

Linking predator diet and prey availability: common murre and capelin in the Northwest Atlantic

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ABSTRACT: We examined the predator–prey interaction between an apex seabird predator, the common murre *Uria aalge*, and capelin *Mallotus villosus*, the primary forage fish in the Northwest Atlantic. Sampling of parental deliveries to murre chicks was carried out during the breeding season on Funk Island, located off northeast Newfoundland, Canada. Concurrent vessel surveys were conducted throughout the murre's diving and foraging range around the colony to characterize the prey field. Results indicated that in years when capelin was abundant in the size range consumed by murre (suitable capelin), murre delivered large and small fish in similar proportions, whereas they delivered more large fish when suitable capelin abundance was low. Considering the relative abundances of small and large suitable capelin, these observations suggest negative prey switching by the predator. Using foraging theory, we derived a model which estimates the probability of delivering a specific prey type (large or small capelin or other prey) to the chick based on prey availabilities. This quantitative model was capable of reproducing the general patterns in the observations. It also allowed estimating the shape of the common murre's multispecies functional response (MSFR) which indicated that this would conform to the definition of prey switching, and could then be classified as a Type 3. From an applied perspective, our results support the use of predator diets as indicators of their food base, but also highlight the need for understanding the shape of the predator's MSFR for quantitative development of these types of applications.

KEY WORDS: Predator–prey · Ecosystem indicator · Functional response · Capelin · *Mallotus villosus* · Common murre · *Uria aalge* · Northwest Atlantic · Seabirds

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INTRODUCTION

Predatory interactions between seabirds and forage species have been the focus of many studies (Randall & Randall 1986, Birkhead & Nettleship 1987, Mehlum & Gabrielsen 1993, Croxall et al. 1999, Barrett 2002, Gaston et al. 2003). This interest is fuelled in part by the idea that seabirds are good trackers of the marine environment and can thus be used as ecosystem indicators (e.g. Montevecchi 1993, Boyd et

al. 2006, Einoder 2009), although phenotypic plasticity may constrain their value as quantitative indicators (Grémillet & Charmantier 2010). On the other hand, interest also arises from the perspective of the prey, as the seabirds' main prey are usually key species in the study systems (Montevecchi & Myers 1996, Barrett & Krasnov 1996, Hunt et al. 1996, Wanless et al. 2005).

The Northwest Atlantic is a productive, Low Arctic ecosystem which underwent dramatic changes in the

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early 1990s (Rice 2002). Its structure is well described as wasp-waist, i.e. a crucial intermediate trophic level is dominated by a single species or at most a handful of species (Bakun 2006). Capelin *Mallotus villosus* fulfils this role in the system, acting as a link between zooplankton and large vertebrates (Lavigne 1996). In the present study, we assess the predator–prey relations between capelin and its dominant avian predator, the common murre *Uria aalge* (Montevecchi 2000).

The common murre, the largest extant auk, has a circumpolar distribution and is one of the most numerous seabirds in the Northern Hemisphere (Ainley et al. 2002). During the breeding season, murre are central place foragers (Orians & Pearson 1979) that deliver a single fish per foraging trip back to the chick. At the species' largest North American colony on Funk Island, they feed mainly on large female, often gravid capelin (Davoren & Montevecchi 2003). Capelin are captured from persistent aggregations around the colony (Davoren et al. 2003a).

Capelin is a small, short-lived pelagic schooling fish with a circumpolar distribution in sub-Arctic and Arctic regions (Vilhjálmsón 1994). The total biomass of capelin stocks off Newfoundland decreased severely during the late 1970s (from 3.6 to 0.5 million t between 1976 and 1979). This decline has been linked to either environmental factors affecting year-class strength (Carscadden 1984), or to the impacts of fishing in the years prior to the stock collapse (Anon 1979); fishing pressure, in conjunction with ecological interactions among fishes, has been identified as an important factor in the collapses of other capelin stocks (Hjermann et al. 2004). The species rebounded to the previous levels observed by 1985 (3.5 million t, acoustic estimate; DFO 1997). A further major reduction in biomass occurred in 1991 (5.78 million t, acoustic estimate in 1990, 0.13 million t in 1991), from which the stock has not recovered (DFO 2010). In addition to this reduction in biomass, its spawning was delayed up to 4 wk and protracted (Nakashima & Wheeler 2002, DFO 2010). Size and age at maturity and somatic condition were reduced (Carscadden & Nakashima 1997, Carscadden & Frank 2002). Furthermore, capelin has shifted its vertical distribution to commonly occupy deeper waters (Mowbray 2002) and exhibited a southward distributional expansion (Frank et al. 1996, Carscadden & Nakashima 1997). These changes in capelin biomass, behaviour, distribution, size/age composition and condition were recorded for the first time in the early 1990s. Until the last capelin assessment (DFO 2010),

all biological characteristics reflected the patterns observed during the 1990s.

Several aspects of murre–capelin interactions in the Northwest Atlantic area have been studied, including the spatial scales at which common murre track capelin aggregations (Davoren et al. 2003b), the influence of conspecific behaviour on the choice of foraging habitat (Davoren et al. 2003b), the aggregative response of common murre to capelin (Piatt 1990), prey searching behaviour (Davoren et al. 2003a), parental allocation of time and energy by breeding common murre (Burger & Piatt 1990, Cairns et al. 1990), and the influence of changes in capelin biology on provisioning of the young (Davoren & Montevecchi 2003, Burke & Montevecchi 2009). Yet, despite the murre's dependence on capelin, a quantitative description of the predator–prey relationship is lacking.

Predation is a key determinant of the structure and dynamics of natural communities; abundance, distribution, and age/size structure of prey and predator populations are influenced by predatory interactions. Quantitative understanding of predator–prey interactions is essential for effective use of top predators as ecosystem indicators, a recurring element in the ongoing efforts to develop ecosystem approaches to fisheries (e.g. Cury & Christensen 2005, Boyd et al. 2006). To infer the (relative) abundances of a top predator's prey from its diet, we must know the function that links them. In this context, the goals of the present study are (1) to jointly analyze the common murre's summer (chick feeding) diet and the availability of its main prey, capelin, and (2) to link these variables using a mechanistically-based mathematical model derived from current foraging theory. Finding the functional relationships between environmental variables (prey abundances) and the responses of a predator aids in interpreting how the predator will respond to its dynamic environment.

MATERIALS AND METHODS

Study area

The present study was carried out between 1995 and 2005 on and around the Funk Island Seabird Ecological Reserve (49° 45' N, 53° 11' W) in the Northwest Atlantic approximately 60 km off the northeast coast of Newfoundland (Fig. 1). During summer, large aggregations of capelin concentrate in inshore coastal areas to spawn (Templeman 1948) following migrations from offshore wintering and feeding

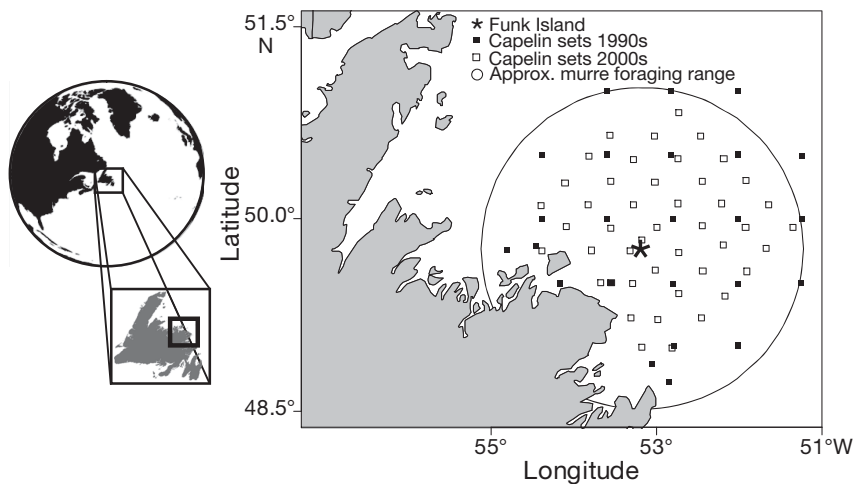


Fig. 1. Study area showing the position of Funk Island, the approximate foraging range of breeding common murre (ca. 140 km), and stations surveyed during 1995–1999 and 2004–2005

areas (Nakashima 1992). Currently, approximately 400 000 pairs of common murre breed on Funk Island (Chardine et al. 2003).

Diet and prey field sampling

Research vessels working in the vicinity of the murre's colony on Funk Island collected data on the prey field (below), soon after dietary samples had been collected from parental murre (Table 1).

We evaluated diet composition from parental deliveries to chicks during the last 7 to 10 d of the ca. 21-d colony-based rearing period. Adult murre carrying fish were caught with a pole net on return to their nests on Funk Island and the food load (single fish) retrieved (Davoren & Montevecchi 2003). Species and total length (Holden & Raitt 1974) were recorded for all prey items.

Common murre rarely deliver fish smaller than 100 mm to their chicks (Birkhead & Nettleship 1987, Barrett 2002, Davoren & Montevecchi 2005), thus we defined suitable capelin for murre as those equal to or longer than 100 mm. We defined 3 prey categories: small capelin (100–140 mm), large capelin (>140 mm) and other prey (every prey other than capelin). In general, the size ranges of capelin employed correspond to mature fish 3 yr and older (>140 mm) and younger immature fish (100–140 mm) (Winters 1982). We used length instead of reproductive condition to classify capelin as fish collected in the trawl surveys during the 1990s were not discriminated by maturity. Also, owing to a slight temporal

mismatch between the diet and prey availability data collections (vessel surveys were conducted a few days after dietary data collection was finished), and because spawning occurs (changing capelin reproductive status from 'gravid' to 'spent') in a short period, the maturity of available prey recorded during surveys would not necessarily reflect maturity while the dietary data were being collected.

Diet was characterized in terms of percentage by number $\%N_{it}$ where i is prey category and t is year (Hyslop 1980). Bootstrap 95% confidence intervals (CIs) were constructed by re-sampling the original diet observations 50 000 times (Efron & Tibshirani 1993).

The prey field within the murre's foraging range was characterized using data from 2 survey programs, the first conducted during 1995 to 1999 (Anderson et al. 2002) and the second during 2004 to 2005. Characteristic positions of the trawl sets made during the surveys in the 1990s and in 2004 to 2005 are shown in Fig. 1. Surveys were conducted in a 360° area (approximate radius 140 km, Fig. 1) around the colony encompassing the maximum foraging range of breeding common murre (123 km during incubation and 80 km during chick rearing; Cairns et al. 1987). All surveys were carried out systematically, using an International Young Gadoid Pelagic Trawl to sample the upper 60 m of the water column, where common murre take most of their prey (Tremblay et al. 2003, Hedd et al. 2009). Prey abundance sampling occurred continuously over 24-h periods. Common murre breeding at Funk Island forage continuously during day and night, although they do so more intensely at dawn and dusk (Regular et al. 2010).

Table 1. Dates of seabird diet and prey field (vessel) sampling

Year	Seabird diet	Prey field
1995	Aug 04–Aug 11	Sep 06–Sep 21
1996	Aug 05–Aug 09	Aug 20–Sep 04
1997	Aug 01–Aug 09	Aug 12–Aug 28
1998	Aug 04–Aug 16	Aug 25–Sep 08
1999	Jul 27–Jul 31	Aug 24–Sep 01
2004	Jul 26–Aug 02	Aug 08–Aug 17
2005	Aug 02–Aug 09	Aug 15–Aug 22

Abundance indices of total (suitable + non-suitable) capelin abundance and other prey were estimated using the delta distribution mean estimator (Pennington 1996). As direct estimations of abundance per size class (i.e. small and large) were not feasible because fish length distributions were not available for every set, we estimated capelin density per size class per year as the product of the Δ -lognormal estimator of total capelin abundance multiplied by the proportion of capelin of a given size class caught in a given year t ($N_{i,t} = \Delta\text{-estimator}_{i,t} \times \text{proportion}_{i,t}$).

Prey abundance estimated this way assumes that the prey are homogeneously distributed and that the murre make use of all their foraging range. Common murre breeding at Funk Island, however, likely use memory and local enhancement as search tactics to locate persistent aggregations of capelin (Davoren et al. 2003a). Results from an assessment of the impact that spatial variability in prey availability and the non-random searching behaviour of the predator have on the model presented in this paper (next section) indicated that the most accurate representation of the murre's perception of its prey field was one in which it forages throughout its foraging range, and there is no prey density threshold above which it feeds on prey aggregations (Buren 2007). This represents the way in which common murre likely integrate information about their prey field over differing spatial (ca. 100 km) and temporal (ca. 2 wk) scales.

THE MODEL

The function that relates consumption to prey availability is the predator's functional response (F_i). It is the amount of prey i consumed by a unit of predator per unit time (searching and handling time). If a predator consumes more than one prey type then the consumption rate for each type of prey will depend on the availability of all possible prey; the function that describes this relationship is a multi-species functional response (MSFR). We based our model on the generalized Holling formulation of the prey-dependent MSFR:

$$F_i = \frac{a'_i N_i}{1 + \sum_{k=sc,lc,ot} h_k a'_k N_k} \quad (1)$$

where h_k is handling time for prey k , N_j is the abundance of prey j in the environment, a'_i is the rate of prey consumption per unit of prey i and searching time (it was termed 'rate of successful search' by

Holling 1965) and sc indicates small capelin, lc large capelin, and ot 'other prey'. The rate of successful search can be interpreted as the predator's prey searching efficiency. If in Eq. (1) a'_i takes the form $a'_i = a_i N_i^{b_i}$ (with a_i and b_i constant coefficients), we obtain a generalized form of the Holling multispecies functional response (Koen-Alonso 2007).

Both Type 2 and Type 3 MSFRs¹ can be obtained with this formulation, depending on the value of the parameter b_i . If $b_i = 0$, then a'_i is independent of prey density and thus the functional response is Type 2, otherwise a'_i is a function of prey density and the functional response is Type 3 (Koen-Alonso 2007). In particular, if $b_i = 1$ then the functional response is a standard Type 3.

The proportion of prey category i in the diet (p_i) can be used as an estimator of the probability of consuming an item of prey category i (i.e. $\hat{\pi}_i = p_i$). Considering that the functional response is a consumption rate, we can define the estimator of the probability of consuming a given prey as:

$$\hat{\pi}_i = p_i = \frac{F_i}{\sum_{k=sc,lc,ot} F_k} = \frac{a'_i N_i}{\sum_{k=sc,lc,ot} a'_k N_k} \quad (2)$$

Note that the proportion of prey category i in the diet is independent of handling time. Therefore, its estimation does not imply the logistical difficulties imposed by the estimation of rates in the field. Most importantly, given that the exponents of the functional response (b_i) are estimated, this approach reveals the shape of the predator's functional response.

Hence, the model we derived to estimate diet composition from the abundance of prey is

$$\hat{\pi}_i = \begin{cases} \hat{\pi}_{sc} = \frac{a_{sc} N_{sc}^{1+b_{sc}}}{a_{sc} N_{sc}^{1+b_{sc}} + a_{lc} N_{lc}^{1+b_{lc}} + a_{ot} N_{ot}^{1+b_{ot}}} \\ \hat{\pi}_{lc} = \frac{a_{lc} N_{lc}^{1+b_{lc}}}{a_{sc} N_{sc}^{1+b_{sc}} + a_{lc} N_{lc}^{1+b_{lc}} + a_{ot} N_{ot}^{1+b_{ot}}} \\ \hat{\pi}_{ot} = \frac{a_{ot} N_{ot}^{1+b_{ot}}}{a_{sc} N_{sc}^{1+b_{sc}} + a_{lc} N_{lc}^{1+b_{lc}} + a_{ot} N_{ot}^{1+b_{ot}}} \end{cases} \quad (3)$$

Diet composition as multinomial distribution

We considered each observed parental delivery (\mathbf{Y}_d) as a single realization from a multinomial ran-

¹Throughout the paper multispecies functional responses (MSFRs) are denoted with arabic numerals, and single species functional responses (SSFRs) with roman numerals

dom variable $\mathbf{Y} = \{y_{sc}, y_{lc}, y_{ot}\}$. The common murre is a single-prey loader, so only one $y_{d,i}$ per parental delivery \mathbf{Y}_d had a non-zero value; if a bird delivered small capelin to its chick in the observed trip, then $y_{d,sc} = 1$ while all other $y_{d,i} = 0$ (i.e. $\mathbf{Y}_d = \{y_{d,sc} = 1, y_{d,lc} = 0, y_{d,ot} = 0\}$).

Let $n_{sc} = \sum_d n_{d,sc}$ denote the number of small capelin delivered and $n = \sum_i n_i$ the sample size. The counts (n_{sc}, n_{lc}, n_{ot}) follow a multinomial distribution. Let π_i denote the probability of delivering the i th prey category in each parental delivery. The multinomial probability mass function is

$$\Pr[n_{sc}, n_{lc}, n_{ot}] = \frac{n!}{n_{sc}! n_{lc}! n_{ot}!} \pi_{sc}^{n_{sc}} \pi_{lc}^{n_{lc}} \pi_{ot}^{n_{ot}} \quad (4)$$

subject to the constraint that $\sum_{i=sc,lc,ot} \pi_i = 1$.

Parameter estimation

The model was fit by maximizing the multinomial log-likelihood function $\ln[\mathbf{L}(\boldsymbol{\theta})] = \sum_{i=sc,lc,ot} n_i \ln \pi_i$ (Agresti 2002). In order to achieve global convergence, the fitting was performed using the enhanced simulated annealing algorithm (Siarry et al. 1997), implemented in a multi-start scheme.

We were interested in testing whether the rate of successful search (a_i) is a function of prey density (and hence whether the functional response is Type 3). In order to do so, we calculated approximate 95% CIs for the parameters by constructing likelihood profiles (Hilborn & Mangel 1997).

RESULTS

Data description

Prey availability. In most years, the most abundant prey was small capelin, with the exception of 1995, when other prey was the most abundant prey category and there were almost no large capelin in the study area (Fig. 2). The most conspicuous characteristic of the abundance estimates is that in some years the abundance of suitable capelin was high ($>10\,000$ ind km^{-2} , in 1997, 1998 and 2004) while in the other years it was low (<5000 ind. km^{-2}). In the years when suitable capelin abundance was high, large capelin was the second most abundant prey, while when suitable capelin abundance was low the second most abundant prey was other prey.

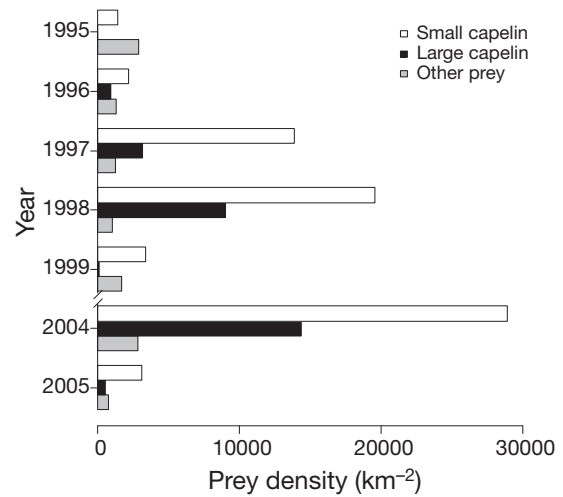


Fig. 2. *Mallotus villosus*. Availability of capelin and other prey of common murre *Uria aalge* in the upper 60 m of the water column within their foraging range around Funk Island, expressed as number of fish km^{-2}

Diet. We retrieved 925 parental prey delivery samples over 7 years, with sample sizes per year ranging from 58 to 289 (Fig. 3). Diet was dominated by capelin in all years. In particular, large capelin dominated the diet in those years (1996, 1999, 2005) when the consumption of small and large capelin was significantly different (i.e. CIs around %N point estimates do not overlap). The contribution of other prey to the overall diet was almost negligible, with the sole exception of the year 1995 when it accounted for 30% of the diet, being the second most important prey (Fig. 3).

Model fit

The fit of the model (expected diet composition estimated from prey abundance; Eq. 3) was very satisfactory (correlation between observed and modelled proportions in the diet, Pearson's $r = 0.96$). It captured most of the characteristics of the time series, some years showing high and others low contrast between the percentage of small and large capelin delivered to chicks (Fig. 3). The percent number of capelin consumed each year was very well estimated throughout the study period with the exception of 1999. In particular, the model exhibited a very good fit to the large capelin data for the years 1995, 1997, 2004 and 2005, a somewhat poorer fit to the 1996 and 1998 data, and a poor fit to the 1999 data. Similarly, the estimates of the percent number of small capelin consumed were accurate for all years, falling within

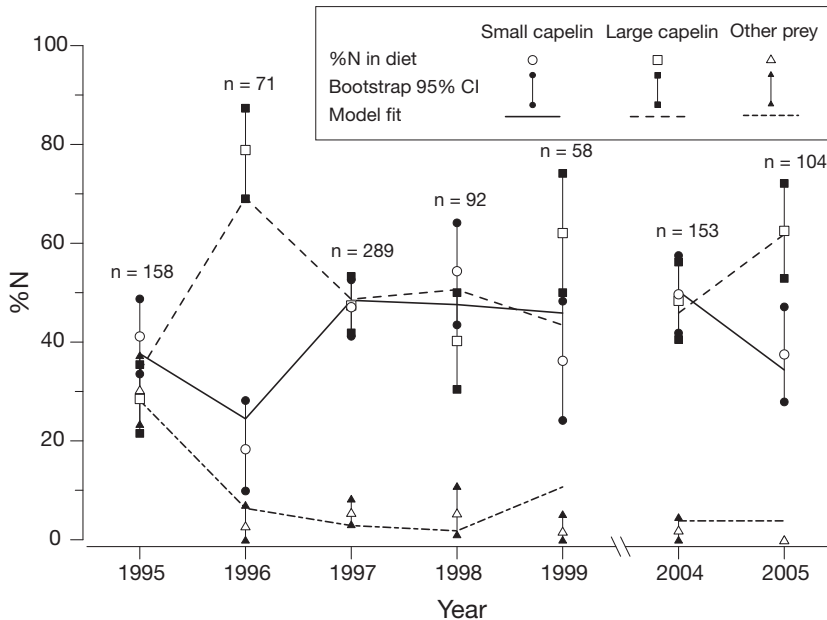


Fig. 3. *Uria aalge*. Common murre diet composition expressed as point estimates of the percentage by number (%N) that small capelin *Mallotus villosus* (100–140 mm), large capelin (>140 mm) and other prey represent in the common murre's diet. The bars indicate bootstrap 95% CI. For easy visualization of overlapping CIs, the tips of the bars are indicated with filled symbols that match the prey type. The lines represent the model fit. Sample sizes of yearly parental deliveries (n) are indicated above the corresponding estimates

the confidence intervals in all cases. The only component of the diet that the model had some difficulty capturing was other prey; during 1996, 1999 and 2004, the residuals had the same order of magnitude as the observed diet. This difficulty does not imply

inability of the model to explain the variability in the diet; rather it reflects uneven sampling throughout the time series. The fitting procedure implemented gives equal weight to each individual observation, and hence, it tends to capture better the pattern for those years with larger sample sizes.

Parameter interpretation

The maximum likelihood estimates of the shape parameters of the functional response with respect to small and large capelin (lower and upper approximate 95% CIs in brackets) were significantly less than zero ($b_{sc} = -0.25[-0.484, -0.005]$, $b_{lc} = -0.7[-0.803, -0.591]$), whereas the shape parameter of the functional response with respect to other prey was negative but not significantly different from zero ($b_{ot} = -0.04[-0.740, 0.700]$). Thus, as the density of prey i increases its consumption becomes increasingly larger until reaching a plateau (Fig. 4a), while the common murre's prey searching efficiency (rate of prey consumption per unit of prey and searching time) becomes increasingly smaller (Fig. 4b).

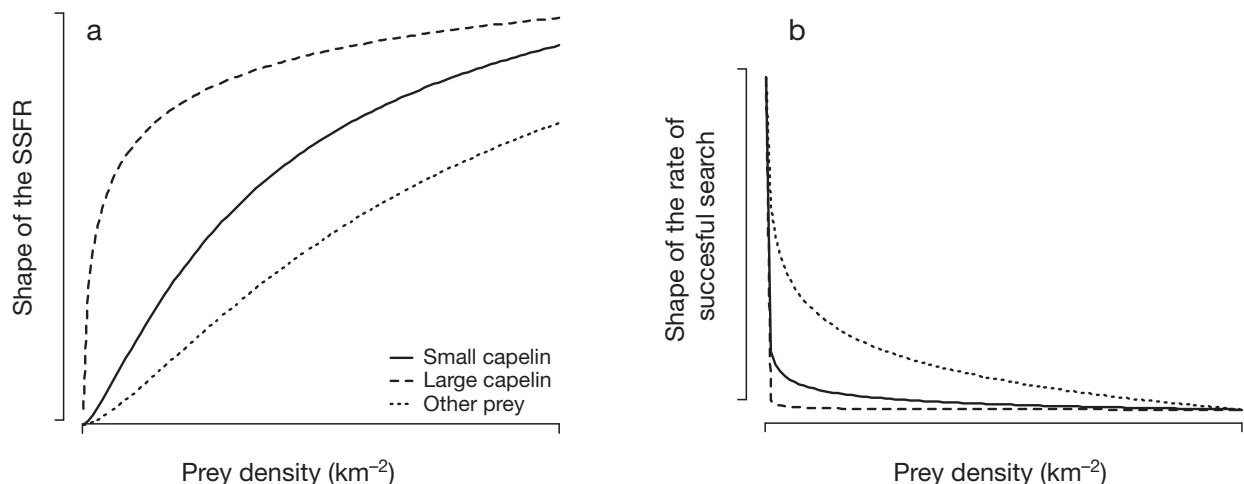


Fig. 4. *Uria aalge*. Shape of common murre (a) marginal single-species functional responses (SSFR) and (b) rates of successful search with respect to small capelin, large capelin and other prey, shown as a function of the availability of those prey. These curves were calculated by making the densities of the 2 prey categories not considered (e.g. in the case of small capelin the prey not considered are large capelin and other prey) equal to their median density during our study period

DISCUSSION

The prey field available to common murres around Funk Island can be schematically characterized in terms of low or high capelin abundance. Most parental deliveries to chicks were capelin throughout the time series, with large capelin being the most important prey in 3 years, and small capelin in 4 years. The model fit the data well, capturing the contrasting patterns in the time series (Fig. 3).

An interesting pattern that emerges from analyzing diet and prey abundance data concurrently is that in the years of high suitable capelin abundance (1997, 1998, 2004) the consumption of small and large capelin was not significantly different; while in years of low capelin abundance (with the exception of 1995) the proportion of large capelin in the diet was significantly larger than that of small capelin. The year 1995 is an exception to this pattern and was unusual in terms of both diet and prey field. Capelin abundance was low (Fig. 2), and its mean length and weight were markedly smaller than in the other years (Nakashima & Slaney 2001). Moreover, other prey accounted for more than 30% of diet (Fig. 3), a striking finding considering that breeding common murres on Funk Island specialize on capelin.

We offer 3 hypotheses to explain this pattern: during the years when capelin abundance is high, (1) common murres have no difficulty in meeting their energy requirements and hence do not need to select for larger prey (note that when the converse of this hypothesis is true, i.e. in low prey availability years murres find it difficult to meet their energetic requirements and hence need to select larger prey, competitors can potentially enhance this difficulty by depleting local prey abundance), (2) common murres' intrinsic selecting ability is decreased, and/or (3) common murres' selecting ability is decreased because capelin show density dependent behaviour, e.g. diel vertical migration or shoaling behaviour may be affected by conspecific density.

The first hypothesis seems the most likely explanation for the observed pattern. Central place foraging theory predicts that as distance, and hence travelling time, from colony to prey patch is increased, the greater must be the energy density of the prey selected by the predator (Orians & Pearson 1979). When feeding conditions are poor, parental common murres increase their foraging effort thus buffering the chicks against these adverse conditions (Burger & Piatt 1990, Wanless et al. 2005). Common murres breeding on Funk Island increased their mean and maximum foraging ranges by approximately 35% in

a year of low capelin availability (2005) compared to a year of high capelin availability (2004) (Burke & Montevecchi 2009). Therefore, the murres' prey delivery patterns can be explained within the context of central place foraging theory (Orians & Pearson 1979): during periods of food shortage they increase foraging effort (travel further from the colony) and, given the high cost of flight for auks (Pennycuik 1987), this would result in greater pressure to deliver larger, more energetically profitable prey to the offspring. Common murres likely select capelin based on size as fish lipid and energy contents are increasing functions of size (Montevecchi & Piatt 1984). This adaptive provisioning strategy buffers chicks from poor prey availabilities and ultimately enhances fledging success and parental inclusive fitness (Hamilton 1964). The hypotheses offered to explain the concurrent pattern in prey abundance and predator's diet may potentially be influenced by differential spatial and depth distribution of large and small capelin and their seasonal movements. Unfortunately, data limitations precluded us from exploring the potential impact these variables may have on the murres' prey selecting abilities.

The empirical patterns described above strongly support the use of common murre's diet as an indicator of suitable capelin (>100 mm) abundance. This idea extends Davoren & Montevecchi's (2003, 2005) perspective of common murres as samplers of female capelin condition, timing of inshore spawning and availability of gravid capelin. However, we do not know if suitable capelin abundance around Funk Island reflects that over the Newfoundland shelf. Further studies are needed to assess the relationship between suitable capelin abundance across different spatial scales.

Functional response

To move the use of predators' diet as indicators of prey availability beyond the interpretation of correlations and generate predictive power we need to know the functional response, i.e. the form of the function that relates prey availability and consumption. The functional response depends on the spatial and temporal scales at which it is measured. Ives et al. (1999) distinguish between a 'behavioural functional response' and a 'population functional response'. The behavioural functional response is the per capita predation rate of a single individual, it often only considers foraging time and its time span is usually very limited (the order ranging from hours

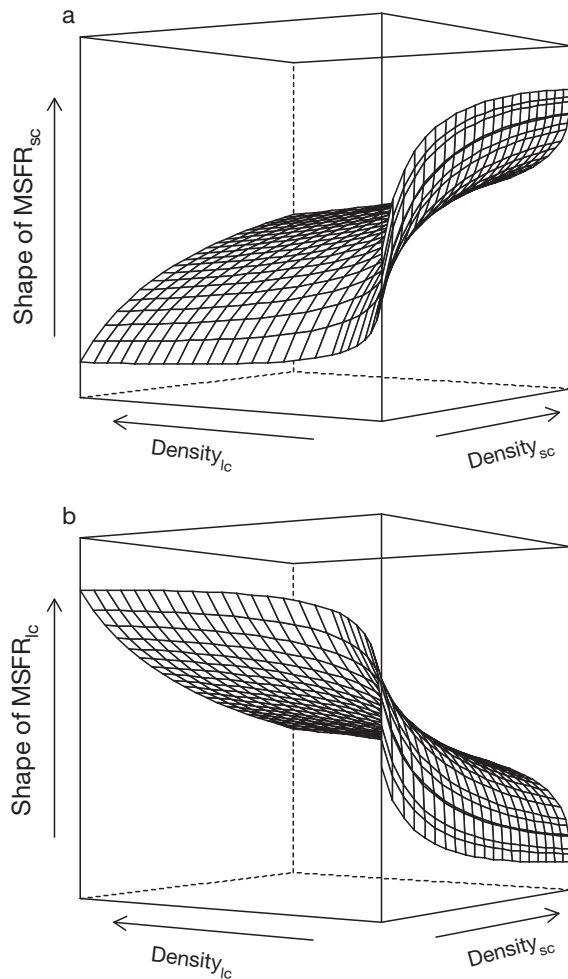


Fig. 5. *Uria aalge*. Shape of the surfaces of the common murre multispecies functional response (MSFR) with respect to (a) small capelin (sc) and (b) large capelin (lc), shown as a function of the availability of those prey. These surfaces were calculated keeping the value of the density of other prey equal to its median density during our study period

to weeks). The population functional response represents the average per capita predation rate of a population of predators, and it implicitly integrates activities other than feeding (e.g. resting, attending offspring, grooming) over a period relevant to the dynamics of the predator population (e.g. breeding season, month, year). Thus, the behavioural functional response is the focus of ethological studies, while it is the population functional response that is of ecological relevance for predator–prey population dynamic studies. The parameters we estimated can thus be considered those of a population functional response, given the temporal (breeding season) and spatial scales (hundreds of km) of the present study.

The surfaces that represent the murre's MSFR are non-linear functions (Fig. 5). The MSFR with respect to small capelin (Fig. 5a) is a monotonic increasing function of the density of that prey and an inverse function of the density of large capelin. At low densities of large capelin (e.g. $N_{lc} = 0$), the curve that represents the marginal single-species functional response with respect to small capelin ($SSFR_{sc}$) is a hyperbolic curve that increases with increasing N_{sc} until reaching a plateau. This general pattern holds for all values of N_{lc} , but as it increases the rate of change of the functional response decreases (Fig. 5a). The same description applies to the MSFR with respect to large capelin (Fig. 5b), interchanging N_{lc} with N_{sc} .

The traditional classification of functional responses is single-species and based on the curve's graphical representation: Type I is a linear increasing function until it reaches an asymptotic value, Type II is a hyperbolic and Type III a sigmoid curve (Holling 1959). On the other hand, the rationale behind published classifications of MSFRs (Gentleman et al. 2003, Koen-Alonso 2007) is based on the potential of a given formulation to produce prey switching (sensu Murdoch 1969).

The maximum likelihood estimates of the shape parameters were negative, indicating that the rate of successful search (a_i) is an inversely dependent function of prey availability. Thus, the MSFR of the common murre allows prey switching and can be classified as Class 2 following Gentleman et al. (2003) or as Type 3 in Koen-Alonso's (2007) framework. Although the MSFR is Type 3 (sensu Koen-Alonso 2007), it is not the standard case ($b_i = 1$) in which marginal single-species functional responses have a sigmoid shape.

It is interesting to note that, had we followed the traditional single-species classification, we would have concluded the functional responses with respect to the 3 prey to be Type II (Fig. 4a). A 2-dimensional version of a MSFR can, in theory, generate a curve that graphically looks like either a Type II or Type III SSFR (Matthiopoulos et al. 2008). In this case, we found a MSFR that allows prey switching and when collapsed to single species looks like a Type II SSFR. This comparison highlights the fact that classifying a MSFR based on graphical criteria can be misleading, underlining the need for the adoption of explicit mathematical criteria for its classification and the importance of evaluating its parameters (most importantly the shape parameter b_i).

Real (1977), in his interpretation of Type III SSFRs, explicitly considered the case when the exponent

$(b_i + 1)$ in the expression of the functional response is in the range $(0, 1)$ (note that Real [1977] used ' n ' to denote the exponent in the expression of the functional response). In this case, he noted that the rate of successful search (a_i) would decrease with increasing prey density. In the present study system, 3 non-mutually exclusive explanations could account for the decreasing searching efficiency: (1) with increasing shoal size, predator avoidance mechanisms of fish improve (Pitcher & Parrish 1993); (2) large prey aggregations may attract seabirds thus promoting interspecific competition (or interference) and disruptions of prey aggregations, and/or (3) the common murre exhibits a negative prey switching behaviour. The last hypothesis would imply that the common murre consumes disproportionately less of a given prey category when that prey is abundant relative to other prey, and disproportionately more when it is relatively rare. We argue that the common murre exhibits negative prey switching based on 2 premises. First, as discussed previously, when food availability is low common murre experience increased pressure to deliver larger capelin. Secondly, in years of low capelin availability large capelin is relatively rare (with respect to small capelin; Fig. 2). Thus, the common murre consumes disproportionately more large capelin when it is rare, thereby complying with the definition of negative prey switching (see also Burke & Montevecchi 2009).

In order for negative prey switching to be adaptive, common murre must adapt chick provisioning rates according to prey availability. When the availability of preferred prey is low and alternative high-quality prey are available, common murre may compensate by shifting their diet and keeping the rate of chick provisioning fairly constant despite adverse conditions (Burger & Piatt 1990). However, when a dietary shift does not occur, common murre increase their foraging effort (by making longer trips and spending more time diving per foraging trip) to provision their chicks with larger prey but at a reduced rate (Birkhead & Nettleship 1987, Monaghan et al. 1994, Uttley et al. 1994). We did not observe chick feeding rates in our study but can infer from the increased effort in a year of low capelin availability (Burke & Montevecchi 2009) and the fact that a dietary shift was not observed (i.e. 'other prey' becoming more prominent in years of low capelin availability), that common murre at Funk Island compensate poor availability of prey by feeding their chicks less often but with more energetically profitable prey items.

Concluding remarks

We used field data to link prey abundance and diet of a top predator quantitatively, describing the shape of the common murre's MSFR. Modelling species interactions represents a step beyond the simple description of patterns and aids in elucidating the mechanisms underlying patterns (Levin 1992), allowing for long-term forecasts of events outside those previously observed. In particular, the knowledge of predatory interactions is an important source of information for strategic ecosystem management (Bax 1998). In that sense, the interaction described in this paper could be used as a building block of a multi-species dynamic model (see Plagányi 2007 for a review on ecosystem models). Furthermore, the MSFR is a vital element in making the important transition from describing concurrent patterns in prey availability and predator diet data to using the murre's diet as a quantitative indicator of capelin abundance.

Acknowledgements. We are grateful to the crews of RV 'Wilfred Templeman', RV 'Teleost', RV 'Gadus Atlantica' and FV 'Lady Easton II', as well as all the people who helped collect the diet data on Funk Island over the years. D. Davis, E. Dalley and C. Burke assisted with data management. J. T. Anderson, B. deYoung and G. K. Davoren provided useful comments and suggestions. We thank B. Nakashima and F. Mowbray for helpful discussions on capelin biology and ecology. The workshops of the Natural Sciences and Engineering Research Council of Canada (NSERC) Strategic Project 'Importance of capelin biology in sustaining trophic interactions in the Northwest Atlantic' provided a fertile setting for discussing the ideas presented in the present study. G. J. Robertson and J. Harwood reviewed earlier version of this manuscript. Thorough reviews by anonymous reviewers improved this manuscript significantly. Funding was provided by an NSERC Strategic Grant (W.A.M., M.K.A., G. K. Davoren, B. de Young, J. T. Anderson), as well as DFO's Species at Risk program, and DFO's Ecosystem Research Initiative (ERI) for the Newfoundland and Labrador Region, the ERI-NEREUS Program.

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