelin in murre (144.1 \pm 0.3; n = 2181) and gannet (144.0 \pm 1.0 mm; n = 116; $t = 0.08$, $P = 0.933$) prey-loads (Fig. 2).

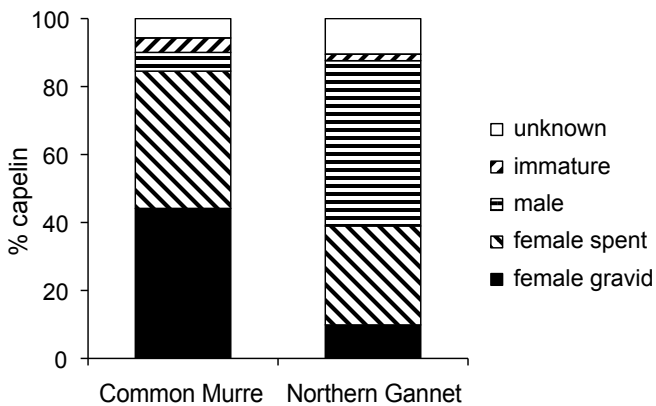


Fig. 1. Composition (by % N) of capelin in the prey-loads of common murrees (n = 2736) and northern gannets (n = 26585) at Funk Island, Newfoundland, 1990–2012.

DISCUSSION

Murrees in the species’ largest North American colony on Funk Island rely heavily on capelin while provisioning chicks (see also Davoren and Montevecchi 2003). For gannets, capelin is an important “default” prey when large warm-water migratory fishes such as mackerel and saury are not available (Montevecchi *et al.* 2009).

The most striking difference between the prey-loads of murrees and gannets was the proportion of female to male capelin. Female capelin outnumbered males roughly 9:1 in murre prey-loads, while the gannet prey-loads contained similar numbers of females and males. Mature capelin segregate by sex into separate shoals before spawning (Davoren *et al.* 2006). Yet, as gannets often had prey-

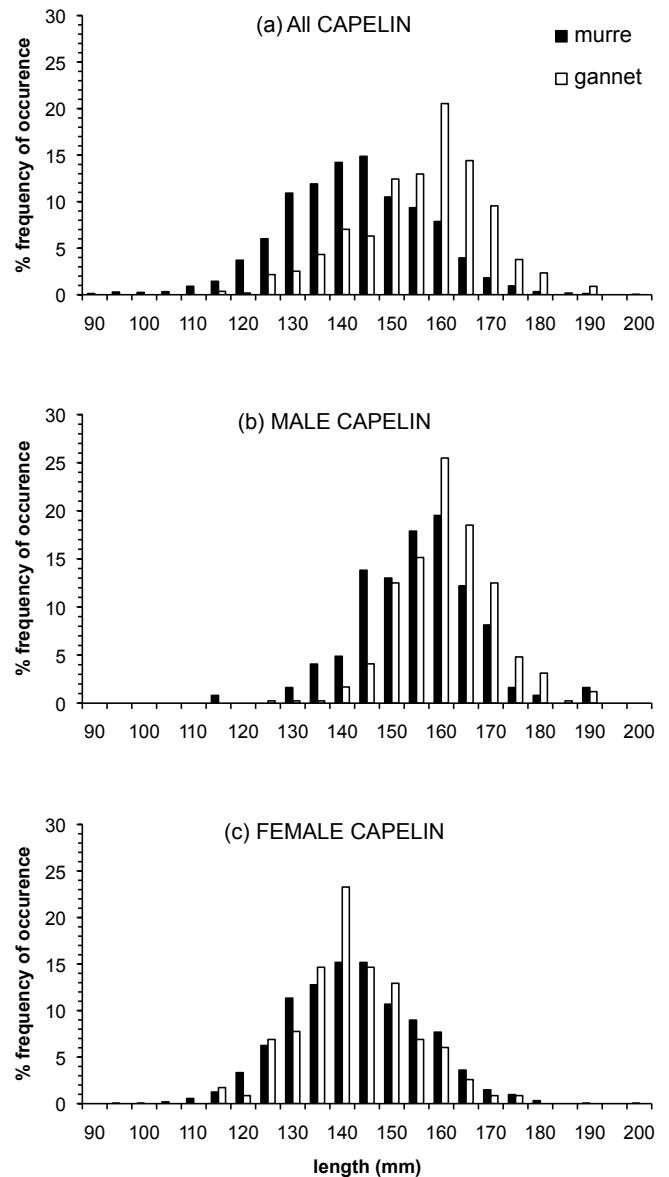


Fig. 2. Length frequency distribution of (a) all capelin (n_{COMU} = 2736; n_{NOGA} = 15849), (b) male capelin (n_{COMU} = 151; n_{NOGA} = 7709) and (c) female capelin (n_{COMU} = 2313; n_{NOGA} = 6177) in murree and gannet prey-loads (1990–2012).

loads containing both sexes, and presumably all capelin available to gannets were also available to murres, the segregation of female and male shoals likely had little influence on our findings.

Of the female capelin, roughly half were gravid in the murre prey-loads compared with only a quarter in the gannet prey-loads. Gravid capelin have the highest energy density of any of the reproductive, sex and age classes of capelin (Montevecchi & Piatt 1984). As murres transport only one fish at a time to offspring, they may target gravid females to provide offspring with maximum energy per unit of parental effort. As well, it may be easier for murres to capture females because they are shorter than males, with less muscle mass and hence slower burst speeds (He 2011). In this respect, it may be significant that the few male capelin in murre prey-loads were significantly smaller than the male capelin in gannet prey-loads. Egg-engorged gravid females are presumably slower and less agile swimmers than non-gravid females (James & Johnston 1998; Figure 3) and shorter males with less muscle mass would have slower burst speeds than larger males (He 2012), possibly facilitating parental foraging efficiency for murres.

Predator swimming speed, however, should not restrict murre prey capture compared with that of gannets. Murre underwater swimming speed ($2.18 \text{ m} \cdot \text{s}^{-1}$; Swennen & Duiven 1991) is faster than that of gannets (up to $1.2 \text{ m} \cdot \text{s}^{-1}$ wing-powered diving speed, $4.3 \text{ m} \cdot \text{s}^{-1}$ or greater plunging speed; Garthe *et al.* 2000). As gannets catch capelin during slower, wing-powered dives, the more rapid murres are presumably at least as able as gannets to catch larger, faster male capelin. Therefore, the small numbers of male capelin in murre prey-loads is likely due to a preference for female fish. Breeding murres may avoid male capelin because they are larger than females (Fig. 2b), as chicks, especially young ones, could have difficulty swallowing larger fish and parents might have more difficulty defending them from theft by neighbouring murres.

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Fig. 3. Common Murre carrying a gravid capelin for its chick on Funk Island, Newfoundland (photo: W.A. Montevecchi)

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