Linking predator diet and prey availability: Common murres and capelin in the Northwest Atlantic

3 authors:

Alejandro Daniel Buren
Fisheries and Oceans Canada
30 PUBLICATIONS **226** CITATIONS

SEE PROFILE

Mariano Koen-Alonso
Fisheries and Oceans Canada
76 PUBLICATIONS **1,311** CITATIONS

SEE PROFILE

William A Montevecchi
Memorial University of Newfoundland
323 PUBLICATIONS **7,284** CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:

Ecosystem Approach to Management and Ecosystem Analyses. View project

Ecosystem Based Management View project

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

Alejandro D. Buren[1,*], Mariano Koen-Alonso[1,2], William A. Montevecchi[1]

[1]**Cognitive and Behavioural Ecology Programme, Departments of Biology and Psychology, Memorial University of Newfoundland, St. John's, Newfoundland A1B 3X9, Canada**
[2]**Northwest Atlantic Fisheries Centre, Fisheries and Oceans Canada, PO Box 5667, St. John's, Newfoundland A1C 5X1, Canada**

ABSTRACT: We examined the predator–prey interaction between an apex seabird predator, the common murre *Uria aalge, an*d capelin *Mallotus villosus, th*e 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 murres (suitable capelin), murres 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

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

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, murres 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 (Vilhjálmsson 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 murres 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 murres to capelin (Piatt 1990), prey searching behaviour (Davoren et al. 2003a), parental allocation of time and energy by breeding common murres (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
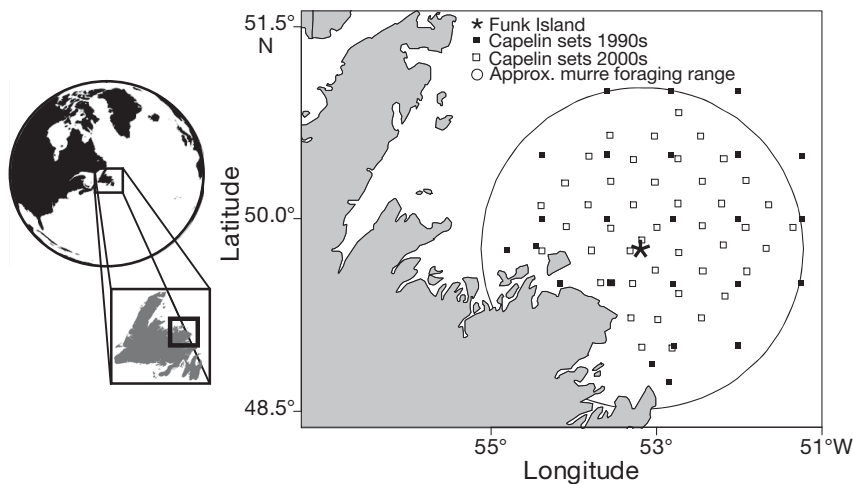
Fig. 1. Study area showing the position of Funk Island, the approximate foraging range of breeding common murres (ca. 140 km), and stations surveyed during 1995–1999 and 2004–2005

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

Diet and prey field sampling

Research vessels working in the vicinity of the murres' colony on Funk Island collected data on the prey field (below), soon after dietary samples had been collected from parental murres (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 murres 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 murres rarely deliver fish smaller than 100 mm to their chicks (Birkhead & Nettleship 1987, Barrett 2002, Davoren & Montevecchi 2005), thus we defined suitable capelin for murres 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 murres' 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 murres (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 murres take most of their prey (Tremblay et al. 2003, Hedd et al. 2009). Prey abundance sampling occurred continuously over 24-h periods. Common murres 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 ($N_{i,t}$ = Δ-estimator$_{i,t}$ × proportion$_{i,t}$).

Prey abundance estimated this way assumes that the prey are homogenously distributed and that the murres make use of all their foraging range. Common murres 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 murres 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_i is the abundance of prey i 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 MSFRs[1] 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

$$\hat{\pi}_i = \begin{cases} \hat{\pi}_{sc} = \dfrac{a_{sc} N_{sc}^{1+b_{sc}}}{a_{sc} N_{sc}^{1+b_{sc}} + a_{lc} N_{lc}^{1+b_{lc}} + a_{ot} N_{ot}^{1+b_{ot}}} \\[2ex] \hat{\pi}_{lc} = \dfrac{a_{lc} N_{lc}^{1+b_{lc}}}{a_{sc} N_{sc}^{1+b_{sc}} + a_{lc} N_{lc}^{1+b_{lc}} + a_{ot} N_{ot}^{1+b_{ot}}} \\[2ex] \hat{\pi}_{ot} = \dfrac{a_{ot} N_{ot}^{1+b_{ot}}}{a_{sc} N_{sc}^{1+b_{sc}} + a_{lc} N_{lc}^{1+b_{lc}} + a_{ot} N_{ot}^{1+b_{ot}}} \end{cases} \quad (3)$$

Diet composition as multinomial distribution

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

---

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 ith prey category in each parental delivery. The multinomial probability mass function is

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

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 $\ln[L(\theta)] = \sum_{i=sc,lc,ot} n_i \ln \pi_i$ (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.
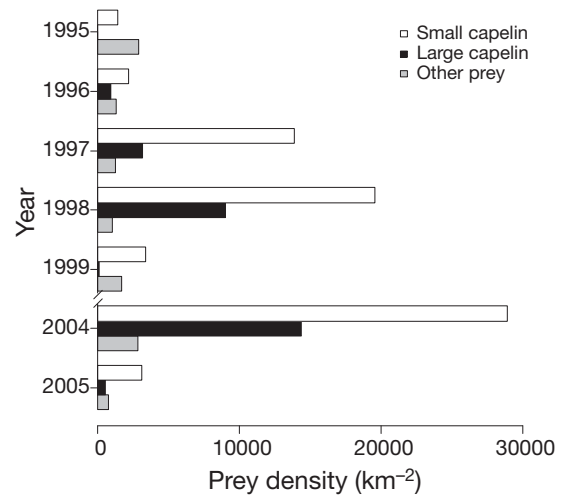

Fig. 2. *Mallotus villosus*. Availability of capelin and other prey of common murres *Uria aalge* in the upper 60 m of the water column within their foraging range around Funk Island, expressed as number of fish km^{-2}

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
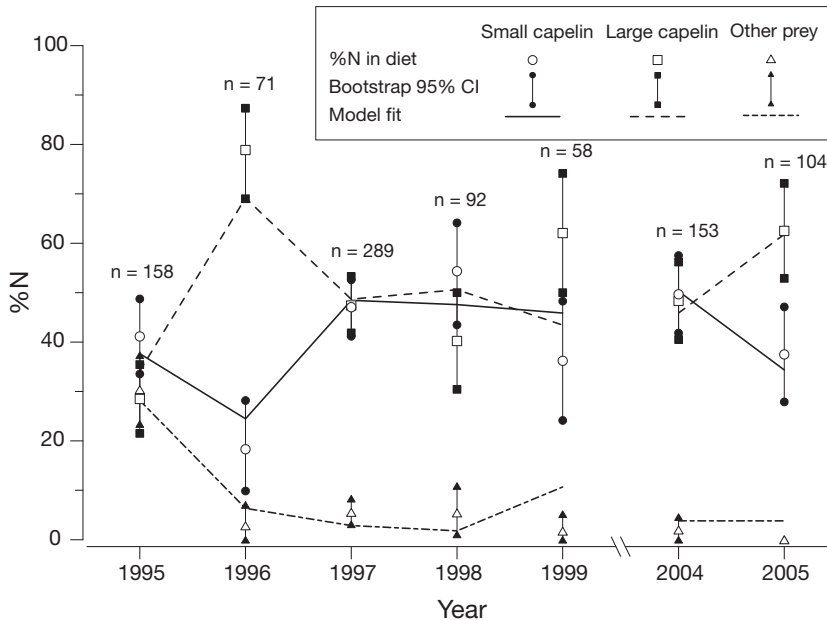
Fig. 3. *Uria aalge.* Common murre diet composition expressed as point estimates of the percentage by number (%N) that small capelin *Mallotus villosus* (100–140 mm), large capelin (>140 mm) and other prey represent in the common murre's diet. The bars indicate bootstrap 95% CI. For easy visualization 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).
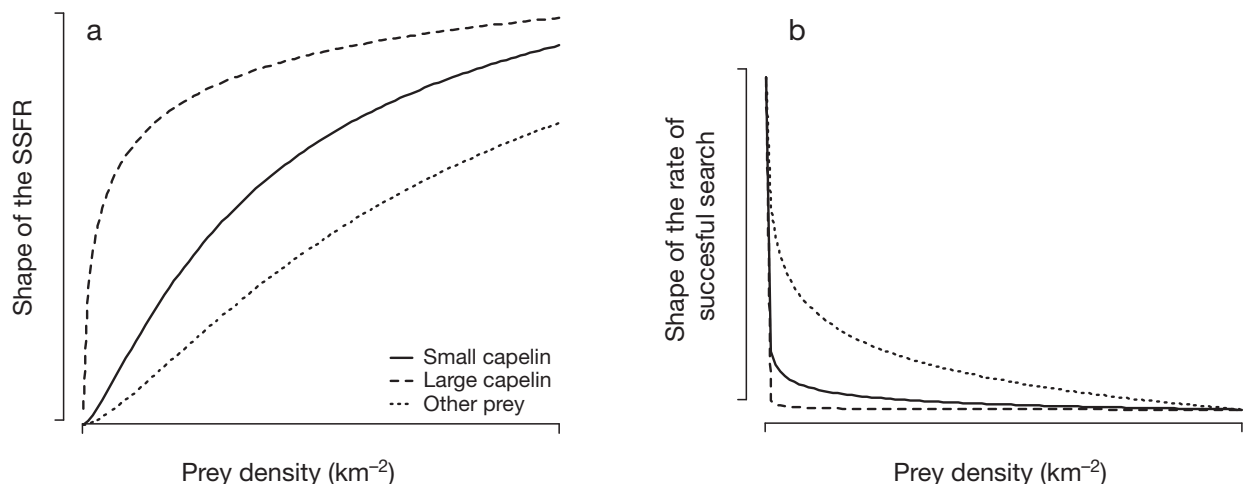

Fig. 4. *Uria aalge.* Shape of common murre (a) marginal single-species functional responses (SSFR) and (b) rates of successful search with respect to small capelin, large capelin and other prey, shown as a function of the availability of those prey. These curves were calculated by making the densities 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 (Pennycuick 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
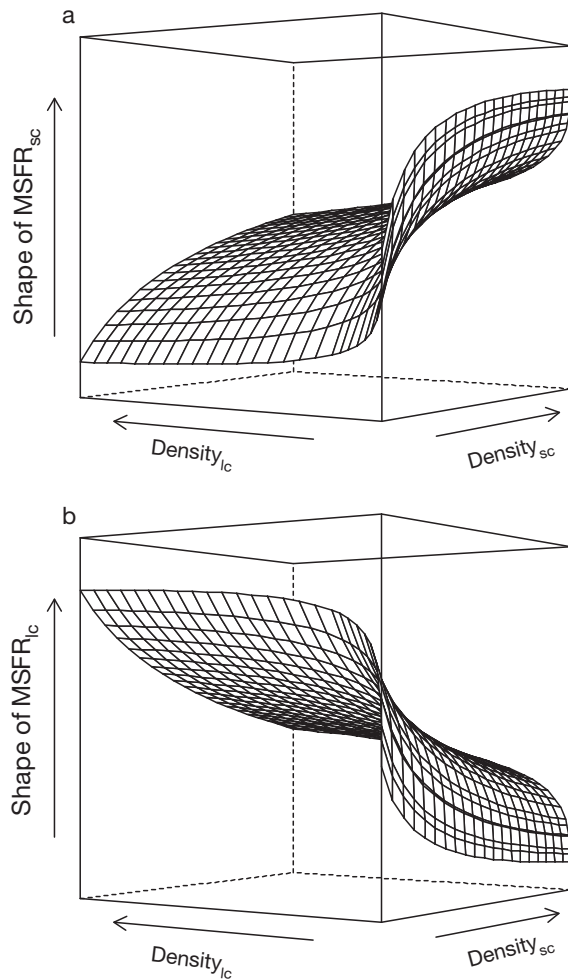
Fig. 5. *Uria aalge.* Shape of the surfaces of the common murre multispecies functional response (MSFR) with respect to (a) small capelin (sc) and (b) large capelin (lc), shown as a function of the availability of those prey. These surfaces were calculated keeping the value of the density of other prey 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 murres 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 murres 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 murres 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 murres 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 murres 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.

LITERATURE CITED

Agresti A (2002) Categorical data analysis. John Wiley & Sons, Hoboken, NJ

Ainley DG, Nettleship DN, Carter HR, Storey AE (2002) Common murre (*Uria aalge*). In: Poole A, Gill F (eds) The birds of North America, No. 666. The Birds of North America, Philadelphia, PA

Anderson JT, Dalley EL, O'Driscoll RL (2002) Juvenile capelin (*Mallotus villosus*) off Newfoundland and Labrador in the 1990s. ICES J Mar Sci 59:917–928

Anon (1979) Int Comm Northwest Atl Fish. Redbook. STACRES Spec Meet Feb 1979

Bakun A (2006) Wasp-waist populations and marine ecosystem dynamics: navigating the 'predator pit' topographies.

Prog Oceanogr 68:271–288

Barrett RT (2002) Atlantic puffin *Fratercula arctica* and common guillemot *Uria aalge* chick diet and growth as indicators of fish stocks in the Barents Sea. Mar Ecol Prog Ser 230:275–287

Barrett RT, Krasnov YV (1996) Recent responses to changes in stocks of prey species by seabirds breeding in the Southern Barents Sea. ICES J Mar Sci 53:713–722

Bax NJ (1998) The significance and prediction of predation in marine fisheries. ICES J Mar Sci 55:997–1030

Birkhead TR, Nettleship DN (1987) Ecological relationships between common murres *Uria aalge* and thick-billed murres *Uria lomvia* at the Gannet Islands, Labrador. III. Feeding ecology of the young. Can J Zool 65:1638–1649

Boyd I, Wanless S, Camphuysen CJ (2006) Top predators in marine ecosystems. Their role in monitoring and management. Cambridge University Press, Cambridge

Buren AD (2007) Modeling the link between prey availability and diet: common murre–capelin interaction during the breeding season. MSc thesis, Memorial University of Newfoundland, St. John's, NL

Burger AE, Piatt JF (1990) Flexible time budgets in breeding common murres: buffers against variable prey abundance. Stud Avian Biol 14:71–83

Burke C, Montevecchi WA (2009) The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. J Zool 278:354–361

Cairns DK, Bredin KA, Montevecchi WA (1987) Activity budgets and foraging ranges of breeding common murres. Auk 104:218–224

Cairns DK, Montevecchi WA, Birt-Friesen VL, Macko SA (1990) Energy expenditures, activity budgets, and prey harvest of breeding common murres. Stud Avian Biol 14: 84–92

Carscadden JE (1984) Population dynamics and factors affecting the abundance of capelin (*Mallotus villosus*) in the Northwest Atlantic. In: Sharp GD, Csirke J (eds) Proceedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources. FAO Fish Rep 291(3), FAO, Rome, p 789–811

Carscadden JE, Frank KT (2002) Temporal variability in the condition factors of Newfoundland capelin (*Mallotus villosus*) during the past two decades. ICES J Mar Sci 59: 950–958

Carscadden JE, Nakashima BS (1997) Abundance and changes in distribution, biology and behavior of capelin in response to cooler water of the 1990s. Proc Internat Sym Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Prog Rep 97-01:457–468

Chardine JW, Robertson GJ, Ryan PC, Turner B (2003) Abundance and distribution of common murres breeding at Funk Island, Newfoundland in 1972 and 2000. Can Wildl Serv Atl Reg Tech Rep Ser 404

Croxall JP, Reid K, Prince PA (1999) Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. Mar Ecol Prog Ser 177: 115–131

Cury PM, Christensen V (2005) Quantitative ecosystem indicators for fisheries management. ICES J Mar Sci 62(Spec Issue):307–310

Davoren GK, Montevecchi WA (2003) Signals from seabirds indicate changing biology of capelin stocks. Mar Ecol Prog Ser 258:253–261

Davoren GK, Montevecchi WA (2005) Did signals from seabirds indicate changes in capelin biology? Reply to

Carscadden (2004). Mar Ecol Prog Ser 285:299–309

Davoren GK, Montevecchi WA, Anderson JT (2003a) Search strategies of a pursuit-diving marine bird and the persistence of prey patches. Ecol Monogr 73:463–481

Davoren GK, Montevecchi WA, Anderson JT (2003b) Distributional patterns of a marine bird and its prey: habitat selection based on prey and conspecific behaviour. Mar Ecol Prog Ser 256:229–242

DFO (Fisheries and Oceans Canada) (1997) Capelin in SA2+Div. 3KL. CSAS Res Doc 1997/29

DFO (2010) Assessment of capelin in SA2+Div. 3KL in 2010. CSAS Sci Advis Rep 2010/090

Efron B, Tibshirani RJ (1993) An introduction to the bootstrap. Chapman & Hall, New York, NY

Einoder LD (2009) A review of the use of seabirds as indicators in fisheries and ecosystem management. Fish Res 95:6–13

Frank KT, Carscadden JE, Simon JE (1996) Recent excursions of capelin (*Mallotus villosus*) to the Scotian Shelf and Flemish Cap during anomalous hydrographic conditions. Can J Fish Aquat Sci 53:1473–1486

Gaston AJ, Woo K, Hipfner JM (2003) Trends in forage fish populations in northern Hudson Bay since 1981, as determined from the diet of nestling thick-billed murres *Uria lomvia.* Arctic 56:227–233

Gentleman W, Leising A, Frost B, Strom S, Murray J (2003) Functional responses for zooplankton feeding on multiple resources: a review of assumptions and biological dynamics. Deep-Sea Res II 50:2847–2875

Grémillet D, Charmantier A (2010) Shifts in phenotypic plasticity constrain the value of seabirds as ecological indicators of marine ecosystems. Ecol Appl 20:1498–1503

Hamilton WD (1964) The genetical evolution of social behaviour. I. J Theor Biol 7:1–16

Hedd A, Regular PM, Montevecchi WA, Buren AD, Burke C, Fifield DA (2009) Going deep: murres dive into frigid water for aggregated, persistent and slow-moving capelin. Mar Biol 156:741–751

Hilborn R, Mangel M (1997) The ecological detective. Confronting models with data. Princeton University Press, Princeton, NJ

Hjermann DO, Ottersen G, Stenseth NC (2004) Competition among fishermen and fish causes the collapse of Barents Sea capelin. Proc Natl Acad Sci USA 101:11679–11684

Holden MJ, Raitt DFS (1974) Manual of fisheries science. Part 2. Methods of resource investigation and their application. FAO Fish Tech Pap 115:1–255

Holling CS (1959) The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Can Entomol 91:293–320

Holling CS (1965) The functional response of predators to prey density and its role in mimicry and population regulation. Mem Entomol Soc Can 97:1–60

Hunt GL Jr Kitaysky AS, Decker MB, Dragoo DE, Springer AM (1996) Changes in the distribution and size of juvenile walleye pollock, *Theragra chalcogramma,* as indicated by seabird diets at the Pribilof Islands and by bottom trawl surveys in the eastern Bering Sea, 1975 to 1993. In: Brodeur RD, Livingston PA, Loughlin TR, Hollowed AB (eds) Ecology of juvenile walleye pollock, *Theragra chalcogramma.* NOAA Tech Rep NMFS 126: 125–139

Hyslop EJ (1980) Stomach content analysis—a review of methods and their application. J Fish Biol 17:411–429

Ives AR, Schooler SS, Jagar VJ, Knuteson SE, Grbic M,

Settle WH (1999) Variability and parasitoid foraging efficiency: a case study of pea aphids and *Aphidius ervi*. Am Nat 154:652–673

Koen-Alonso M (2007) A process-oriented approach to the multispecies functional response. In: Rooney N, McCann KS, Noakes DGL (eds) Fundamental ecology, Vol I. From energetics to ecosystems: the dynamics and structure of ecological systems. Springer, Dordrecht, p 1–36

Lavigne DM (1996) Ecological interactions between marine mammals, commercial fisheries and their prey: unravelling the tangled web. In: Montevecchi WA (ed) Studies of high-latitude seabirds. 4. Trophic relationships and energetics of endotherms in cold ocean systems. Can Wildl Serv Occas Pap 91:59–71

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73:1943–1967

Matthiopoulos J, Smout S, Winship AJ, Thompson D, Boyd I, Harwood J (2008) Getting beneath the surface of marine mammal fisheries competition. Mammal Rev 38:167–188

Mehlum F, Gabrielsen GW (1993) The diet of high-arctic seabirds in coastal and ice-covered, pelagic areas near the Svalbard archipelago. Polar Res 12:1–20

Monaghan P, Walton P, Wanless S, Uttley JD, Burns MD (1994) Effects of prey abundance on the foraging behaviour, diving efficiency and time allocation of breeding guillemots *Uria aalge.* Ibis 136:214–222

Montevecchi WA (1993) Birds as indicators of change in marine prey stocks. In: Furness RW, Greenwood JD (eds) Birds as monitors of environmental change. Chapman & Hall, London, p 217–266

Montevecchi WA (2000) Seabirds. In: Bundy A, Lilly GR, Shelton PA (eds) A Mass balance model of the Newfoundland-Labrador Shelf. Can Tech Rep Fish Aquat Sci 2310:15–18

Montevecchi WA, Myers RA (1996) Dietary changes of seabirds reflect shifts in pelagic food webs. Sarsia 80:313–322

Montevecchi WA, Piatt JF (1984) Composition and energy contents of mature inshore spawning capelin (*Mallotus villosus*): implications for seabird predators. Comp Biochem Physiol A 78:15–20

Mowbray F (2002) Changes in the vertical distribution of capelin (*Mallotus villosus*) off Newfoundland. ICES J Mar Sci 59:942–949

Murdoch WW (1969) Switching in general predators: experiments on predator specificity and stability of prey populations. Ecol Monogr 39:335–354

Nakashima BS (1992) Patterns in coastal migration and stock structure of capelin (*Mallotus villosus*). Can J Fish Aquat Sci 49:2423–2429

Nakashima BS, Slaney BW (2001) Spawning and early development of capelin (*Mallotus villosus*) at Bellevue Beach, Trinity Bay in 1999. In: Anonymous (ed) Capelin in SA2 + Div. 3KL during 1999. CSAS Res Doc 2001/161, p 75–87

Nakashima BS, Wheeler JP (2002) Capelin (*Mallotus villosus*) spawning behaviour in Newfoundland waters — the interaction between beach and demersal spawning.

ICES J Mar Sci 59:909–916

Orians GH, Pearson NE (1979) On the ecology of central place foraging. In: Horn DJ, Stairs GR, Mitchell RD (eds) Analysis of ecological systems. Ohio State University Press, Columbus, OH, p 155–177

Pennington M (1996) Estimating the mean and variance from highly skewed marine data. Fish Bull 94:498–505

Pennycuick CJ (1987) Flight of seabirds. In: Croxall JP (ed) Seabirds: feeding ecology and role in marine ecosystems. Cambridge University Press, Cambridge, p 43–62

Piatt JF (1990) The aggregative response of common murres and Atlantic puffins to their prey. Stud Avian Biol 14: 36–51

Pitcher TJ, Parrish JK (1993) Functions of shoaling behaviour in teleosts. In: Pitcher TJ (ed) Behaviour of teleost fishes. Chapman & Hall, London, p 363–439

Plagányi E (2007) Models for an ecosystem approach to fisheries. FAO Fish Tech Pap 447, FAO, Rome

Randall RM, Randall BM (1986) The diet of jackass penguins *Spheniscus demersus* in Algoa Bay, South Africa, and its bearing on population declines elsewhere. Biol Conserv 37:119–134

Real LA (1977) The kinetics of functional response. Am Nat 111:289–300

Regular PM, Davoren GK, Hedd A, Montevecchi WA (2010) Crepuscular foraging by a pursuit-diving seabird: tactics of common murres in response to the diel vertical migration of capelin. Mar Ecol Prog Ser 415:295–304

Rice J (2002) Changes to the large marine ecosystem of the Newfoundland-Labrador shelf. In: Sherman K, Skjoldal HR (eds) Large marine ecosystems of the North Atlantic. Elsevier Science, Amsterdam, p 51–103

Siarry P, Berthiau G, Durbin F, Haussy J (1997) Enhanced simulated annealing for globally minimizing functions of many-continuous variables. ACM Trans Math Softw 23: 209–228

Templeman W (1948) The life history of the caplin (*Mallotus villosus* OF Müller) in Newfoundland waters. Bull Nfld Gov Lab 17:1–151

Tremblay Y, Cherel Y, Oremus M, Tveraa T, Chastel O (2003) Unconventional ventral attachment of time-depth recorders as a new method for investigating time budget and diving behaviour of seabirds. J Exp Biol 206: 1929–1940

Uttley JD, Walton P, Monaghan P, Austin G (1994) The effects of food abundance on breeding performance and adult time budgets of guillemots *Uria aalge.* Ibis 136: 205–213

Vilhjálmsson H (1994) The Icelandic capelin stock. Rit Fiskideildar 13:1–281

Wanless S, Harris MP, Redman P, Speakman JR (2005) Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. Mar Ecol Prog Ser 294:1–8

Winters GH (1982) Life history and geographical patterns of growth in capelin (*Mallotus villosus*) of the Labrador and Newfoundland area. J Northw Atl Fish Sci 3:105–114