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4. Trophic relationships and  
energetics of endotherms in cold  
ocean systems**

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Number 91  
Canadian Wildlife Service**

Papers presented at the Marine Birds and Mammals in Arctic Food Webs Symposium held at Memorial University of Newfoundland, St. John's, Newfoundland, in April 1992 and jointly sponsored by the Canadian Wildlife Service and Memorial University of Newfoundland

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**Cover photo:** Common Murres and capelin, Funk Island, Newfoundland (W.A. Montevecchi)

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# Introduction

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*Biopsychology Program, Departments of Psychology and Biology and Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, Newfoundland A1B 3X9*

The 1992 Canadian Wildlife Service/Memorial University of Newfoundland symposium on "Marine Birds and Mammals in Arctic Food Webs" was the third such venture of its kind, following joint symposia that were held in 1986 (Montevecchi 1987) and in 1989. Papers from these symposia provided the basis for a new series of publications within the Canadian Wildlife Service Occasional Papers series — "Studies of high-latitude seabirds" (Gaston and Elliot 1991; Montevecchi and Gaston 1991; Diamond et al. 1993). The present publication is the fourth one in this series.

The symposium held in St. John's during 1992 focused on ecosystem-level considerations of marine endotherms. Most presentations took a multispecies orientation. Specifically, papers presented here address topics in feeding ecology, energetics, and multispecies indication of prey conditions.

During the early 1990s, when this symposium was held, human-induced effects on seabirds in the Northwest Atlantic were considerable. A Canadian "fisheries moratorium" initiated in 1992 eliminated massive tonnages of "artificial" food sources of offal available to scavenging seabirds. As at least a partial consequence (see below), the levels of predation by Great Black-backed Gulls *Larus marinus* and Herring Gulls *L. argentatus* on other seabirds have been extraordinary (Regehr 1995; Russell and Montevecchi 1996; H.M. Regehr, W.A. Montevecchi, and J.W. Chardine, unpublished data). In the longer term, populations of *Larus* gulls will most probably be negatively affected by this fishery closure (Howes and Montevecchi 1993).

Also during this period, the Northwest Atlantic exhibited decadal anomalous cold sea surface temperatures (Montevecchi and Myers 1992, 1995b; Drinkwater et al. 1994). Heavy arctic ice cover occurred during some of these springs. Cold surface water events were associated with (1) delayed inshore migrations of capelin *Mallotus villosus*, (2) widespread reproductive failures of Black-legged Kittiwakes *Rissa tridactyla* and *Larus* gulls along the Newfoundland coast, (3) delayed breeding (but good success) of pursuit-diving alcids, and (4) dietary shifts among Northern Gannets *Sula bassana* (Montevecchi and Myers 1992, 1995b; Casey 1994; Neuman 1994; Regehr 1995; Rodway 1995; M.S. Rodway, J.W. Chardine, and W.A. Montevecchi, unpublished data). Similarly, poor production by seabirds

in Alaska has also been associated with cold-water events and unusual ice cover in the Chukchi Sea (Springer et al. 1984), as well as with warm surface water perturbations (e.g., Baird 1990).

As in the Northwest Atlantic, many studies have documented divergences in the reproductive success of surface-feeding and pursuit-diving seabirds during years of poor food availability (see Montevecchi 1993). The papers by Monaghan et al. and Barrett in this volume substantiate the informational value of well-integrated multispecies studies of the feeding and reproductive ecology of seabirds. Monaghan et al.'s investigation in the Shetland Isles is an exemplary multidisciplinary study in which seabird and fisheries biologists collaborated in synoptic studies of avian feeding and breeding ecology and prey (sand lance *Ammodytes* spp.) abundances, age classes, and spatial and temporal distributions in the colony vicinity. Despite a 40-fold increase in the density of sand lance between 1990 and 1991, neither surface-feeding kittiwakes nor pursuit-diving murre showed any dietary changes, but they did exhibit increases in foraging effort when density in this "single-prey" system was low (see also Burger and Piatt 1990; Barrett and Krasnov 1996). Kittiwakes exhibited complete reproductive failure in 1990, whereas murre showed much less marked differences in success between years. The contribution by Barrett has the distinction of documenting a situation in which surface-feeding kittiwakes exhibited better reproductive success than pursuit-diving Atlantic Puffins *Fratercula arctica* in the Northeast Atlantic during the 1980s, when there was a common shortage of herring *Clupea harengus*. The take-home message from these studies and others like them is that comprehensive multispecies, multidisciplinary approaches to indication of prey conditions are more robust and more informative than single-species efforts. For example, some situations in which surface feeders and pursuit divers feed on the same prey and in which surface feeders reproduce less well lead to hypotheses about oceanographic influences on the distribution of pelagic fishes — for example, thermal barriers to the vertical and migratory movements and hence availability of prey (Montevecchi and Myers 1995a, 1995b; Barrett and Krasnov 1996). Interspecific comparisons suggest further that surface-feeding piscivores are more sensitive to surface water perturbations than are surface-feeding planktivores, a

general pattern that is consistent with the larger clutch sizes of the former.

Chapdelaine and Brousseau show how Razorbills *Alca torda* provisioning chicks in a "two-prey" (sand lance and capelin) system provide different energy inputs to offspring, depending on the proportions of these prey in food deliveries. This study affords a good contrast with Monaghan et al.'s "single-prey" (sand lance) system carried out at the Shetlands. Razorbills exhibited high fledging success that was positively associated with interannual variation in daily provisioning rates.

With regard to inter- and intraspecific spatial and temporal comparisons, Hatch has contributed an important methodological paper on the analysis and interpretation of concordance among seabird population parameters. Concordance among parameters, such as breeding success among years, areas, and species, can, when carefully applied, imply similarity of ecological factors affecting performance. Conversely, discordant relationships suggest that similar underlying ecological relationships may not be involved. Attempts to rigorously analyze long-term and large-scale data sets are often impeded by missing values, and Hatch presents ways to maximize the utility of available data. These techniques will aid in evaluating information obtained from seabirds concerning changing conditions in the marine environment — for example, hypotheses about the differential effects of pelagic prey distributions on surface-feeding and pursuit-diving seabirds.

Using doubly labelled water to study the energy expenditures of Common Murres *Uria aalge* during chick rearing, Gabrielsen reported an average daily energy expenditure of 2200 kJ, which was 3.8 times the resting metabolic rate (RMR). Substantial variation (fourfold differences) among the field metabolic rates (FMRs) of individual murres yielded FMR/RMR ratios that ranged from 1.7 to 6.8. This variation was considered consistent with the hypothesis that murres exhibit flexible parental foraging efforts at sea (FMR was well correlated with time at sea) in response to changing prey conditions (Burger and Piatt 1990). As chick success remained high across a range of foraging efforts, Gabrielsen suggested that for murres, breeding success, provisioning rate, and chick growth may not reflect food availability in the colony vicinity, but that time at sea per day was a good indicator of parental foraging effort. Gabrielsen also estimated that Common Murres consumed prey equal to about 43% of their body mass per day and presented water influx rate data suggesting that parental murres digest as much food as possible at sea before returning to the colony to provision chicks (see also Cairns et al. 1990).

Lavigne's contribution rounds out the symposium collection with a comprehensive synthesis of the interactive roles of science, management, and conservation strategies in understanding interactions between commercial fisheries, marine mammals, and their prey. Lavigne argues that besides research directing more attention to population size, age structure, and size at age, more scientific effort needs to be aimed at understanding trophic interactions at the ecosystem level. Traditional approaches to estimating fish populations as well as predator harvests have taken single-species approaches, which, as indicated above, are inadequate and inferior to multispecies approaches (Harwood 1983). Moreover, prey

harvest data need to be integrated in the spatial contexts of the movements of large marine predators; for example, harp seals *Phoca groenlandica* in the Northwest Atlantic spend much, if not most, of the year outside of the range of northern cod *Gadus morhua*. When capelin stocks collapsed in the Barents Sea in the mid-1980s, harp seals moved out of their range and showed up in record numbers along the North Norwegian coast. Interestingly, in the 1990s, harp seals have been observed in exceptional numbers in the coastal waters of Newfoundland.

The current roles of scientists in public education leave much room for development, especially with regard to realistically addressing ecological uncertainty. At present, we cannot predict the effects of increasing or decreasing marine mammal populations on either the abundance of their prey or commercial fisheries harvests. Ecological uncertainty ensures the inevitability of scientific errors (Ludwig et al. 1993), and experience shows clearly that such errors need to be biased in favour of conservation rather than economic expediency. Bearing this in mind, wildlife, fisheries, and ecosystem management must be seen as what it really is — the control of human harvests, pollution, and disturbance by quotas, bag limits, habitat protection, licensing programs, etc., to ensure long-term sustainable harvests and preservation — and as what it is not — the regulation of animal populations. There is no scientific evidence that the culling of large marine predators has ever benefited a commercial fishery, and even the commercial extinction of northern cod in eastern Canada does not seem to have led to an increase in capelin, a primary prey of the cod. So, in addition to focusing on scientific knowledge, comprehensive programs of conservation biology need to critically examine management policies and the economic orientations that drive them. Until ecological concerns override short-term economic scenarios, we will continue to disrupt ecosystem integrity. The issues raised by Lavigne are especially timely, as much of the current debate about harp seal exploitation in the Northwest Atlantic focuses on their "presumed," yet unsupported, impacts on northern cod stocks. In view of past performance, it is clear that we have more to gain by acting on our ignorance and invoking cautious environmental interactions than by acting on our limited knowledge and overexploiting and disrupting renewable natural resources.

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# The influence of changes in food abundance on diving and surface-feeding seabirds

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## Abstract

Breeding parameters of Black-legged Kittiwakes *Rissa tridactyla* and Common Murres *Uria aalge* breeding in Shetland in 1990 and 1991 were examined in conjunction with studies on the distribution, abundance, and age composition of sand lance (*Ammodytes* spp.), their main prey in the area. There was a 40-fold difference in sand lance density between years, and the distribution and age composition of the fish also differed markedly. Although the diet composition of the birds did not differ between years, differences were found in the breeding success, colony attendance, foraging trip durations, and overall activity budgets. These findings are discussed in relation to the differing foraging strategies of the two seabird species and the use of seabirds as indicators of changes in marine fish populations.

## Résumé

On a examiné les paramètres de reproduction des populations reproductrices de Mouettes tridactyles *Rissa tridactyla* et de Marmettes de Troil *Uria aalge* du Shetland pour 1990 et 1991, ainsi que les résultats d'autres études portant sur la distribution, l'abondance et la composition par âge du lançon (*Ammodytes* sp.), principale proie de ces espèces dans la région. On a déterminé que la densité de la population de lançons s'était multipliée par 40, et la distribution de même que la composition par âge affichaient également des variations marquées. Bien que l'alimentation de ces oiseaux n'ait pas varié, on a observé certaines variations dans le taux de reproduction, l'importance des colonies, la durée des migrations entraînées par la quête de nourriture et les bilans d'activité globaux. Ces résultats sont traités à la lumière des différentes stratégies de recherche de nourriture adoptées par les deux espèces et du fait que les oiseaux marins constituent des indicateurs des variations dans les populations de poissons marins.

## 1. Introduction

Many aspects of seabird biology may be influenced differentially by changes in the availability of their marine food, and we therefore need to understand the nature and

pattern of such responses if seabirds are to be successfully used as indicators of changes in the marine environment. Cairns (1987, 1992) put forward putative relationships between food supply and a number of seabird parameters — in particular, adult survivorship, breeding success, chick growth, colony attendance, and adult activity budgets — and suggested the range of food availabilities over which these parameters are likely to be sensitive. This has provided a useful theoretical framework that can be used to examine responses within and among species. The latter aspect is particularly important in using seabirds as bioindicators, as, owing to differential flexibility in their time and energy budgets, some seabird species may be capable of behavioural changes that effectively buffer certain aspects of their breeding biology against at least moderate changes in food supply (e.g., Furness and Ainley 1984; Burger and Piatt 1990). Such differences in sensitivity both between species and between measurable parameters need to be taken into account.

A number of additional factors also need to be considered in assessing the usefulness of seabirds as indicators of changes in marine fish populations. In many situations, a variety of potential prey species may occur. In the absence of good data on the hierarchy of prey preferences, dietary shifts cannot be used to deduce which component of the prey spectrum has altered in availability. Furthermore, independent data on food abundance are rarely available. The fish taken by seabirds are often not the basis of a commercial fishery, and thus fisheries-derived estimates of prey populations do not exist. Even where such estimates are available, the location and scale over which they have been calculated are rarely appropriate. Specific studies of seabird prey in the vicinity of study colonies, in conjunction with good data on the foraging ranges of seabird species, are required. Such studies are expensive and time consuming and are usually outside the scope of most seabird research.

Seabirds breeding in the Shetland Isles are largely dependent on a single prey species, the lesser sand lance *Ammodytes marinus* (e.g., Martin 1989; Monaghan et al. 1989a, 1989b; Hamer et al. 1991). For most seabird species, no other suitably sized, energy-rich prey occur in the area (Kunzlik 1989). During the 1980s, Shetland seabirds experienced dramatic reductions in breeding success. This was coincident with a decline in sand lance

stocks (Bailey et al. 1991). A fishery for sand lance had occurred around Shetland since 1974, and considerable controversy arose over whether and to what extent the seabird breeding failures resulted from overfishing of the sand lance stock (Monaghan 1992). This has led to the undertaking of detailed studies of both the fish and the bird populations. Considerable changes occurred in sand lance abundance between 1990 and 1991. This effectively acted as a natural experiment, giving us the opportunity to compare the response of diving and surface-feeding seabirds with known changes in prey abundance in a relatively simple, single-prey situation. Here we present data on the changes in the fish population between the two years and compare the response of the surface-feeding Black-legged Kittiwake *Rissa tridactyla* with that of the pursuit-diving Common Murre *Uria aalge*.

## 2. Methods

The study was conducted at Sumburgh Head, South Mainland of Shetland (59°51.2'N, 1°16.4'W; Fig. 1). Data were collected on both fish and bird populations in May–August 1990 and 1991.

### 2.1 Assessment of fish abundance and distribution

The distribution of sand lance and other seabird prey within 40 km of Sumburgh Head was investigated via dedicated ship cruises from 18 June to 26 July 1990, from 8 to 21 May 1991, and from 25 June to 13 July 1991. Sampling thus took place during the main seabird chick-rearing periods in each year and additionally during the incubation period in 1991. A 21-m fishing vessel was used for surveys that ran from Sumburgh to Fair Isle (see Fig. 1). Fish distribution and density were investigated from echosounder and echointegration surveys. An echotrace area/echointegral relationship for sand lance was used to estimate relative abundance on a linear 0–1 scale as follows. Corresponding measurements of combined shoal area and echointegrals for 15-minute integration runs were compared. Shoal area was estimated from the vertical height and length of echotraces, and then corrections for beam width and position in the water column were applied (see Forbes and Nakken 1972). Data used were derived from one survey during a period when 0-group sand lance, 8–11 cm in length, dominated catches (25 June – 1 July 1991). Shoal area and echointegration values were significantly correlated ( $r^2 = 0.74$ ,  $P < 0.001$ ; Fig. 2), and this relationship was used to derive estimates of sand lance density from echotrace area per kilometre travelled.

For the purpose of analysis, survey areas were divided into  $9 \times 4.5$  km blocks to examine large-scale distribution and  $2 \times 2$  km blocks to examine distribution within 5 km of the coast. Cruise tracks passed through the centre of each block, and a mean density of fish per kilometre travelled was estimated as outlined above. Surveys lasted between five and eight hours and were timed to coincide with the peak in sand lance activity in the water column (06:00–14:00).

Bottom trawling was also used to derive catch per unit effort (CPUE) data at Voe, a known sand lance ground close (<5 km) to Sumburgh (Fig. 1). Fish were

also sampled in mid- and surface waters using a pelagic trawl (PT 154) and in the sediment using a modified scallop dredge (1991 only). Length composition of the sample was recorded at sea, and otoliths were collected for later age analysis.

### 2.2 Seabird parameters

Data on diet, breeding success, activity budgets, and colony attendance were collected from both seabird species at study plots at Sumburgh Head (Fig. 1). The kittiwake data were collected from a study plot of 47 breeding pairs in 1990 and 52 in 1991; for murre, a sample of 133 pairs in the study colony was observed in 1990, and 117 in 1991. Activity budget and colony attendance data were obtained from dawn to dusk hide watches on subsamples of nests (03:00–23:00). Kittiwakes were observed on seven days during incubation and seven days during chick rearing in 1990 and on five and nine days in 1991, respectively; for murre, the corresponding figures were five and five days in 1990 and 12 and five days in 1991. Dietary data were collected by observation of prey carried to chicks in the bill by murre and from examination of regurgitates of adult kittiwakes caught at the nest. Foraging locations were obtained by radio-tracking; three murre were tracked during 21 foraging trips in 1990 and six during 31 trips in 1991, and 13 kittiwakes were tracked during 43 trips in 1990 and nine during 117 trips in 1991. Triangulations were obtained by the combined use of two tracking stations. Full details of methodologies for kittiwakes can be found in Hamer et al. (1993) and Wanless et al. (1992), and for murre in Uttley et al. (1994) and Monaghan et al. (1994). Where data are normally distributed, means  $\pm$  1 s.e. are given; medians and interquartile ranges are given for nonnormal distributions.

## 3. Results

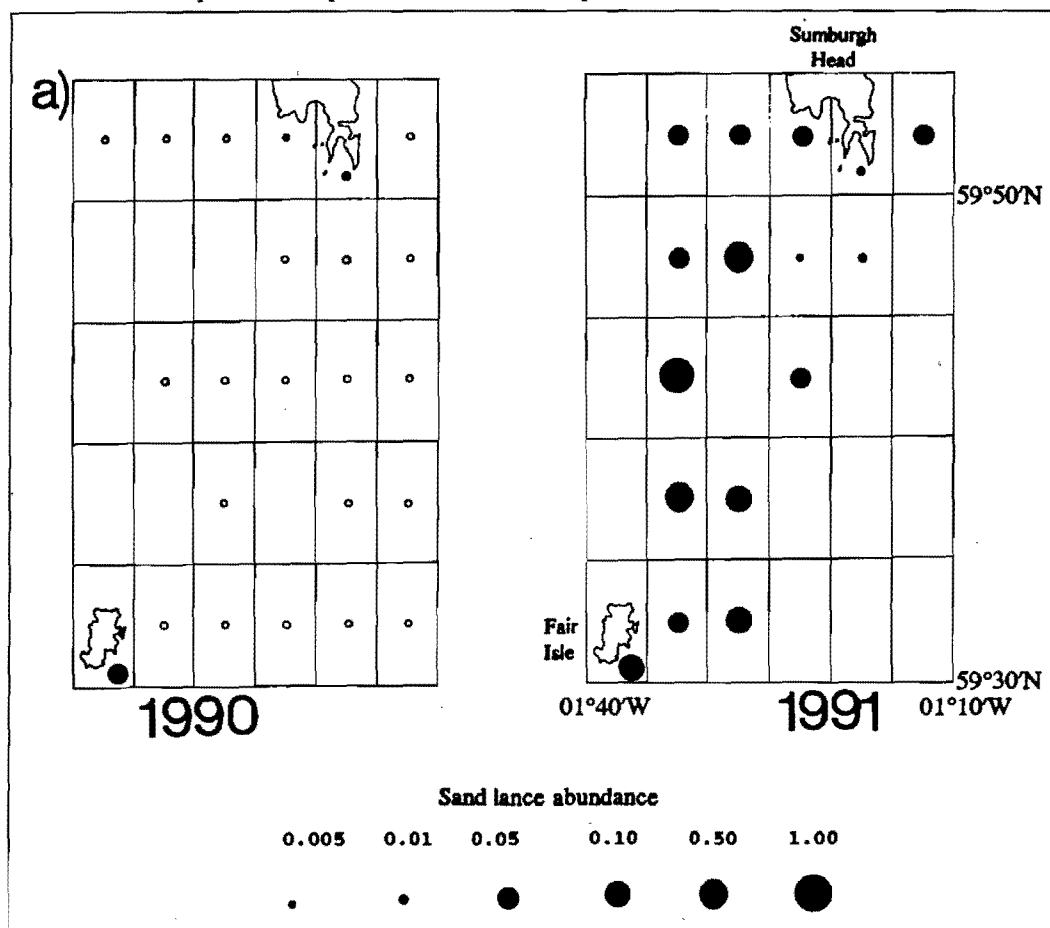
### 3.1 Sand lance population changes

#### 3.1.1 Abundance and distribution

The acoustic surveys showed that sand lance were much more abundant and had a far wider distribution in 1991 than in 1990 (Fig. 1). In 1990, between Sumburgh and Fair Isle, sand lance were found only within 5 km of the coast around Sumburgh (Fig. 1a), the highest densities occurring within 2 km (Fig. 1b), in depths of <50 m. Abundance in this area was, however, relatively low. A larger concentration of sand lance was found just south of Fair Isle (Fig. 1a), a distance of around 40 km from the seabird study colonies. In contrast, in 1991, sand lance were both more abundant and much more widespread. High concentrations of sand lance were found between Sumburgh Head and Fair Isle (depths 80–100 m), as well as inshore around Sumburgh (Figs. 1a and 1b). The acoustic surveys clearly demonstrated a marked difference in sand lance abundance during the early chick-rearing period (late June and July) in the inshore Sumburgh area between the two years (area sampled 59°50'–59°52'N, 01°15'–01°20'W; 1990 mean =  $0.002 \pm 0.001$  units/km,  $n = 5$  surveys; 1991 mean =  $0.005 \pm 0.0012$  units/km,  $n = 7$  surveys). In addition, mean CPUE for bottom trawl

**Figure 1**

(a) The distribution and relative abundance of sand lance within the foraging area used by the seabirds. These data are based on three echosounder surveys carried out in each year between 25 June and 1 July, the early chick-rearing period. Abundance is shown on a grid basis, each grid square being  $9.26 \times 4.63$  km. Squares with open circles are areas sampled but where no sand lance were found



catches tended to be markedly greater in 1991 than in 1990 at the sand lance ground sampled (Table 1).

Overall, the acoustic surveys give relative estimates of sand lance density per kilometre travelled for the Sumburgh – Fair Isle region shown in Figure 1a as  $0.00461 \pm 0.00384$  units/km for 1990 and  $0.215 \pm 0.054$  units/km for 1991.

### 3.1.2 Age composition

There was a particularly striking difference in the age composition of catches at the Voe ground between the two years. In 1990, all sand lance present there during the seabird chick-rearing period in late June and July were one or two years old ( $>1+$ ); in contrast, in 1991, 0-group sand lance dominated catches at Voe (Table 1) and at other grounds in south Shetland that were also sampled at this time. In addition, pelagic trawl catches from offshore stations ( $>10$  km from Sumburgh) in 1991 consisted solely of 0-group sand lance. Although the  $>1+$  fish were relatively abundant at Voe in May 1991, numbers had declined by late June, presumably because of movement of fish of this age group into the sediment or offshore (Table 1). Dredge sampling in 1991 indicated that whereas trends in dredge CPUE were similar to those in trawl CPUE, the relative proportion of  $>1+$  sand lance occurring in the sediment increased by mid-July (Wright and Bailey

1993). In contrast to 1991,  $>1+$  fish were abundant in late June 1990, although they had almost disappeared by July. This indicates a difference in the timing of withdrawal of this age class from the water column in the two years. Furthermore, in early to mid-July, this age class was also considerably more abundant in 1991 than in 1990 (Table 1).

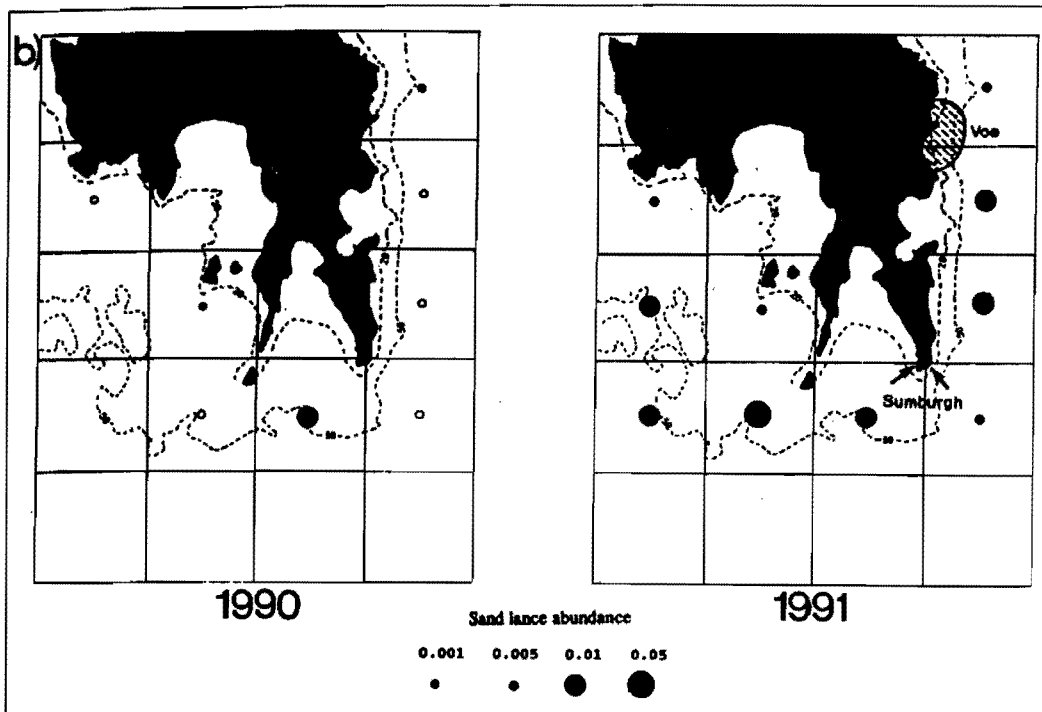
The length frequencies of 0-group fish showed that two subcohorts of 0-group sand lance were present around south Shetland at the beginning of the chick-rearing period (22 June – 1 July) in 1991 (Fig. 3). The median length of the older and more numerous subcohort was significantly larger than that of 0-group sand lance caught at the same time of year in 1990 (total length, 1990 median = 70 mm, range 65–85 mm,  $n = 100$ ; 1991 median = 95 mm, range 55–120 mm,  $n = 100$ ; Mann-Whitney/Wilcoxon's test,  $W = 15022.0$ ,  $P < 0.0001$ ).

### 3.1.3 Size and position of shoals

Information on the position and size of shoals in the water column obtained from acoustic surveys indicated that dense sand lance shoals rarely extended to within 10 m of the surface in any area (median shoal size = 0.001, range 0.001–0.05 relative acoustic units). Shoals extending into the top 10 m comprised 17% of all shoals recorded in south Shetland in 1990 and 7.5% in 1991.

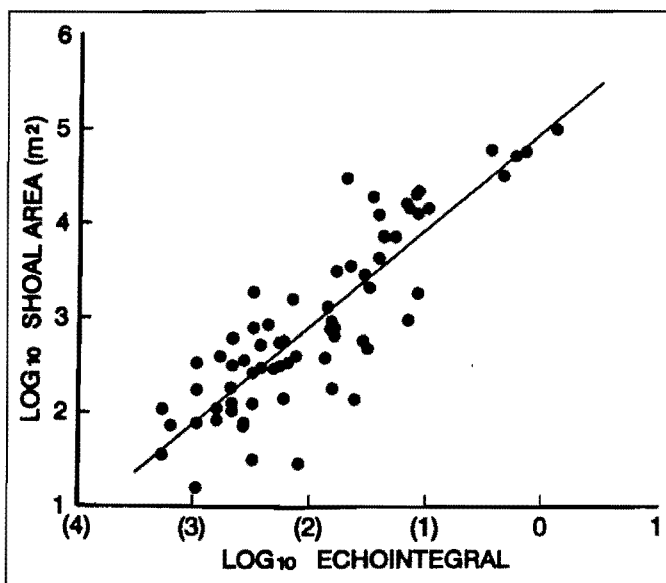
**Figure 1 (cont'd)**

(b) Details of sand lance distribution and relative abundance in the area close to Sumburgh Head, as measured by transects on 26 June in each year. Grid here is 2-km squares. The location of the study colonies at Sumburgh Head is shown, as is the sand lance ground sampled at Voe. Depth contours (m) are also shown



**Figure 2**

The relationship between sand lance shoal area and echointegration value for simultaneous 15-minute integration runs (data transformed to log +1 values)



Owing to their size, however, the component of shoals in the top 10 m formed only about 7% and 3%, respectively, of the total sand lance biomass in 1990 and 1991. Given the difference in the abundance of fish between the two years, it is clear that very few fish occurred near the surface in 1990. In both years, over 80% of detected shoals occurred in mid-water between 04:30 and 12:00.

### 3.2 Responses of seabirds

#### 3.2.1 Diet composition

Only limited data were collected on kittiwake diets in 1990, as few of the handled birds regurgitated food. However, all of the seven regurgitates in 1990 and all of the 27 collected in 1991 consisted of small sand lance, indicating that, in both years, the bulk of the kittiwake diet was 0-group sand lance. Similarly, for murres, about 80% of the prey brought to chicks in both years were sand lance; these fish were up to 16 cm in length, suggesting that they were a mixture of 0-group and older age classes.

#### 3.2.2 Breeding success

Timing of breeding for the kittiwake did not differ between years, although average laying date for the murre was four days earlier in 1991 than in 1990 ( $P < 0.001$ ; Uttley et al. 1994). Table 2 gives details of the breeding success of both species in the two years. In kittiwakes, there was no significant difference in clutch size or hatching success, but the proportion of young fledging was radically different in the two years, with total breeding failure occurring in 1990. The difference in breeding success was much less marked in murres; there was again no difference in hatching success, but, whereas 22% of hatched young failed to fledge in 1990, all but 2% fledged in 1991. However, there was no significant difference between years in the average number of young fledged per pair.

#### 3.2.3 Colony attendance

The eggs of both species were incubated more or less continuously in both years. In both species, at least

**Table 1**  
Catch per unit effort (CPUE) of sand lance at the Voe ground, near Sumburgh Head (see Fig. 1)

	CPUE <sup>a</sup>						
	1990			1991			
	25 June	2 July	21 July	21 May	28 June	7 July	13 July
0-group	0	0	0	0	116 868	371 270	325 448
>1+	203 395	185	207	172 147	22 901	17 185	17 506

<sup>a</sup> Average of two 30-minute trawls.

**Table 2**  
The average breeding success of kittiwakes and murres in 1990 and 1991, based on birds producing eggs

	Year	n	Clutch size	% hatching	% fledging	Mean chicks fledged/pair
Kittiwake	1990	47	1.60	81.3	0	0
	1991	52	1.45	79.7	84.6	0.98
Murre	1990	133	—	76.0	78.0	0.59
	1991	117	—	72.0	98.0	0.70

one adult generally attends the young at the nest site for around three weeks after hatching — in murres, until the young leave the breeding site. In the kittiwake, older young are occasionally left unattended at the nest site, especially in larger broods (see Galbraith 1983; Coulson and Johnson 1993). At Sumburgh, young murres were continuously attended by at least one parent in both years. One kittiwake parent attended the young throughout the chick-rearing period in 1991, but in 1990 young were periodically left unattended by the second week after hatching (Fig. 4). A further measure of adult attendance at the colony is given by the amount of time pairs spend together at the breeding site when changeovers of the adults occur. In kittiwakes, this was very brief, generally less than one minute in both years. In murres, parental overlap differed considerably between years, being on average around five times longer in 1991 than in 1990 (Fig. 5).

#### 3.2.4 Activity budgets

The average durations of foraging trips made by each species during incubation and chick rearing are shown in Figures 6a and 6b. For both species, there was a significant difference between years for both periods, with trips being longer in 1990 than in 1991. In kittiwakes, foraging trips were around three times longer in both periods; for the murre, incubation trips averaged 20% longer in 1990, but chick-rearing trips more than twice as long.

The radio-tracking data demonstrated that both species foraged farther from the colony in 1990 than in 1991. This was most marked in the kittiwake, which, in 1990, generally foraged more than 40 km from the colony and out of range of the receiving equipment. In 1991, virtually all tracked trips were within 5 km of the colony. The directions and locations of these foraging trips are shown in Figures 7a and 7b. Although the murres foraged relatively close inshore in both years, the average distance travelled from the colony was around 7 km in 1990 and only 1 km in 1991. Foraging locations are shown in Figure 8, and the average overall proportion of time spent per day at sea and at the colony by the two species in 1990

and 1991 is shown in Figure 9, based on data collected at the colonies. Both species devoted less time to foraging in 1991 than in 1990; the difference was most marked in the murres, which spent around half of their time at the colony in 1990, but around two-thirds in 1991. In neither year was over 50% of time spent foraging, the chicks always being attended by at least one parent. In kittiwakes, over 60% of time was devoted to foraging in 1990, effectively meaning that chicks were left unattended for part of the time.

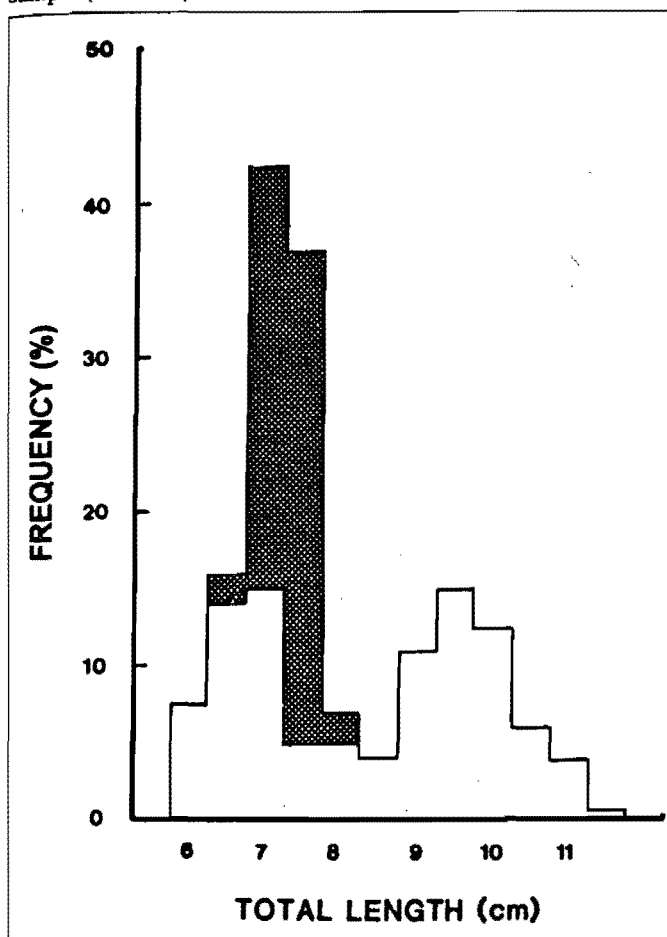
#### 4. Discussion

In terms of examining the response of seabirds to changes in prey abundance, the situation in Shetland is relatively simple, in that it is effectively a single-prey situation. Changes in the abundance of sand lance therefore represent changes in seabird food abundance. Clearly, the distribution of sand lance both horizontally and vertically will influence availability, but, unless dramatic density-dependent changes occur in the behaviour of the fish, availability is likely to covary with abundance.

Survey results showed marked changes in the abundance, distribution, size, and age composition of sand lance in the vicinity of Sumburgh Head between 1990 and 1991. The density of sand lance within 40 km of the seabird colonies was more than 40 times greater in 1991 than in 1990. Very few 0-group sand lance were present in the area in 1990, whereas these were abundant and widespread both close inshore and within the area south of Sumburgh (as shown in Fig. 1a) in 1991. This picture is consistent with Scottish Office Agriculture and Fisheries Department surveys for the Shetland area as a whole carried out in August each year (SOAFD, unpubl. data); these estimate the recruitment of 0-group sand lance in 1991 as the highest since such surveys began in 1984, whereas 1990 was one of the lowest during this period. Furthermore, the bulk of the 0-group fish were larger in 1991 than in 1990, indicating a difference in prey quality as well as in abundance and distribution.

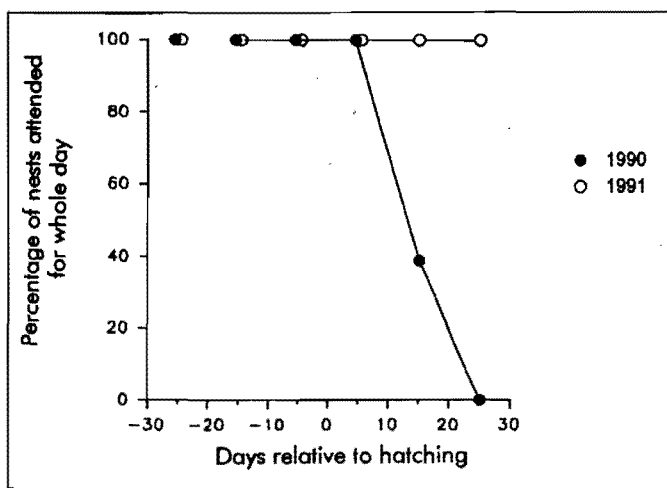
**Figure 3**

Length frequency distribution of 0-group sand lance caught in the Sumburgh area on 25 June 1990 and 28 June 1991. Shaded section is 1990 sample ( $n = 282$ ), and unshaded section is 1991 sample ( $n = 1056$ )



**Figure 4**

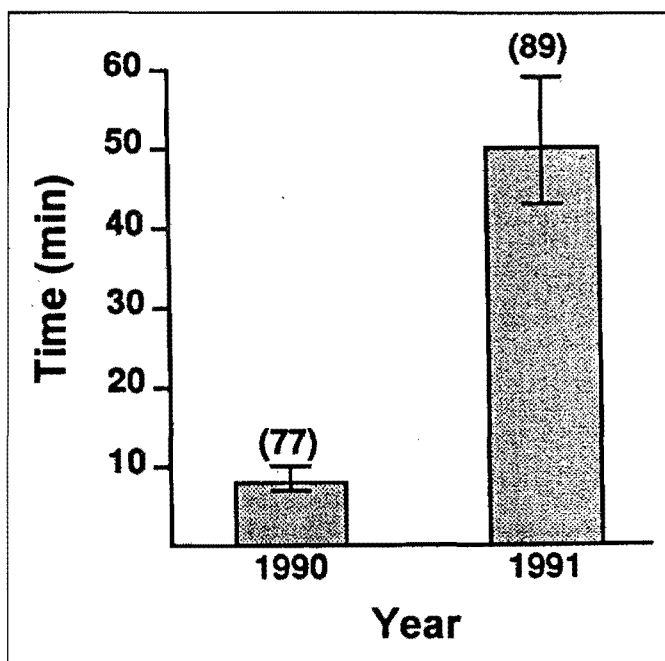
The proportion of kittiwake nests attended for the whole day at Sumburgh in 1990 and 1991 (based on nests with live chicks)



Thus, the difference in the sand lance population around Sumburgh between 1990 and 1991 was considerable and would be expected to have marked effects on the breeding seabirds. The surface-feeding kittiwake seems to be largely dependent on 0-group fish, whereas murre take a combination of 0-group and older

**Figure 5**

The median time (and interquartile ranges) that pairs of murre spent together at the nest site during changeovers (sample sizes are in parentheses)



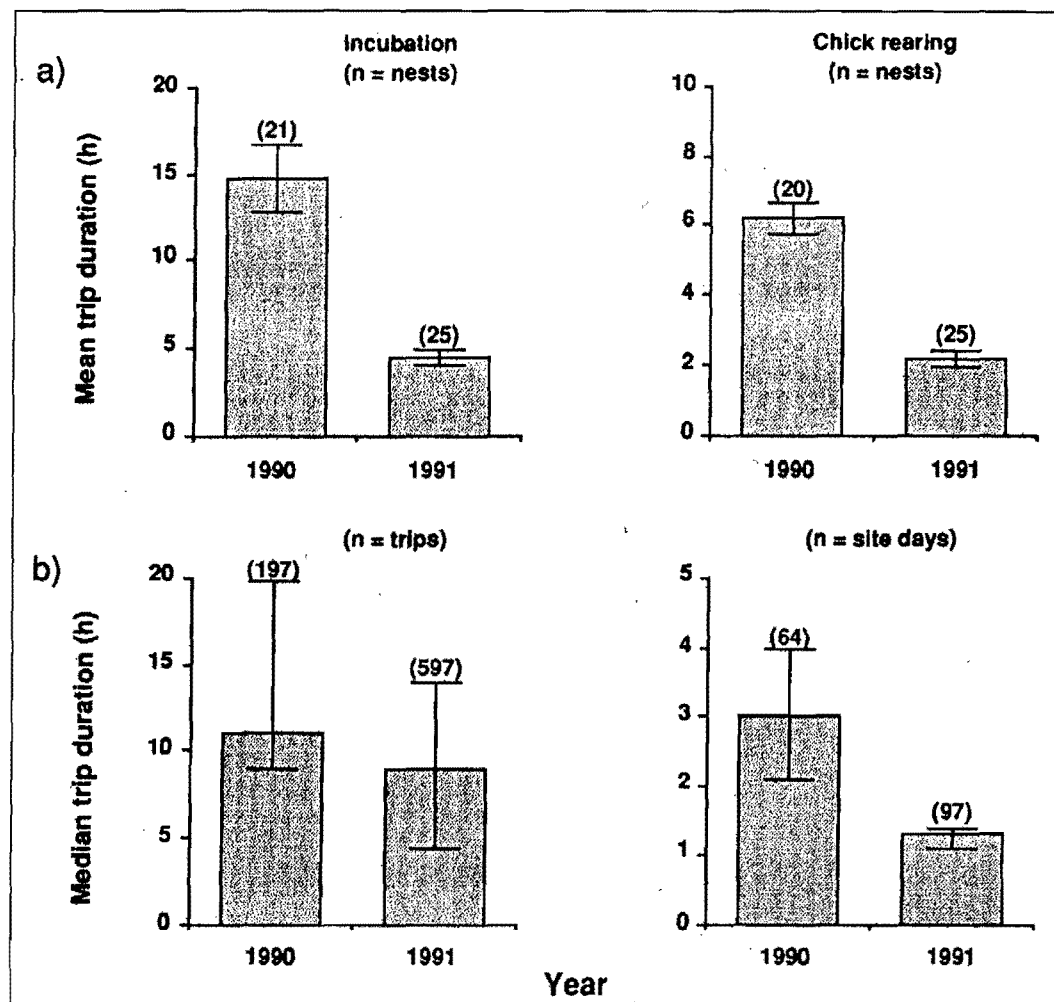
sand lance. The difference in abundance of 0-group fish would therefore be expected to have the greatest effect on the kittiwake. The older fish appear to enter the sediment in advance of the 0-group fish, as was reflected in the age composition of commercial fishery catches of sand lance in the Shetland area, in which very few older fish occurred in July (Warburton 1983). As can be seen from this study, the timing of this withdrawal is clearly variable and may be linked to growth rate. Older sand lance therefore generally become less available, at least to surface-feeding seabirds, during mid- to late chick rearing. However, despite their withdrawal into the sediment earlier in 1991, the older fish still remained relatively more abundant during chick rearing in that year than in 1990. The change in age and size composition of sand lance was reflected in the size of prey fed to murre chicks in the two years; in 1991, fewer sand lance in the 16-cm size class were fed to chicks (Uttley et al. 1994), presumably because it was more profitable for murre to feed on the relatively large and abundant 0-group class.

Despite the large difference in sand lance abundance, there was no change in the diet of either species. This is largely due to the absence of suitable alternative prey and demonstrates that, in such a situation, seabird diet composition tells us relatively little about prey abundance. The effect on breeding success varied between the two seabird species. As is the case in most seabird studies, the extent of nonbreeding is unknown. In both species, those birds that did attempt breeding produced normal clutches and incubated and hatched the eggs successfully even when food supplies were very poor. Foraging trips during incubation were longer in 1990, but the effect was considerably more marked in the kittiwake than in the murre. This difference presumably reflects differences both in their capacity and need to increase foraging effort and foraging range during the egg



**Figure 6**

(a) The mean ( $\pm 1$  s.e.) durations of trips made by kittiwakes at different stages of breeding in each year. (b) The median duration (and interquartile ranges) of trips made by murres at different stages of breeding in each year (sample sizes are in parentheses). Differences between years are significant in both species (see Uttley et al. 1994 and Hamer et al. 1993 for a detailed examination of trip durations between years;  $P < 0.001$  in all cases)



formation and relatively undemanding incubation period and in the relative abundance of  $>1+$  sand lance during the early part of 1990.

During the chick-rearing period, on the other hand, foraging trip duration and foraging range increased considerably in both species. In the murres, this was effected through a reduction in the time that off-duty birds spent at the colony with their partners, and not at the expense of attending chicks. Our data on the activity of murres at sea showed that diving effort increased considerably in the poor food conditions (Monaghan et al. 1994). In the kittiwake, even when food was abundant, pairs spent little time together at the colony, as has been found in other studies (e.g., Coulson and Johnson 1993); increased foraging time therefore did mean leaving chicks unattended, thereby increasing thermoregulatory costs, risk of predation, and risk of attack by other kittiwakes.

The difference in foraging range of the two seabird species in the two years is particularly interesting and in line with the information on prey distribution. Kittiwakes in 1990 had to travel over 40 km from the breeding colony, and the fish survey data confirm that this distance was necessary in order to reach relatively dense sand

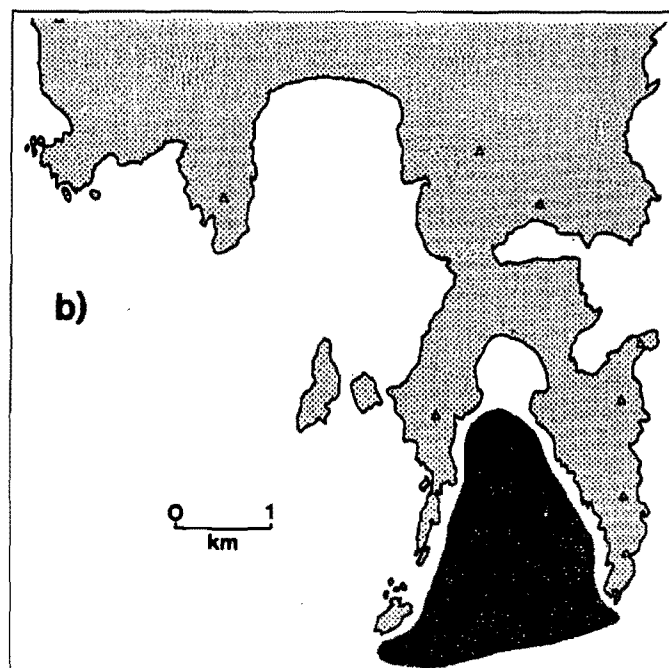
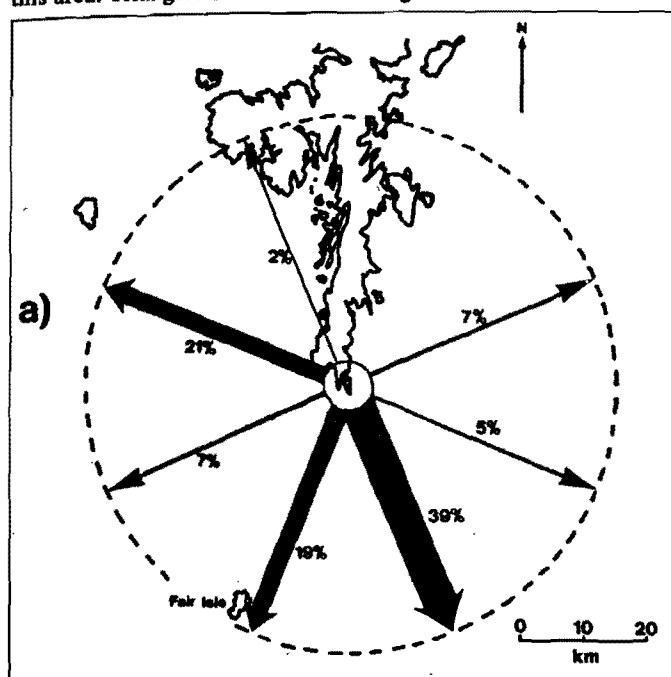
lance shoals. Whereas sand lance shoals at the surface were comparatively rare in both years, this would be exacerbated in the year of low abundance; shoals were also small in that year. As shoal density may influence the probability of kittiwakes detecting fish in surface waters, it may therefore have been necessary for the seabirds to travel to an area where shoals of sufficient density occurred. The shorter foraging range of murres may reflect both a capacity to feed on lower-density shoals and possibly also an ability of diving birds to disturb the sediment on the bottom, thereby causing the temporary emergence of buried sand lance. If such behaviour occurs, this would have increased the availability of  $>1+$  sand lance to murres in the inshore area around Sumburgh during chick rearing in 1990.

The more than 40-fold difference in prey abundance experienced by seabirds in this study represents two extremes of the range on which Cairns' (1987) models are based, and thus we cannot test the accuracy of the shape of his proposed response curves. However, it is clear from this study that the parameters most affected vary between species, and this highlights interspecific differences in the flexibility of time budgets



**Figure 7**

(a) The directions of foraging trips made by radio-tracked kittiwakes from Sumburgh in 1990. The dotted line indicates the 40-km detection distance of the receiving equipment, and virtually all trips were out of range (see Wanless et al. 1992 for a detailed examination of these trips). (b) The foraging area (shaded) used by kittiwakes in 1991; only four out of 117 tracked trips were outside this area. Triangles on land are tracking stations



and sensitivity to changes in food supply, as suggested by Burger and Piatt (1990). In kittiwakes, fledging success and foraging trip lengths were most affected, and, although the magnitude of the effect on adult activity budgets was relatively small, the desertion of chicks at an early age had considerable consequences for the survival of chicks. In murres, the most marked effect was on the amount of time that off-duty birds spent at the colony; their capacity to increase foraging effort without decreasing chick attendance effectively buffered breeding success against the poor food supply. Although this study shows that seabirds have considerable potential as indicators of changes in fish populations, such interspecific differences in responses need to be taken into account in determining the appropriate species or combination of species to be used and the parameters to be monitored.

#### Acknowledgements

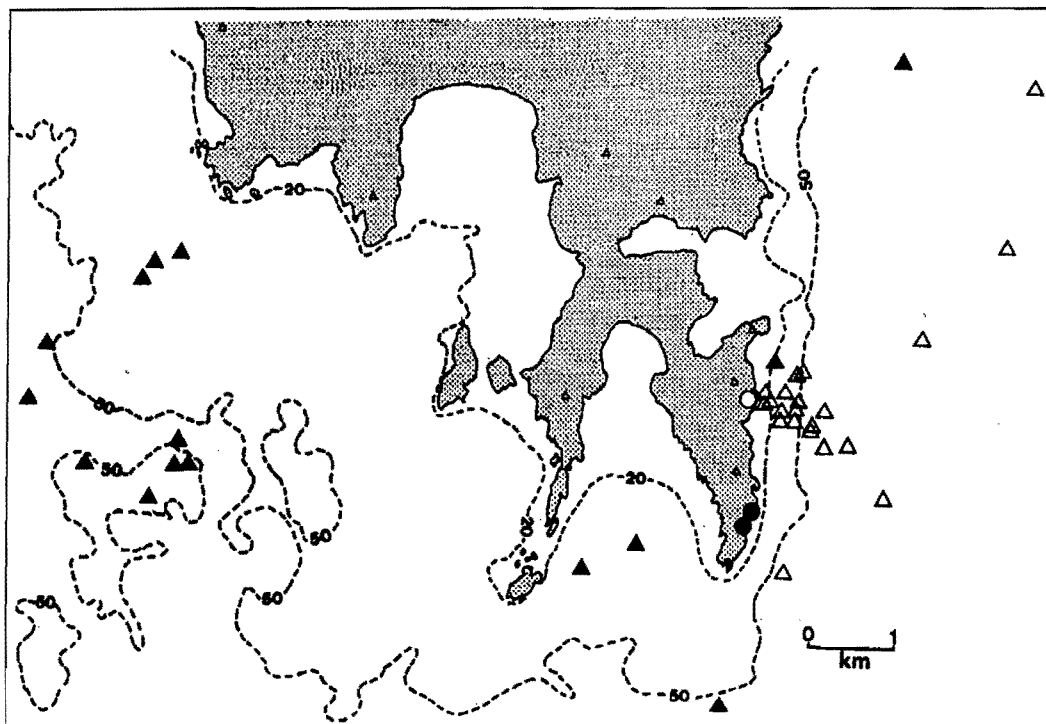
This seabird research study was funded by the Natural Environment Research Council, and the fish research by the Department of the Environment, the Nature Conservancy Council for Scotland, the Scottish Office, the World Wide Fund for Nature, Cadbury's Public Limited Company, and the Royal Society for the Protection of Birds, and we are grateful for their support. We are also grateful to Sarah Wanless, Keith Hamer, Martin Burns, John Morris, Martin Heubeck, David Okill, Wylie Horn, Anne Etheridge, Howard Towll, Malcolm Smith, and the crew of the *Ardent* for help with data collection in the field.

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**Figure 8**

The locations of foraging areas used by radio-tracked murre in 1990 and 1991. Locations were obtained by triangulation. Solid triangles are 1990 locations, open triangles 1991 locations. Depth contours (m) are also shown. Triangles on land are tracking points, solid dots 1990 colonies, open dot 1991 colony



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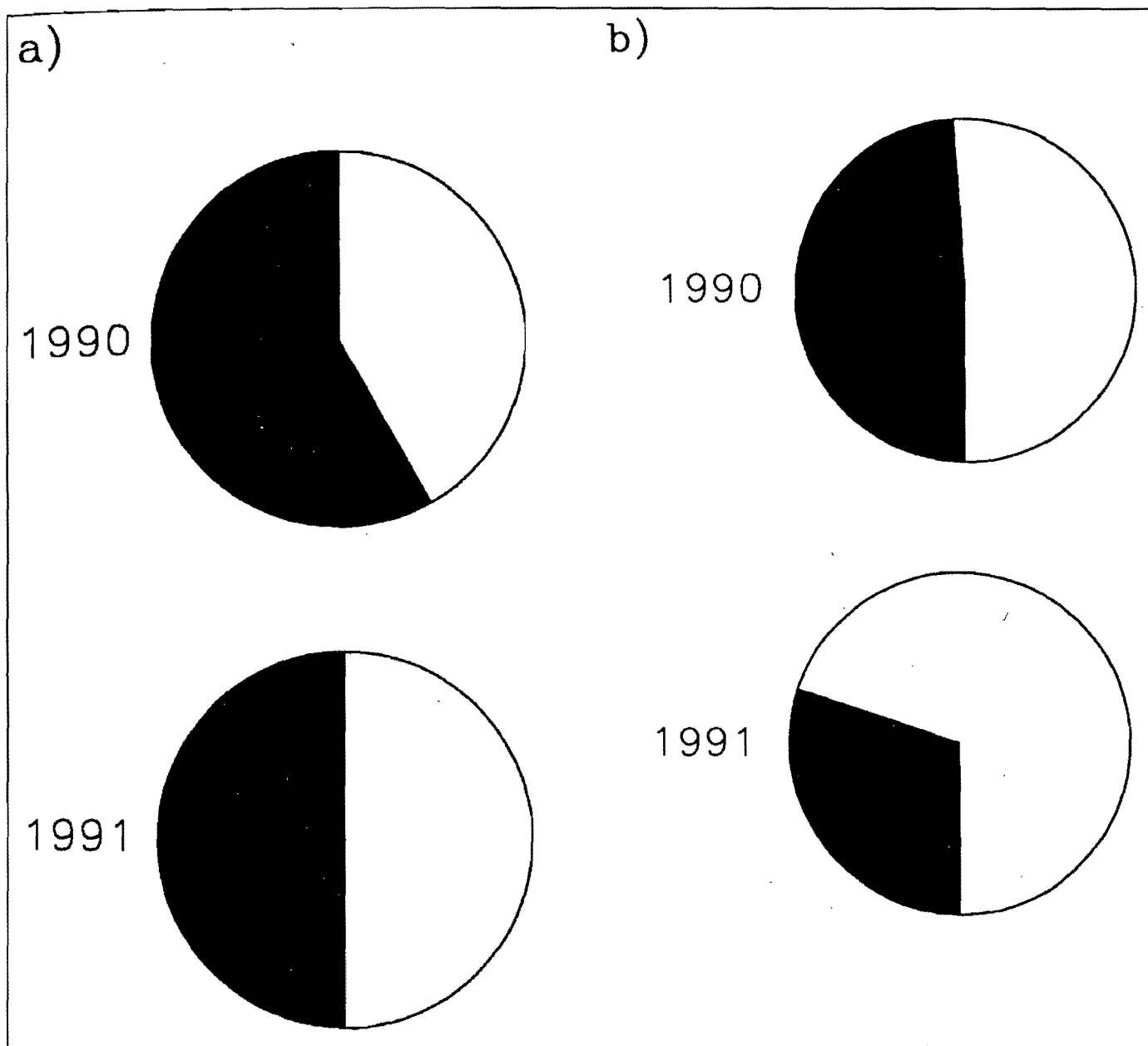
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**Figure 9**

Average proportion of time spent at the colony (unshaded) and at sea (shaded) by (a) breeding adult kittiwakes and (b) murres at Sumburgh in 1990 and 1991



# Prey harvest, chick growth, and production of three seabird species on Bleiksøy, North Norway, during years of variable food availability

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## Abstract

During the 1980s, when stocks of the Atlanto-Scandian herring *Clupea harengus* were very low, Black-legged Kittiwakes *Rissa tridactyla* had higher breeding success than Atlantic Puffins *Fratercula arctica* on two North Norwegian colonies. This finding is contrary to the general hypothesis that surface feeders will suffer more than pursuit divers in times of common food shortages. Studies on Bleiksøy, Nordland, in 1985–1988 showed that kittiwakes found a plentiful supply of glacier lanternfish *Benthoosema glaciale*, an energy-rich, mesopelagic myctophid that the puffins failed to exploit when their preferred prey was absent in 1986. It is suggested that the puffin is sometimes too constrained in its feeding habits to switch to other prey when its preferred prey is not available.

## Résumé

Durant les années 1980, période où les stocks de hareng de l'Atlantique de la région de la Scandinavie étaient très faibles, la Mouette tridactyle *Rissa tridactyla* affichait un taux de reproduction plus élevé que celui du Macareux moine *Fratercula arctica* dans deux colonies de la Norvège septentrionale. Ces résultats entrent en contradiction avec l'hypothèse généralement avancée selon laquelle les oiseaux qui se nourrissent à la surface de l'eau souffrent davantage des pénuries de nourriture que ceux qui plongent et poursuivent leurs proies sous l'eau. Des études menées sur la Bleiksøy, en Norvège, de 1985 à 1988 ont indiqué que les Mouettes tridactyles disposaient d'abondantes quantités de lanternes glaciales *Benthoosema glaciale*, espèce des profondeurs infrapélagiques appartenant à la famille des *Myctophidae* et possédant une valeur énergétique importante dont les Macareux moines n'ont pas su tirer avantage en 1986, lorsque leur proie préférée accusait une pénurie. Il semble que des habitudes alimentaires trop ancrées empêchent le Macareux moine d'opter pour d'autres proies dans de telles circonstances.

## 1. Introduction

Seabirds prey mainly on shoaling fish and crustaceans, and several studies have linked breeding success with food availability (Cairns 1987). A reduction in prey availability will, for example, result in an increase in the adults' breeding effort and decreases in chick growth and breeding success (Cairns 1987). Such an effect will, however, depend on a number of factors, including feeding habits, foraging ranges, time available to forage, tolerance to temporal changes in food availability, and food-searching techniques (Furness and Ainley 1984). For example, because of the greater depth of water column available for foraging, diving species might be expected to suffer less than surface-feeding species during periods of a common food shortage, as demonstrated by Harris and Riddiford (1989).

In northern Norway, many of the colonial seabirds seem to depend on a few selected prey species during the breeding season. These prey species include Atlanto-Scandian herring *Clupea harengus*, sand lance (*Ammodytes* spp.), and capelin *Mallotus villosus* (Røv 1984; Barrett et al. 1985; Furness and Barrett 1985; Anker-Nilssen 1987; Barrett and Furness 1990). In the 1950s and 1960s, herring and sand lance were the most important puffin prey on Lovunden (66°20'N, 12°20'E) (Myrberget 1962). Since the collapse of the Atlanto-Scandian herring stocks in the late 1960s, Atlantic Puffins *Fratercula arctica* on a nearby island, Hernyken (67°26'N, 11°52'E), at Røst in the Lofotens, have had breeding failures, with nearly all chicks starving to death in all but five seasons until 1990 (Anker-Nilssen 1987; Anker-Nilssen and Barrett 1991). Similarly, about 270 km northeast of Røst, on Bleiksøy (69°17'N, 15°53'E), breeding success in Atlantic Puffins ranged from total failure to poor in four (1981, 1982, 1986, 1987) of seven seasons (1981–1983, 1985–1988) (Barrett et al. 1985; Barrett and Rikardsen 1992). The breeding failures on Røst and Bleiksøy were all attributed to low food availability as a result of low herring stocks (Barrett et al. 1985; Anker-Nilssen and Barrett 1991).

Simultaneous studies of Black-legged Kittiwakes *Rissa tridactyla* showed that whereas puffins had total breeding failures on Røst in 1980–1982, kittiwakes raised 0.3, 0.6, and 0.5 chicks/nest ( $n = 576, 487, \text{ and } 462$  nests, respectively) in the same years (Barrett 1984). This is low

**Table 1**

Growth parameters of kittiwake and Shag chicks on Bleiksøy (1986) and on Hornøya<sup>a</sup> (1980, 1981) (based on Ricklefs 1967)

	Asymptote A (g)	Adult mass W (g)	Growth rate		
			R = A/W	K <sup>b</sup>	t <sub>10-90</sub> (d)
<b>Kittiwake</b>					
Bleiksøy 1986	396	392 <sup>c</sup>	1.01	0.20	21.9
Hornøya 1980	418	431	0.97	0.20	22.4
Hornøya 1981	422	431	0.98	0.18	24.4
<b>Shag</b>					
Bleiksøy 1986	1750	1792 <sup>d</sup>	0.98	0.16	28.3
Hornøya 1980	1725	1851	0.93	0.17	24.9
Hornøya 1981	1730	1851	0.93	0.18	24.4

<sup>a</sup> Source: Barrett 1983; Barrett et al. 1986.

<sup>b</sup> K = growth constant.

<sup>c</sup> Adult mass, Bleiksøy = 392 ± 36 g, n = 193.

<sup>d</sup> Adult mass, Bleiksøy = 1792 ± 179 g, n = 66.

compared with the results of other European studies of kittiwakes (1–1.4 chicks/nest) (Coulson and Thomas 1985; Harris 1988), but kittiwakes were still more successful than the puffins. Similarly, on Bleiksøy, kittiwake breeding success was good every season between 1985 and 1988 (e.g., 1.2 chicks/nest in 1986), whereas puffins experienced total breeding failures in 1986 and nearly total failures in 1987 (Barrett 1989, 1991; Barrett and Rikardsen 1992).

These results are in contrast to the general hypothesis that surface feeders will suffer more than pursuit divers in times of food shortage. This paper concentrates on the food availability and breeding success of puffins and kittiwakes on Bleiksøy in 1986, when the difference in the production between the two species was the greatest observed during a four-year study of the birds breeding there (Barrett 1991). Comparisons are also made with data from a contemporary study of the Shag *Phalacrocorax aristotelis* on Bleiksøy.

## 2. Methods

### 2.1 Chick growth and adult weight

Sixty marked puffin burrows on Bleiksøy were checked every three days from 2 July 1986 (approximate date of hatching), and 43 chicks of known age were weighed at the same interval until 29 July 1986, as well as on 17 August 1986. Chicks in 43 Shag nests and 52 kittiwake nests were also weighed every three days until near fledging. All chicks were weighed using Pesola spring balances, and their wing and culmen lengths were measured using a stopped rule and vernier calipers, respectively. Further details are given in Barrett (1989) and Barrett and Rikardsen (1992). Adults were weighed using Pesola spring balances.

### 2.2 Food samples

Details of puffin food sampling and weighing are given in Barrett and Rikardsen (1992). Data were collected by frightening food-carrying adults as they approached their burrows and picking up any food dropped. Kittiwake food was sampled either by stomach pumping (Wilson 1984) adults caught on the nest

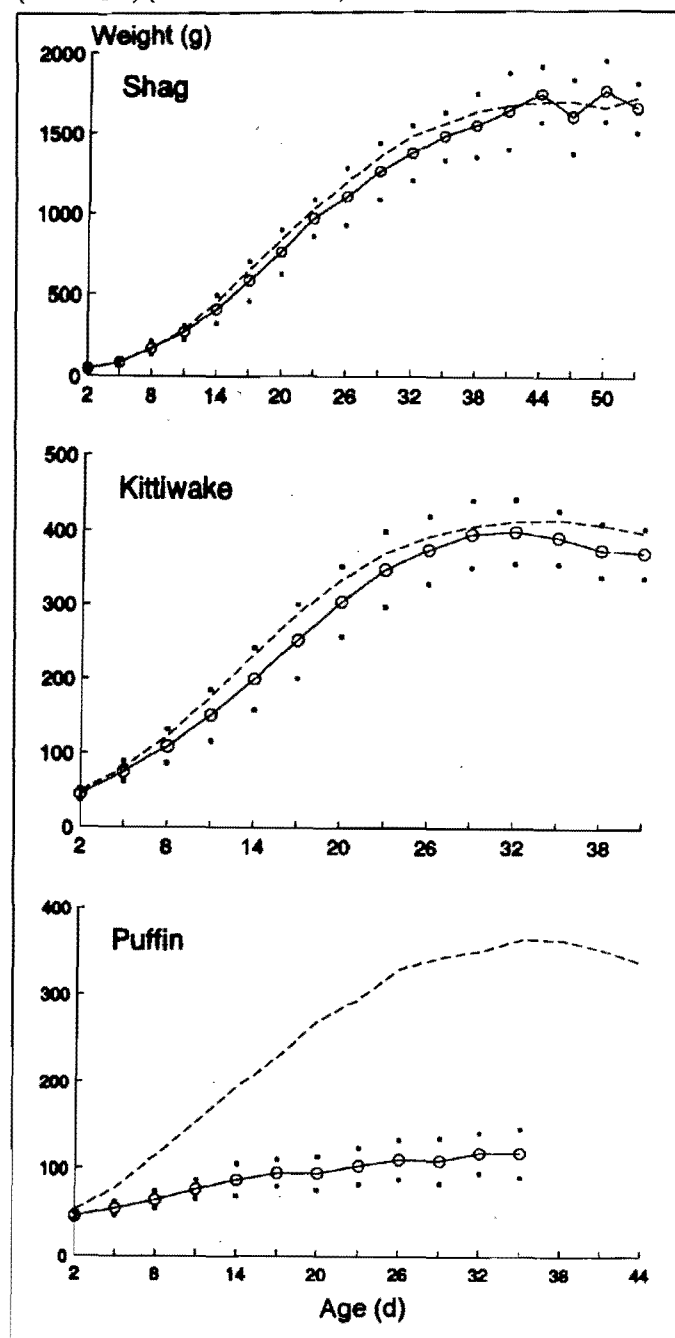
("pumped regurgitations") or by collecting loads regurgitated by adults or chicks during handling ("voluntary regurgitations"). The former consisted generally of hard parts only (otoliths, bones, etc.), whereas the latter consisted of more complete food loads, thereby lending themselves to a more rigorous, volumetric analysis. Shag food was sampled through the collection and analysis of regurgitated pellets (Barrett et al. 1990). Each sample was sorted under a binocular microscope. Fish were identified to the lowest possible taxon by sagittal otoliths (using Breiby 1985; Härkönen 1986; personal otolith collections), and invertebrates were identified by various hard parts (e.g., chitinous mandibles of polychaetes or beaks of cephalopods). The Shannon-Weaver index (Tramer 1969) was used as a measure of seasonal diet diversity based on all samples collected. For further details on the analyses (e.g., estimation of fish lengths, numerical presentations) of regurgitation/pellet contents, see Barrett et al. (1990).

## 3. Results

### 3.1 Chick growth and fledging success

In 1986, kittiwake and Shag chicks on Bleiksøy grew at rates similar to those at Hornøya, NE Norway, in 1980 and 1981, when and where food was considered to be abundant (Furness and Barrett 1985) (Table 1; Fig. 1); the growth of puffin chicks at Bleiksøy, however, was considerably retarded compared with that at Hornøya (Fig. 1). The fledging success of kittiwakes on Bleiksøy was high (1.2 chicks/nest, n = 52), whereas only one (of 43 = 2%) underweight puffin chick was alive on 17 August 1986. The other puffin chicks died within 37 days of hatching, by which time they had reached a mean mass of only 118 ± 23 g (n = 9), or approximately 25% of adult mass (= 464 ± 36 g, n = 336; pers. obs.). At that age, puffin chicks normally weigh 70–80% of adult mass (Barrett et al. 1985). Culmen and wing growth were also much reduced. Owing to the loss of Shag chicks in observation nests through disturbance, it was impossible to measure their fledging success. Growth was normal, however, and there was no indication of food-related mortality, as was seen in the puffins.

**Figure 1**  
Growth curves of Shag, kittiwake, and puffin chicks on Bleiksøy in 1986 (solid line  $\pm$  SD [squares]) compared with those from another North Norwegian colony, Hornøya, in 1980–1981 (dotted line) (from Barrett 1983)



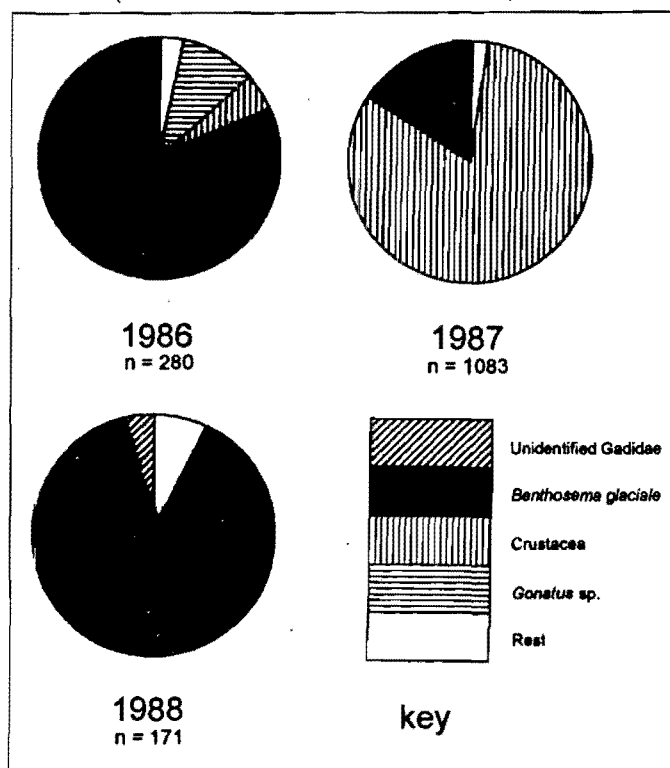
### 3.2 Food

The glacier lanternfish *Benthosema glaciale* occurred in 51 of the 57 regurgitations collected from kittiwakes and made up over 80% of the 280 items recorded, with the squid (*Gonatus* sp.) and crustaceans making up most of the remainder (Table 2; Fig. 2). The Shag diet was also relatively specialized, with pollock *Pollachius virens* occurring in 71 of the 79 pellets and, together with the sand lance, constituting >80% of the 2044 items found (Table 2; Fig. 3). The Shannon-Weaver indices of diet diversity for kittiwakes and Shags were 0.34 and 0.52, respectively. In contrast, the puffins fed

**Table 2**  
Frequency of occurrence of food items in kittiwake, Shag, and puffin food samples at Bleiksøy in July 1986

	No. of samples containing each item		
	Kittiwake (n = 57)	Shag (n = 79)	Puffin (n = 107)
Clupeidae (unidentified)		4	
<i>Clupea harengus</i>	2		67
<i>Mallotus villosus</i>		2	1
<i>Benthosema glaciale</i>	51		6
Gadidae (unidentified)	2		1
<i>Pollachius virens</i>		71	20
<i>Melanogrammus aeglefinus</i>			20
<i>Ammodytes</i> sp.	2	27	33
<i>Cyclopterus lumpus</i>			6
<i>Anarhichas</i> sp.			6
<i>Sebastes</i> sp.		5	34
<i>Myoxocephalus scorpius</i>		32	
Pleuronectidae (unidentified)		3	12
Unidentified fish	10	13	
<i>Gonatus</i> sp.	8		17
Polychaetes	1	27	1
Crustacea	10	17	5

**Figure 2**  
Percentage (by number) of the most common prey species regurgitated by kittiwake adults and chicks on Bleiksøy in June and July 1986–1988. Total number of prey items is given below each date (number of fish = number of otoliths/2)

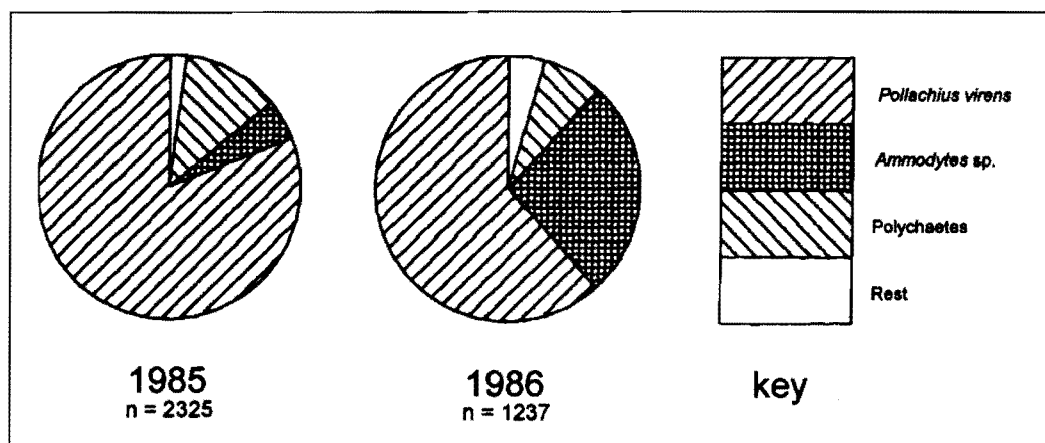


their chicks on a wider variety of items (diversity index = 0.87), with only one species, herring, making up >25% (by mass) of the 557 g of prey species collected (Table 2; Fig. 4).

Nearly all fish caught by puffins in 1986 were postlarval forms or small fry (herring 30–50 mm, pollock 20–35 mm, sand lance 40–75 mm; Fig. 5), whereas Shags caught 0- and I-group pollock (up to about 200 mm) and I- to IV-group sand lance (50–160 mm) (Barrett et al. 1990;

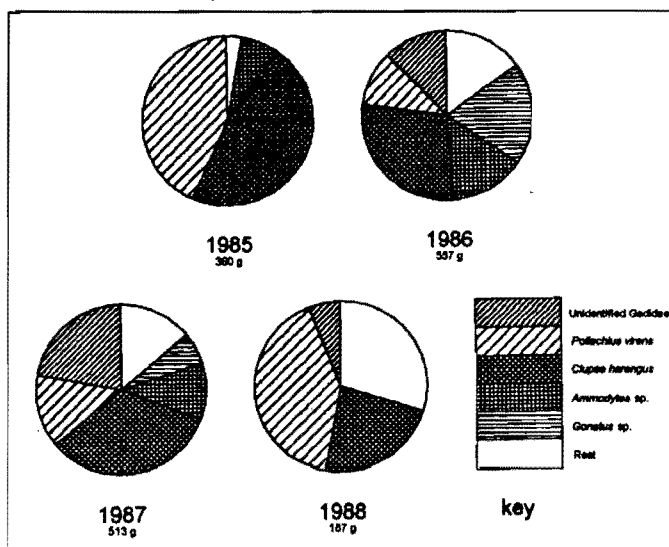
**Figure 3**

Percentage (by number) of the most common prey species eaten by Shags on Bleiksøy in July 1985–1986. Total number of otoliths is given below each date (from Barrett et al. 1990)



**Figure 4**

Percentage (by mass) of the most common prey species fed to puffin chicks on Bleiksøy in 1985–1988. Total weight of food samples is given below each date (from Barrett 1991; Barrett and Rikardsen 1992)



Barrett 1991). The calculated mean length of lanternfish caught by kittiwakes was  $58.2 \pm 8.1$  mm ( $n = 235$  otoliths).

#### 4. Discussion

The parallels between the situation at Røst in the early 1980s and that on Bleiksøy are striking, with puffin breeding success being lower than that of the kittiwake. The parallels are carried further in the puffin by the simultaneous breeding failures at both colonies in 1986 and 1987 and low to good breeding success in 1985 and 1988 (Anker-Nilssen and Barrett 1991; Barrett 1991; Anker-Nilssen 1992).

There was considerable variation in the diet of puffin chicks in 1986, with no one species dominating at any one time. Load weights were generally low, and chick provisioning rates remained below those needed to maintain normal chick growth and survival (about 100 g/d) (Barrett and Rikardsen 1992). The situation was little better in 1987, when, although chick survival was better

(approximately 60%), chicks at fledging were at least 65 days old, in poor condition, and often still covered in down (Barrett and Rikardsen 1992).

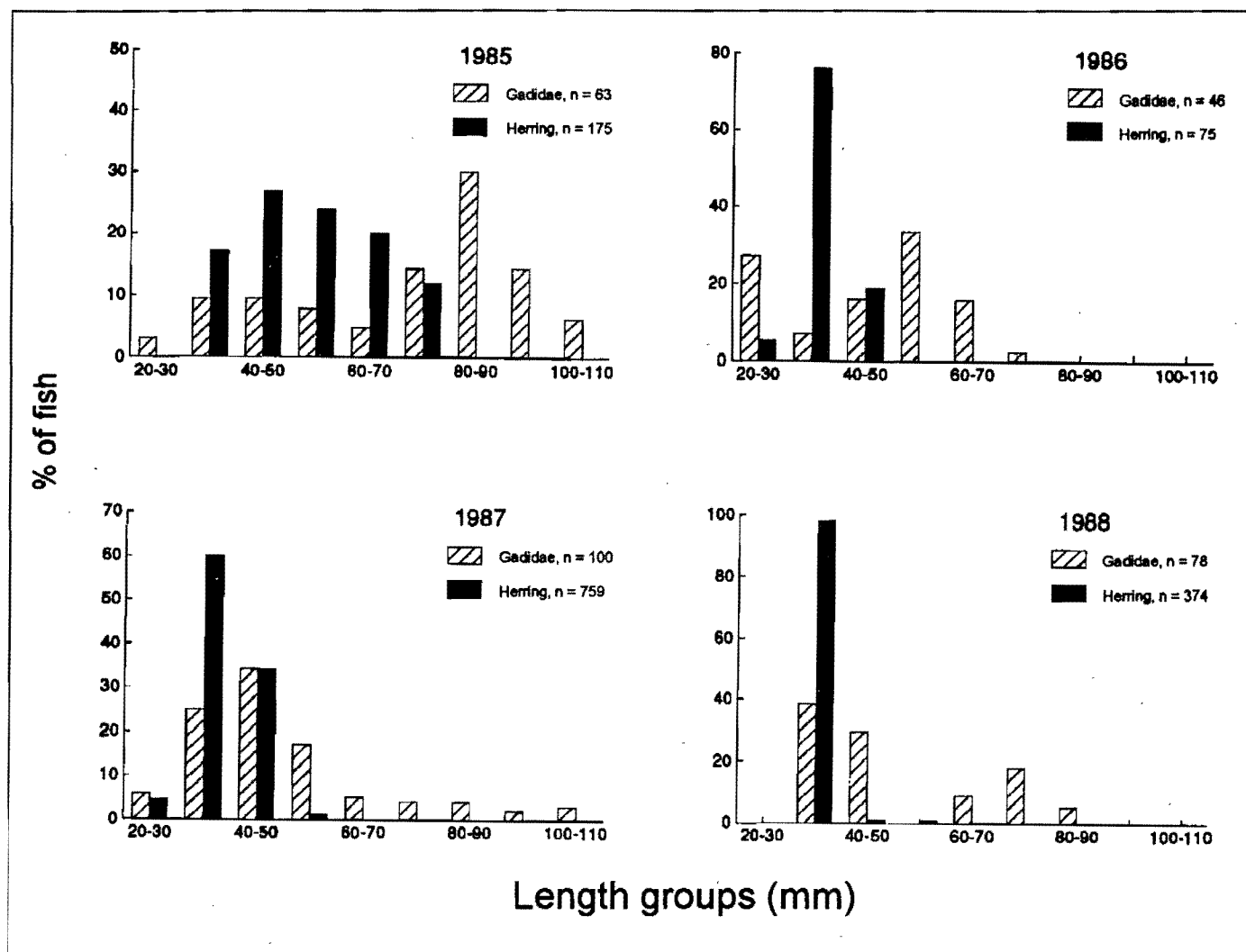
Herring and pollock are probably key prey species for the puffin at Bleiksøy (Barrett et al. 1985); however, although these fish were present in the samples brought ashore in 1986 and 1987, the majority were small larval or postlarval forms ( $<50$  mm; Fig. 5) and therefore of little dietary value. In 1985, puffins found larger (herring:  $\bar{x} = 50 \pm 12$  mm,  $n = 175$ ; pollock:  $\bar{x} = 66 \pm 22$  mm,  $n = 63$ ) and thus better-quality fry of both species, and chick growth and survival were consequently better (Barrett 1991).

Kittiwakes had a very different diet; in 1986–1988, lanternfish totally dominated nearly all the samples collected. Although euphausiids and amphipods were numerically dominant in 1987 (Fig. 2), they occurred in only about 50% of the 60 samples, with one sample containing 580 (65%) of the 893 crustaceans found. Furthermore, volumetric analyses of voluntary (as opposed to pumped) chick regurgitations ( $n = 26$ ) showed that lanternfish made up 60% of the samples. Lanternfish are very rich in lipids (68% dry weight; Falk-Petersen et al. 1986) and have an energy content (*B. pterotum*, about 5 kJ/g wet weight; Haque et al. 1981) similar to that of more traditional seabird prey in the same size range.

The glacier lanternfish is the most common myctophid in the northern North Atlantic. It is mesopelagic, occurring offshore at depths of 150–500 m during the day (Gjøsæther 1973), well out of reach of most seabirds. Off Bleiksøy, mesopelagic fish are often recorded at depths of 300–500 m (S. Sundby, pers. commun.). Lanternfish have a conspicuous diel vertical migration, rising to the upper 100 m of the water column at night; some actually reach the surface (Halliday 1970; Sameoto 1988), thereby becoming available to both pursuit divers and surface-feeding predators. For example, in the Northwest Atlantic, lanternfish are the most common prey of Leach's Storm-Petrels *Oceanodroma leucorhoa*, a surface feeder and the most abundant breeding bird in the region. Myctophids are also a common prey of Black-legged Kittiwakes in the Bering Sea (Schneider and Hunt 1984; Hatch et al. 1993). However, lanternfish have not previously been recorded as

**Figure 5**

Size frequency distribution of Gadidae (hatched) and herring (solid) caught by puffins on Bleiksøy in 1985–1988



a major prey species of breeding kittiwakes or any other seabird in the far Northeast Atlantic (Belopol'skii 1957; Barrett et al. 1985; Furness and Barrett 1985; Barrett and Furness 1990), probably because of the contrasting daylight regimes. The Northwest Atlantic and Bering Sea observations were both south of the Arctic Circle, where myctophids may rise to the surface at night. In North Norway, nearly all seabird colonies are well north of the Arctic Circle and therefore have continuous daylight throughout the breeding season. Such light would normally keep myctophids deep in the water column (Roe and Badcock 1984).

How, then, do kittiwakes gain access to these deep-water fish? Off Bleiksøy, the ocean floor topography is unusual, in that the continental shelf — while far offshore along most of the Norwegian coast — veers in to within 10 km of the shore, well within the kittiwakes' normal foraging range (about 50–60 km, Pearson 1968; 27 km, Furness and Barrett 1991). Nowhere else along the Norwegian coast is the continental shelf as close to shore as this. Off the coast, both the inshore coastal current and the offshore Atlantic water flow northwards, with Atlantic water currents reaching approximately 1–2 knots (50–100 cm/s) (S. Sundby, pers. commun.). In the area, several troughs in the continental slope cross the direction of flow

and probably deflect the north-going current up the slope and to the surface. With such current speeds and vertical mixing, lanternfish whose swimming speed is in the order of only 5–10 cm/s (Karnella and Gibbs 1977; Go 1980, cited in Roe 1983) are thus likely to be forced to the surface. The area involved may not be large, but it could provide a steady supply of a rich food source to surface feeders. This could account for the generally good breeding success of kittiwakes on Bleiksøy.

Why, then, did puffins not exploit these lanternfish? Admittedly, lanternfish are small (50–60 mm at Bleiksøy) compared with prey brought in by puffins in good years (e.g., 1985; Fig. 5); however, considering the high energy content of lanternfish, it would seem worthwhile for puffins to exploit what seems to be a locally abundant food source rather than the small pollock and herring that they actually brought in.

Shags, too, seemed to fare better than puffins in 1986–1988, although breeding success was quantified in 1987 and 1988 only (1.2 and 0.7 fledglings/nest, respectively) (Barrett 1991). In contrast to kittiwakes, Shags fed on at least two of the same species as puffins (pollock and sand lance; Figs. 3 and 4). However, Shags caught larger fish than did puffins.



Puffins feed their chicks on a wide variety of prey species, but there is evidence of some selectivity. In most colonies, puffin food loads are dominated by one or a few energy-rich, small, pelagic schooling species, such as sprat *Sprattus sprattus*, herring, sand lance, and capelin (Belopol'skii 1957; Harris 1984; Barrett et al. 1985; Nettleship 1991; Hatch and Sanger 1992). When such prey is not available, poorer-quality items are caught. However, the results of this study are enigmatic, in that, in the absence of suitably sized herring, puffins on Bleiksøy did not select what seems at the outset to have been a reasonable and plentiful alternative, namely lanternfish. Instead, they chose fish of lower calorific value.

On Shetland, as well, puffins stood out as being more sensitive to food declines than might have been anticipated (Furness and Barrett 1991). During the late 1980s, they were among the species, which included kittiwakes, most affected at Foula by the declines in sand lance. Other species, such as Common Murres *Uria aalge* and Shags, were not affected.

This suggests that the puffins are sometimes very constrained in their feeding habits and cannot switch to other prey when their preferred prey becomes unavailable. In this case, it seems that they do not forage in areas used by kittiwakes during the breeding season.

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# Diet of Razorbill *Alca torda* chicks and breeding success in the St. Mary's Islands, Gulf of St. Lawrence, Quebec, Canada, 1990–1992

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## Abstract

Between 1990 and 1992, sand lance (*Ammodytes* spp.) and capelin *Mallotus villosus* were the two main prey of Razorbill *Alca torda* chicks on the St. Mary's Islands in the Gulf of St. Lawrence. Sand lance represented 64–78%, by number, of prey delivered by adults, but only 31–46% of total intake by weight. Conversely, capelin accounted for 21–36% of delivered prey by number and 53–69% by weight. Capelin contributed more than sand lance to the energy supply of growing young. The weights of sand lance loads were similar from year to year, whereas capelin loads were heavier in 1992 than in 1990 and 1991. The mean number of feeds was similar in all years, between 3.1 and 3.8 feeds per chick per day. Daily intake was estimated to range from 35 g/chick (251 kJ) in 1990 and 1991 to 50 g/chick (357 kJ) in 1992. Fledging success was 88.2% in 1990, 87.2% in 1991, and 95.1% in 1992.

## Résumé

Le lançon (*Ammodytes* spp.) et le capelan *Mallotus villosus* ont constitué les deux principales proies des poussins du Petit Pingouin *Alca torda* dans les îles Sainte-Marie dans le golfe du Saint-Laurent entre 1990 et 1992. En terme de nombre, le lançon représentait 64 à 78% des proies apportées par les adultes, tandis que selon le poids il constituait 31 à 46% de la masse totale consommée. En contrepartie, la proportion de capelan était de 21 à 36% en terme de nombre et 53 à 69% du point de vue de la masse. À cause de sa masse et de sa valeur calorifique élevée, le capelan contribue plus que le lançon dans l'apport énergétique nécessaire à la croissance des jeunes. Les poids des bouchées de lançon étaient similaires entre les années tandis que les bouchées de capelan étaient plus pesantes en 1992 comparativement à 1990 et 1991. Les taux moyens d'alimentation ont été similaires entre les années et s'établissaient entre 3,1 et 3,8 repas/poussin/jour. L'estimation de la consommation journalière a été de 35 g/poussin (251 kJ) en 1990 et 1991 comparativement à 50 g/poussin (357 kJ) en 1992. Le succès à l'envol a été de 88,2%, 87,2% et 95,1% en 1990, 1991 et 1992 respectivement.

## 1. Introduction

It is estimated that only 15 000 pairs of Razorbills *Alca torda* breed in two main regions in North America: southern Labrador and the North Shore of the Gulf of St. Lawrence (Nettleship and Evans 1985). On the North Shore of the Gulf of St. Lawrence, alcid populations dropped sharply between 1960 and 1982 (Moisan and Fyfe 1967; Nettleship and Lock 1973; Chapdelaine 1980; Chapdelaine and Brousseau 1984) and then increased over the last decade (Chapdelaine and Brousseau 1991).

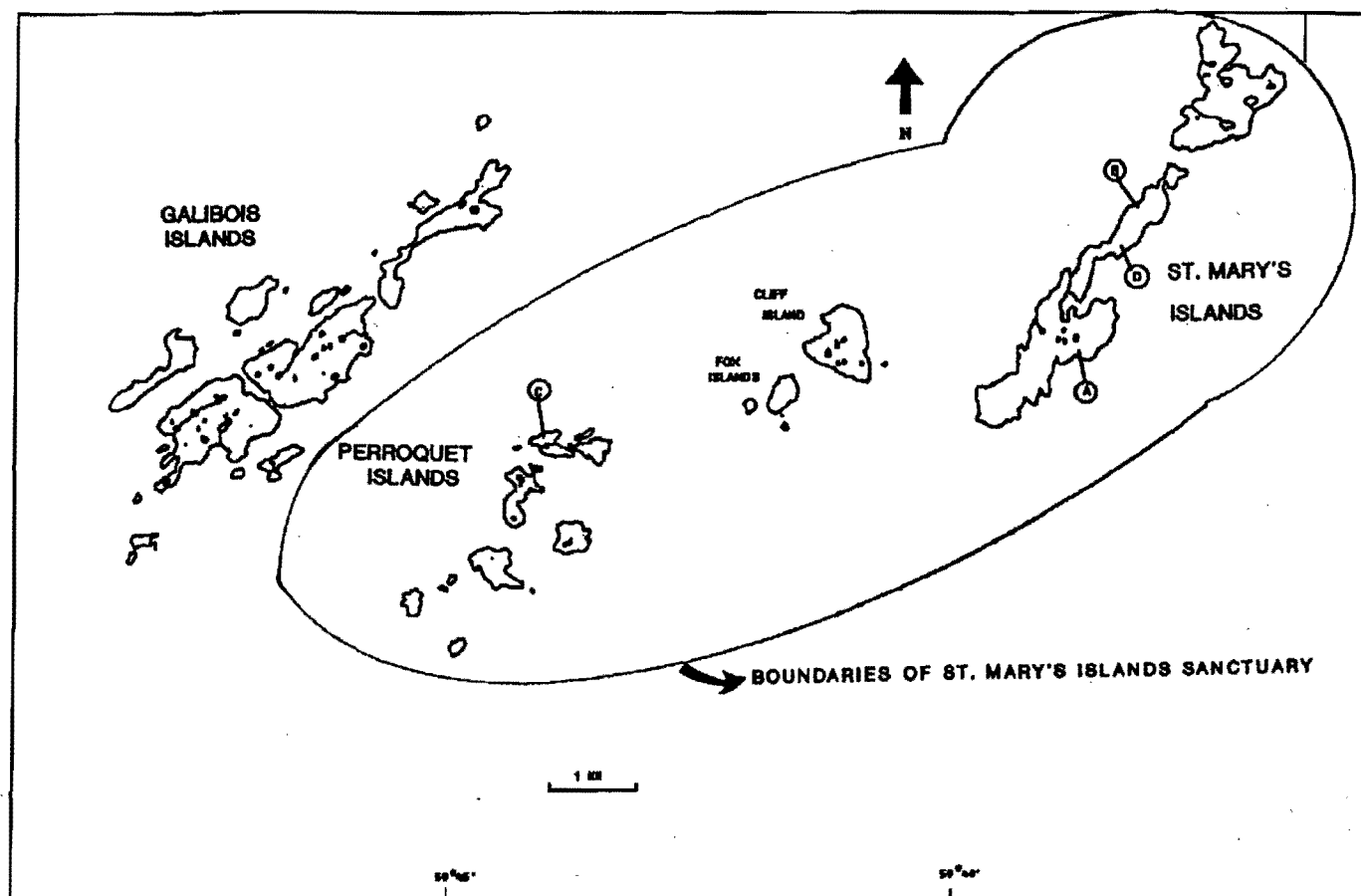
The reasons for such long-term changes are not always clear, but data on the relationship between predators and prey are often useful in understanding the changes (Hunt et al. 1991). The diet of seabird chicks varies by species, location of colony, and year and reflects changes in the relative abundance of fish species caught in the feeding areas by adults (Cairns 1987; Furness 1987; Montevecchi et al. 1987). The quality and quantity of prey delivered to chicks influence breeding success and population change (Cairns 1992). The objectives of the present study were to characterize the diet of young Razorbills in the St. Mary's Islands, calculate the energy intake of chicks, and determine breeding success between 1990 and 1992. We have also compared our findings with those of similar studies of Razorbills that breed elsewhere in the North Atlantic.

## 2. Study area and methods

The St. Mary's and Perroquet islands are part of a system of migratory bird sanctuaries on the North Shore of the Gulf of St. Lawrence (Fig. 1). There are 11 islands in the archipelago; their topography is characterized by rather rounded hills with very few cliffs. The alcid community is composed of four species, Common Murre *Uria aalge*, Razorbill, Black Guillemot *Cepphus grylle*, and Atlantic Puffin *Fratercula arctica*, which nest in dense colonies.

All observations on feeding and food were made from hides (labelled A, B, C, and D; Fig. 1) located within 1–5 m of nest sites. Observers were able to positively identify more than 97% of prey brought in by adults and count the number of fish in each load. The length of each prey item was estimated by comparison with the length between the tip of the bird's bill and the end of the white

**Figure 1**  
Location of study sites A–D



line that extends to just in front of the eye ( $59.3 \pm 1.80$  mm,  $n = 21$ ). We estimated weights of sand lance (*Ammodytes* spp.) and capelin *Mallotus villosus* using the equations of Koehler et al. (1969) and Lambert and Bernier (1989) (see Appendix 1). We used Birkhead and Nettleship's (1987) caloric values of these fish.

We carried out 16-hour watches (04:00–20:00) over the entire chick-rearing period at hides A (17 nests) and B (eight nests) (1990–1992). At hides C (21 nests) (1990–1991) and D (17 nests) (1992), watches were eight hours in duration (08:00–16:00). In 1992, hide C was replaced by hide D, because a red fox *Vulpes vulpes* prevented most seabirds from nesting near hide C. Owing to the nature of the nest sites, many of which shared common entrances, we were not always able to determine to which chick the adults were delivering the food. We inspected all nests before each observation session to determine the exact number of chicks in each. The feeding rate was defined as the number of food deliveries observed per chick per day. To calculate a chick's daily intake, we divided the estimated total mass of all loads of fish delivered in a day by the number of chicks.

Breeding success was determined by using several nest sites in the archipelago. Nests, identified by numbers painted on nearby rocks, were divided into two categories, depending on the amount of disturbance we caused: (1) nests where we observed food and weighed chicks every two days, and (2) nests that were visited only three times each year (see Nisbet and Drury 1972; Chapdelaine and

Laporte 1982). Hatching success was calculated by comparing the number of chicks hatched with the number of nests containing an egg, and fledging success was defined as the number of chicks that left the nest in relation to the number of chicks that hatched. At sites visited only three times, fledging success was defined as the number of chicks that reached 12 days of age divided by the number of chicks that hatched. Net productivity was estimated by comparing the number of "fledged" chicks with the number of nests containing an egg.

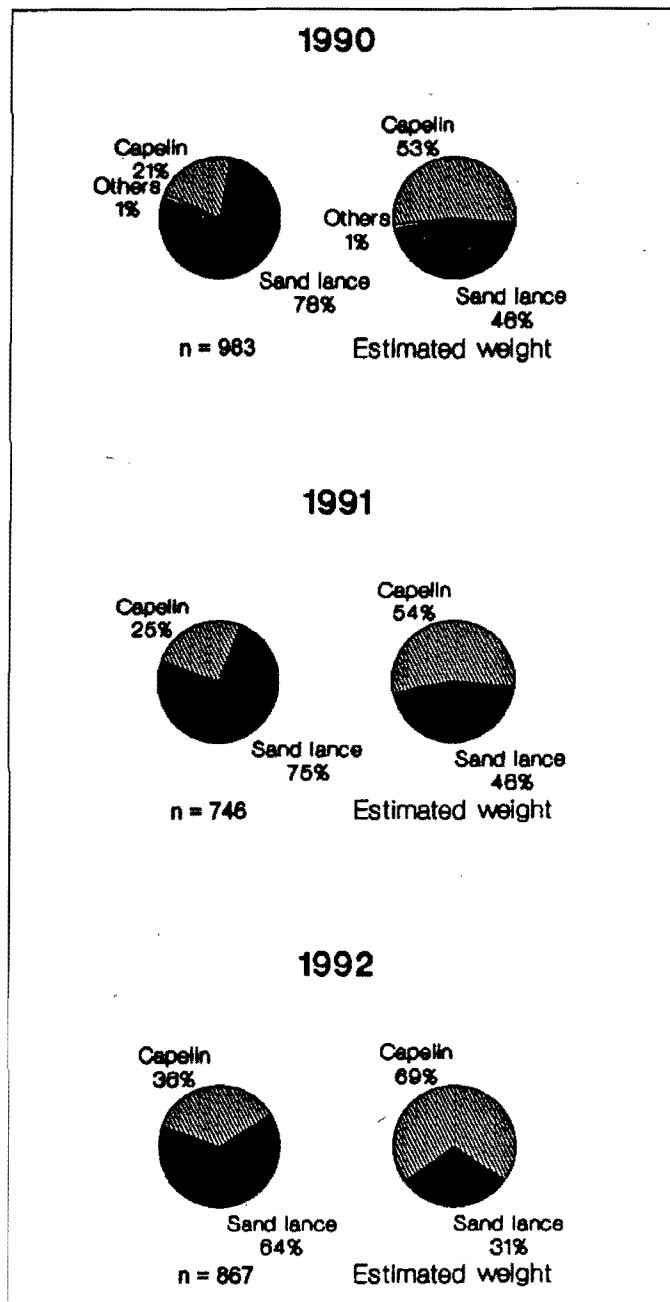
All data were tested for normality, using Shapiro-Wilk statistics (SAS Institute Inc. 1985). If the distribution was not normal, we used the median as the measurement of central tendency; if the distribution was nonparametric, the Kruskal-Wallis (K-W) and Mann-Whitney U-tests were used. In "normal" circumstances, parametric tests were used.

### 3. Results

#### 3.1 Diet of chicks

In all three years of the study, sand lance was the most frequently observed prey (64–78%), followed by capelin (21–36%). However, by mass, capelin was the most important prey (53–69%), followed by sand lance (31–46%) (Fig. 2). Rainbow smelt *Osmerus mordax* and Atlantic herring *Clupea harengus harengus* were also identified, but only in 1990, and only in very small

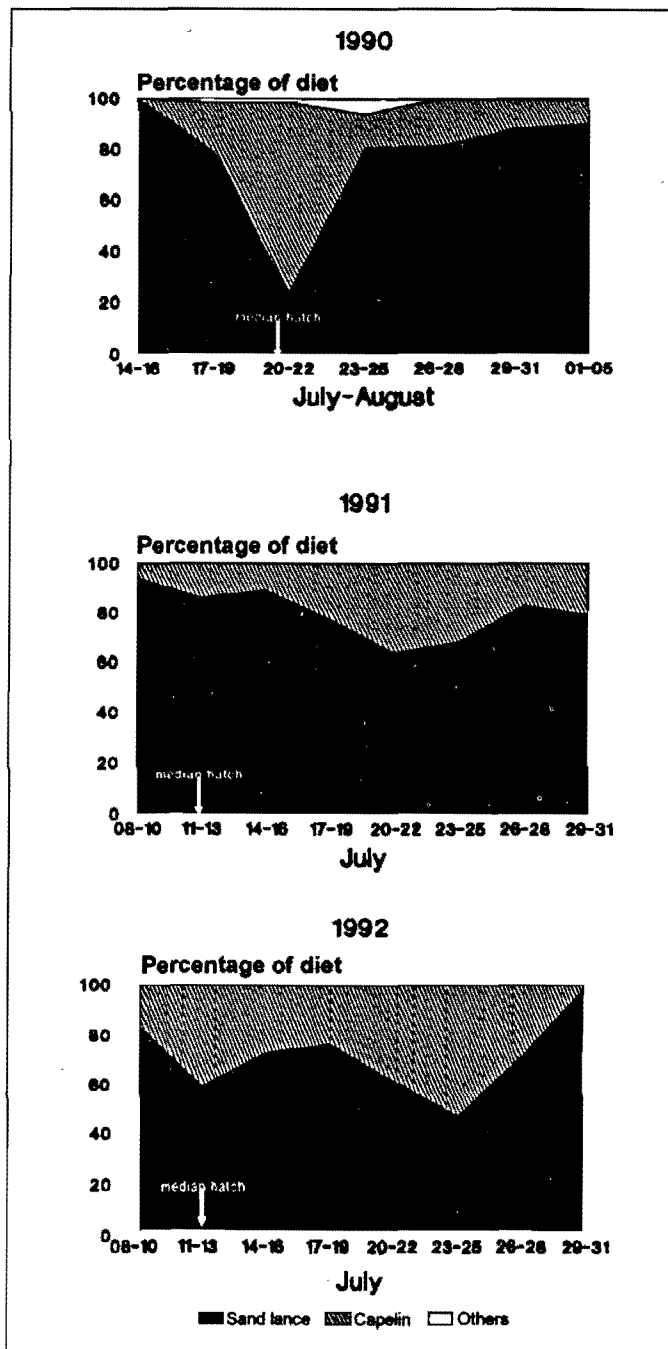
**Figure 2**  
Percent composition, by number and mass, of fish fed to Razorbill chicks at St. Mary's Islands, Gulf of St. Lawrence, Quebec, 1990–1992



numbers. Capelin mass was higher than sand lance mass in 1992, but not in 1990 or 1991.

The proportions of sand lance and capelin varied seasonally over the three years (Fig. 3). In 1990, capelin were observed at peak frequency just after the median hatching date (20 July); in 1991, the peak occurred well after the median hatching date (13 July). In 1992, there were two peaks, one at the median hatching date (12 July) and another towards the end of the chick-rearing period (24 July). The proportion of capelin remained relatively high throughout the 1992 season compared with 1990 and 1991.

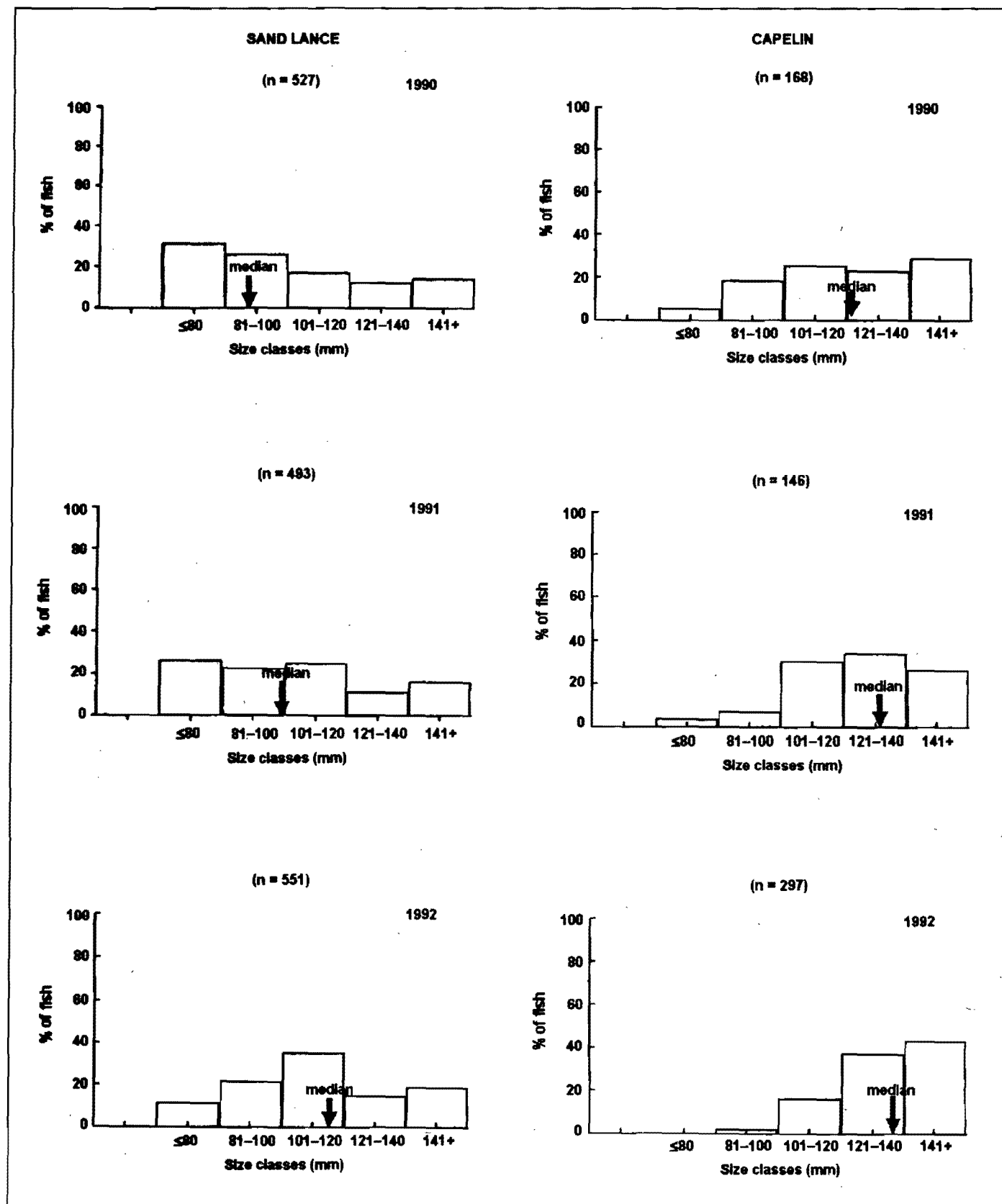
**Figure 3**  
Temporal change (1990–1992) in the numerical proportions of prey in the Razorbill chicks' diet at St. Mary's Islands, Gulf of St. Lawrence, Quebec



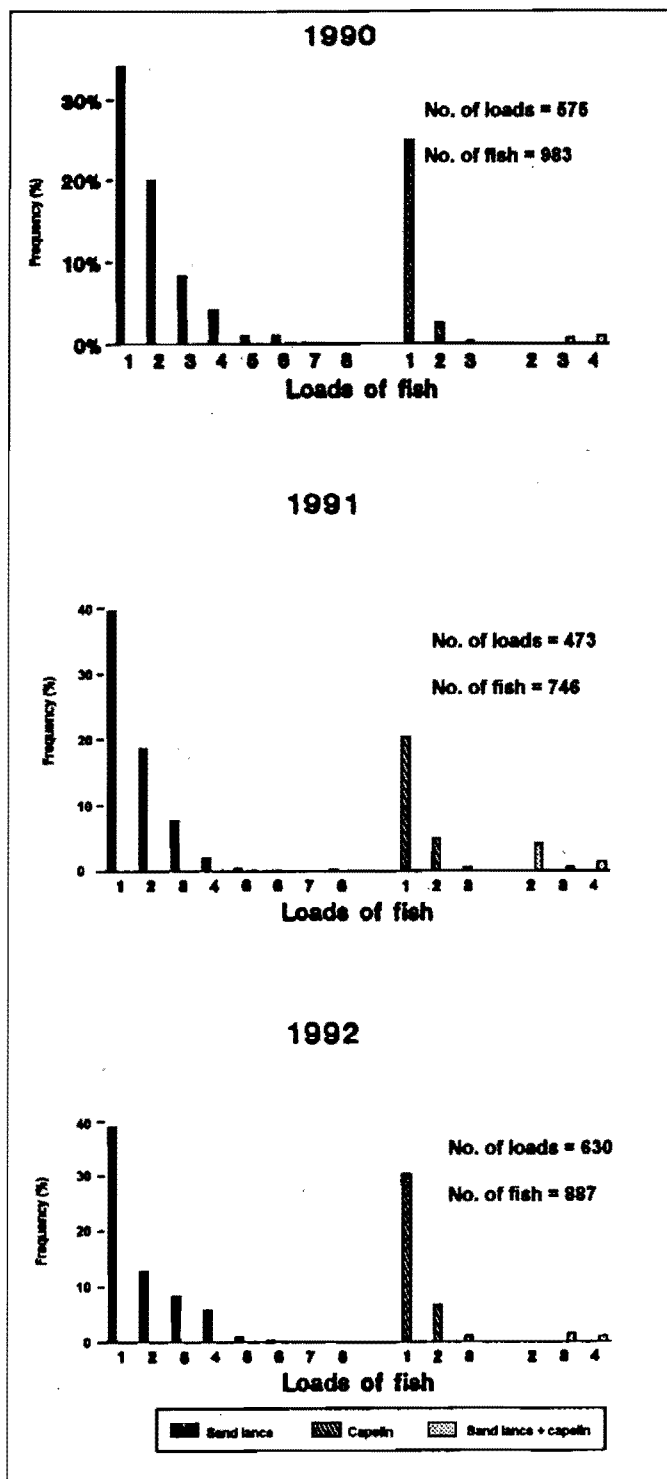
### 3.2 Characteristics of prey and loads

Sand lance ranged in length between 27 and 237 mm over the course of the three years, and median lengths differed significantly from year to year (K-W,  $H = 74.2$ ,  $P < 0.05$ ). In 1992, sand lance were significantly longer (median = 118.6 mm,  $n = 551$ ) than in 1990 (median = 89.0 mm,  $n = 527$ ; U-test,  $z = -8.43$ ,  $P < 0.0001$ ) (Fig. 4). The mass of sand lance estimated according to the length-to-mass relationship ranged between 0.8 and 21 g, and estimated median masses varied significantly from year to year (1990 = 2.7 g; 1991 = 3.5 g; 1992 = 5.0 g; K-W,  $H = 74.2$ ,  $P < 0.05$ ).

**Figure 4**  
Size classes of sand lance and capelin fed to Razorbill chicks, 1990–1992

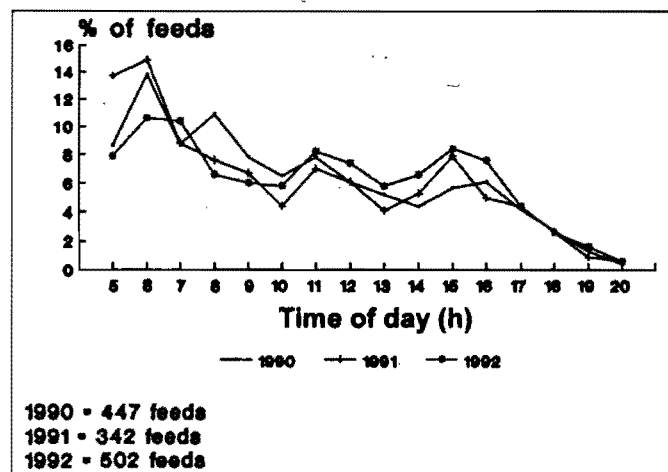


**Figure 5**  
Frequency of number of prey in loads of sand lance and capelin



Capelin lengths ranged between 45 and 207 mm, and median lengths also varied significantly from year to year (K-W,  $H = 45.7$ ,  $P < 0.05$ ). In 1992, capelin were significantly longer (median = 138.2 mm,  $n = 297$ ) than in 1990 (median = 123.1 mm,  $n = 168$ ; U-test,  $z = -6.28$ ,  $P < 0.0001$ ) and 1991 (median = 133.4 mm,  $n = 146$ ; U-test,  $z = -4.17$ ,  $P < 0.001$ ) (Fig. 4). The estimated mass of capelin ranged between 2 and 67 g, and median masses varied significantly from year to year (1990 = 15.9 g; 1991 = 19.8 g; 1992 = 21.8 g; K-W,  $H = 45.7$ ,  $P < 0.05$ ).

**Figure 6**  
Diurnal pattern of feeding (% feeds/h) of young Razorbills. Data from all-day watches combined for all years



Adults may carry one or more prey in their bills. Loads consisting of a single fish were most frequent over the three years, although loads of one to eight sand lance and one to three capelin were observed (Fig. 5). The proportion of loads of single to loads of two or more sand lance significantly differed from year to year ( $\chi^2 = 22.74$ , 2 df,  $P < 0.001$ : 34% in 1990, 39% in 1991 and 1992). The proportion of loads of single to loads of two or more capelin also varied from year to year ( $\chi^2 = 9.94$ , 2 df,  $P < 0.05$ : 25% in 1990, 20% in 1991, and 30% in 1992). Very few mixed (sand lance and capelin) loads were observed (Fig. 5).

Overall, the median mass of sand lance loads ranged from 0.8 to 31.2 g over the three years studied, with no significant difference from year to year (1990 = 6.4 g,  $n = 275$ ; 1991 = 6.4 g,  $n = 278$ ; 1992 = 6.8 g,  $n = 364$ ; K-W,  $P > 0.3$ ). Median loads ranged between 2 and 83 g and significantly increased from year to year (1990 = 17.6 g,  $n = 157$ ; 1991 = 21.8 g,  $n = 120$ ; 1992 = 26.5 g,  $n = 240$ ; K-W,  $H = 44.3$ ,  $P < 0.001$ ). Load masses were positively associated with the number of items in the loads. For sand lance, loads of three to six fish were heaviest; for capelin, loads of two or three were heaviest (Table 1).

### 3.3 Timing and frequency of feeding and energy intake

Because we had simultaneous 16-hour watches at study sites A and B, which is about the total period of daylight at that time of year, we combined results for the two sites. Generally speaking, the frequency of feeding was high early in the morning and gradually slowed down towards afternoon (Fig. 6). We recorded a positive and significant correlation between years (1990 and 1991,  $r_s = 0.87$ ,  $P < 0.001$ ; 1990 and 1992,  $r_s = 0.77$ ,  $P < 0.001$ ; 1991 and 1992,  $r_s = 0.92$ ,  $P < 0.001$ ).

Overall, young Razorbills were fed about three times a day. Feeding rates peaked later in the season, then decreased towards the end of the chick-rearing period (Fig. 7). There were no significant differences in the mean numbers of feeds at different study sites in each year (F,  $P_s > 0.05$ ). By combining all the feeding rates at the study

**Figure 7**  
Feeding rates at various study plots in 1990, 1991, and 1992

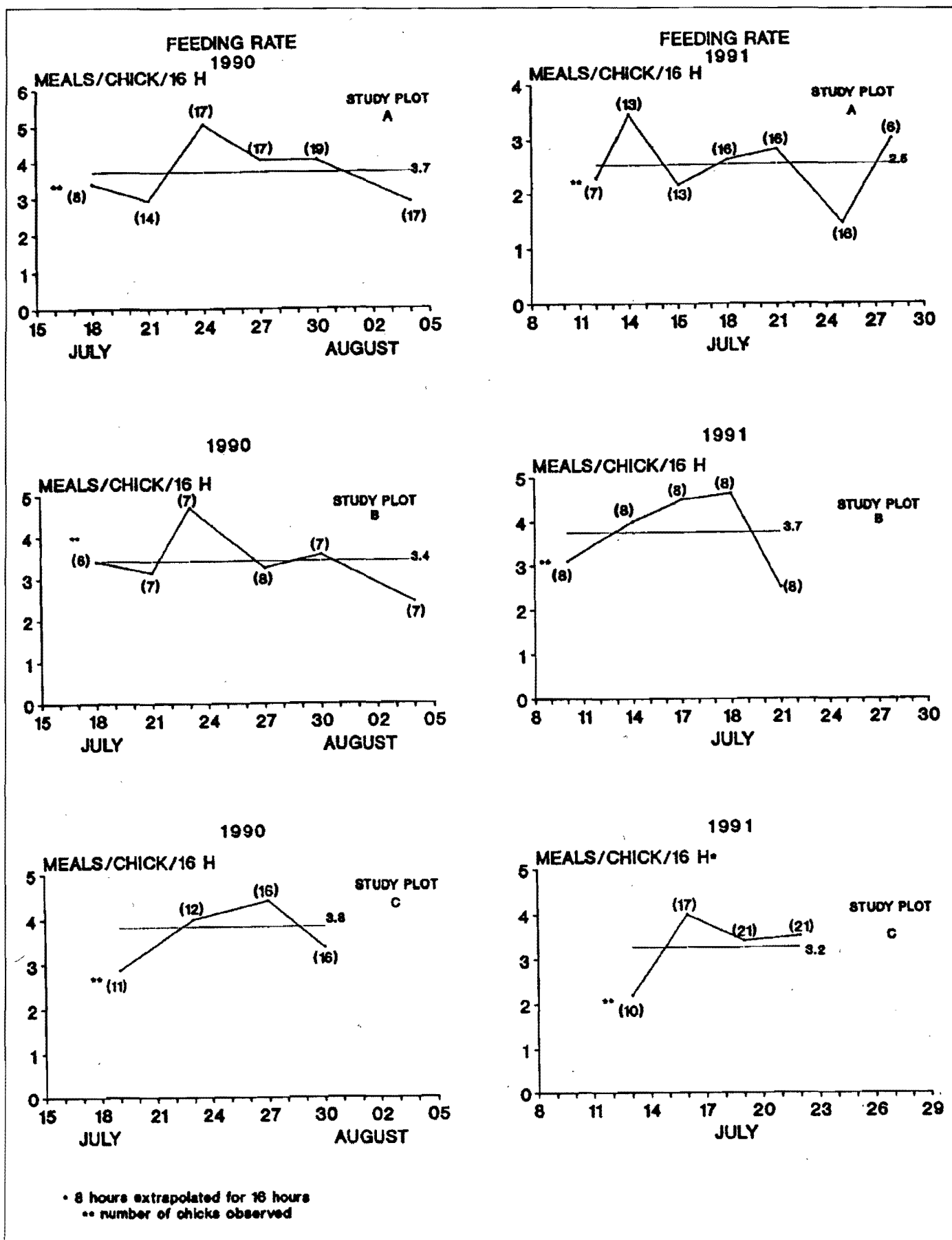
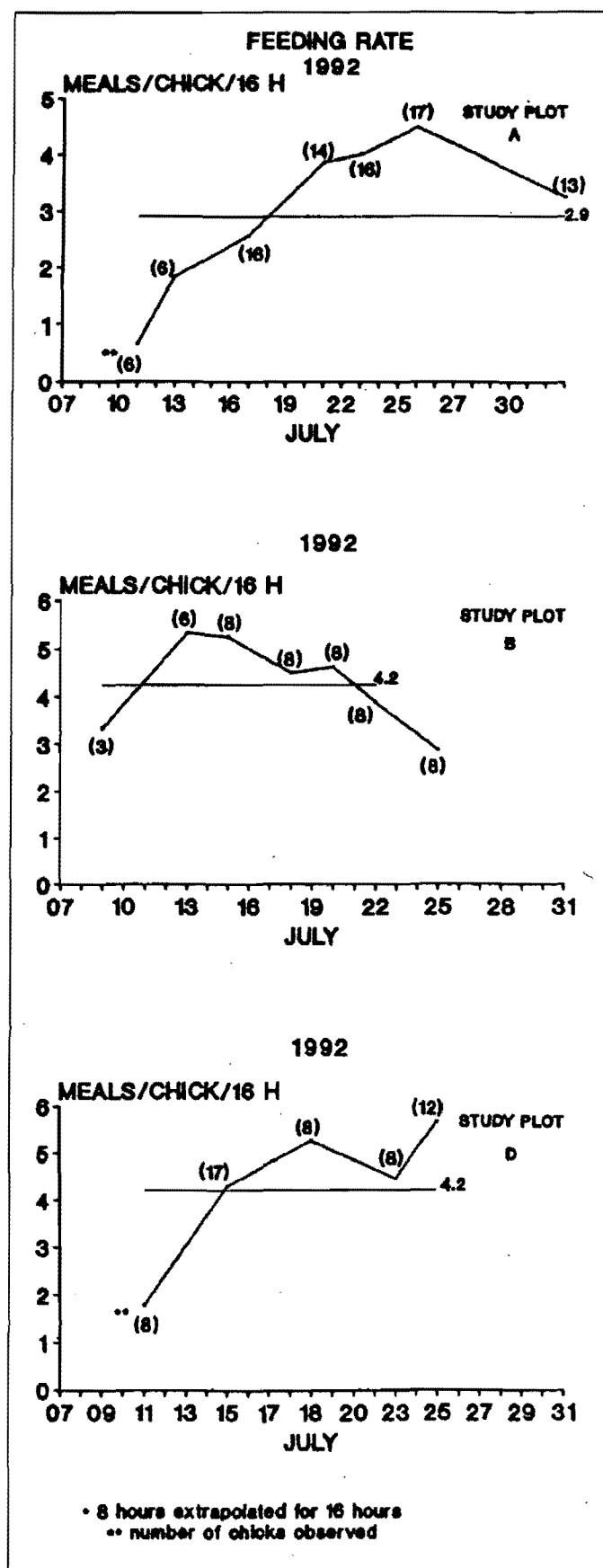




Figure 7 (cont'd)  
Feeding rates at various study plots in 1990, 1991, and 1992



sites by year, the mean number of feeds per chick per day did not vary significantly among years (3.6 in 1990, 3.1 in 1991, and 3.8 in 1992).

We estimated the chicks' daily intake and its energy value on the basis of the mean load weights, prey composition (see above), and caloric value of prey (Birkhead and Nettleship 1987). In 1990 and 1991, mean daily intake was approximately 35 g/chick, compared with 50.2 g/chick in 1992 (Table 2). This difference was due to the major role of capelin in the diet of chicks in 1992. The mean estimated daily intakes, in terms of their energy equivalents, were 251 kJ in 1990 and 1991 and 357 kJ in 1992. Based on a rearing period of 18 days, we estimate total intake per chick at 4514 kJ in 1990, 4525 kJ in 1991, and 6433 kJ in 1992 (Table 2). Because of the large amount (by mass) of capelin consumed each year and its high energy value, capelin contributes more than sand lance to the chicks' energy supply (Table 2). Nevertheless, caution is warranted in the choice of energy equivalents of prey from the literature, because variation of energy densities among species, seasons, and regions contributes to error in energy extrapolations (Montevecchi and Piatt 1984). Other factors, such as analytical methods and dehydration of seabird prey during transport to the colony, could also contribute to the variation in intake values obtained by different authors (Montevecchi and Piatt 1987).

#### 3.4 Breeding performance

There were no significant differences in any of the reproductive success parameters between the sites disturbed to different extents in any of the years ( $\chi^2$ ,  $P > 0.5$ ) (Table 3). Fledging success was slightly but nonsignificantly higher in 1992 (95.1%) than in 1990 (88.2%) and 1991 (87.2%).

#### 4. Discussion

Prior to this study, the only information available on the diet of young Razorbills in the Gulf of St. Lawrence was that of Bédard (1969), based on a sample of 31 fish, 93.5% of which were sand lance and 6.5% capelin. Elsewhere in North America, Birkhead and Nettleship (1983) mentioned that the two main prey of young Razorbills at the Gannet Clusters, Labrador, were sand lance (80%) and capelin (10–20%); they also reported herring and eelpout (*Lycodes* spp.) as minor prey species. Elsewhere in the Northwest Atlantic, in Greenland, Salomonsen (1950) reported that capelin was the main prey of Razorbill chicks. The diet of Razorbills in the Northeast Atlantic reveals a different pattern. Harris and Wanless (1986) reported that sand lance made up more than 98% of the diet of chicks in a three-year study on the Isle of May, Scotland; other prey species mentioned were herring and rockling (*Ciliata/Gaidropsarus* spp.). In the Barents Sea, sand lance and capelin were the main prey at Hornøya, a colony in northern Norway (Barrett 1984; Furness and Barrett 1985; Barrett and Furness 1990).

In this study, we have shown the importance of the contribution of capelin to the diet of young Razorbills. Although capelin were observed more frequently and were

**Table 1**  
Median masses of different-sized loads of fish in 1990–1992

Median masses of different sized loads of fish in 1990–1992									
Load size	1990		1991		1992		H <sup>c</sup>	P	
	Median mass (g) <sup>a</sup>	n <sup>b</sup>	Median mass (g)	n	Median mass (g)	n			
<b>Sand lance</b>									
1	4.6 (2.2–7.7)	131	5.0 (3.4–6.9)	170	5.0 (3.8–6.9)	236	9.17	0.01**	
2	7.2 (4.3–10.5)	84	7.1 (5.1–10.0)	80	7.8 (5.6–23.4)	82	2.38	0.30	
3	8.7 (5.3–18.0)	30	10.4 (8.1–14.1)	35	12.5 (8.8–19.2)	34	4.13	0.12	
4	12.2 (6.8–16.7)	19	8.0 (7.8–11.6)	9	15.4 (11.6–16.4)	11	4.95	0.08	
5	14.0 (8.1–26.3)	3	7.8 (6.0–10.3)	3	–	–	–	–	
6	10.0 (2.6–11.4)	7	–	–	–	–	–	–	
7	–	–	–	–	–	–	–	–	
8	4.8	1	–	–	–	–	–	–	
<b>Capelin</b>									
1	15.9 (10.8–25.6)	143	21.4 (14.3–26.5)	96	21.8 (19.8–26.5)	191	38.93	0.0001**	
2	36.8 (30.4–51.2)	11	29.1 (24.2–36.1)	22	48.3 (41.6–53.0)	42	12.88	0.001**	
3	59.3 (59.3–71.2)	3	32.8 (20.9–44.7)	2	61.4 (47.3–79.7)	7	3.78	0.15	

<sup>a</sup> Interquartile range in parentheses.

<sup>b</sup> n = sample size.

<sup>c</sup> Kruskal–Wallis test among years.

\*\* significant at P < 0.05.

**Table 2**  
Caloric and food intake of Razorbill chicks at the St. Mary's Islands in 1990–1992

Year	Mean mass of loads (g)	Feeding rates (loads/day)	Daily intake		Total food (g) and caloric intake (kJ) per chick during rearing period	
			g	kJ <sup>a</sup>	g	kJ
1990	9.7	3.6	34.9	250.8	628	4514
1991	11.3	3.1	35.0	251.4	630	4525
1992	13.2	3.8	50.2	357.4	878	6433

<sup>a</sup> Caloric values of sand lance = 6.8 kJ/g, capelin = 7.5 kJ/g; based on Birkhead and Nettleship (1987).

**Table 3**  
Reproductive success of Razorbill at St. Mary's Islands in study plots with low disturbance (A) and high disturbance (B)

	No. of eggs	Hatching success		Fledging success		Net produc- tivity (%)
		No.	%	No.	%	
<b>1990</b>						
A	75	60	(80.0)	54	(90.0)	72.0
B	83	67	(80.7)	58	(86.6)	69.9
Total	158	127	(80.4)	112	(88.2)	70.9
<b>1991</b>						
A	99	80	(80.8)	71	(88.8)	71.8
B	112	92	(82.1)	79	(85.9)	70.5
Total	211	172	(81.5)	150	(87.2)	71.1
<b>1992</b>						
A	86	65	(75.6)	63	(96.9)	73.3
B	116	97	(83.6)	91	(93.8)	78.4
Total	202	162	(80.2)	154	(95.1)	76.2
<b>1990-1992</b>						
A	260	205	(78.8)	188	(91.7)	72.3
B	311	256	(82.3)	228	(89.1)	73.3
Total	571	461	(80.7)	416	(90.2)	72.8

larger in 1992 than in 1990 and 1991, fledging success did not vary among years (Table 3), nor did maximum weights or mean weights at fledging (Table 4).

It is possible that our mean daily intake estimate of 50.2 g/chick in 1992 is an overestimate, as there were 12 observations in 1992, compared with two in 1990 and

**Table 4**  
Mean maximum and fledging masses and mean fledging ages of Razorbill chicks at St. Mary's Islands, 1990–1992

Year	Mean maximum mass		Mean fledging mass		Mean fledging age	
	g	n <sup>a</sup>	g	n	d	n
1990	212.4 ± 19.1	17	207.0 ± 22.5	16	17.9 ± 1.8	16
1991	213.0 ± 20.4	35	199.3 ± 23.4	31	18.5 ± 1.6	31
1992	203.9 ± 20.8	46	195.8 ± 23.7	44	18.1 ± 1.9	43

<sup>a</sup> n = sample size.

Note: All interannual variation is nonsignificant.

1991, of adults eating fish that chicks had rejected as if they were satiated. However, these observations are based on only three chicks that could be directly observed. Harris and Wanless (1986) estimated the daily intake of Razorbill chicks on the Isle of May to be 21 g/chick (150 kJ, mean based on three years of study). These estimates are much lower than ours (mean daily intake = 39.5 g/chick or 286 kJ), but they can probably be explained by the difference in masses of adults and chicks in the two regions. The mean mass of adults in the British Isles is estimated to be 630–637 g (Lloyd 1976; Harris and Wanless 1986), and the mean mass of chicks at fledging is approximately 175 g (Lloyd 1979). In the St. Mary's Islands, the mean mass of adults is 728 ± 51 g (n = 353; this study), and the mean mass of fledglings is 199.2 ± 24 (n = 91). It is therefore expected that the energy require-

ments of Razorbills in the St. Mary's Islands would be higher and that they would eat more. Moreover, larger adults are certainly able to carry heavier prey loads.

Harris and Wanless (1989) calculated a mean hatching success rate of 71.5%, a mean fledging success rate of 92.1%, and a mean net productivity of 0.66 young per pair, based on studies of nine colonies located in the northern Atlantic Ocean, North Sea, and Baltic Sea (Paludan 1947; Keighley and Lockley 1948; Brun 1958; Plumb 1965; Bianki 1967; Bédard 1969; Ingold 1974; Lloyd 1979; Chapdelaine and Laporte 1982; Barrett 1984; Harris and Birkhead 1985). Moreover, their study of Razorbills breeding on the Isle of May, conducted between 1981 and 1987, found a mean hatching success rate of 72% and a mean fledging success rate of 85%. In every case the authors mentioned, hatching success was lower than fledging success. This study is no exception (Table 3). With a mean fledging success rate of 90.2% over the three years of the study of Razorbill breeding success on the St. Mary's Islands, we feel that feeding conditions during the chick-rearing period were excellent. Chapdelaine and Laporte (1982) reported a net productivity of 61% in 1978, when the population of this species was at a very low level and no growth trend was indicated. In 1988, however, a substantial increase had been reported, and corresponding net productivity was 74% (Chapdelaine and Brousseau 1991). The mean net productivity of 73% for the 1990–1992 period suggests that the population will continue to increase over the next five years.

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## Appendix 1

Length (L)/mass regressions used to estimate the mass of sand lance (Koehler et al. 1969) and capelin (Lambert and Bernier 1989) delivered to Razorbill chicks:

Mass of sand lance =  $209 \times 10^{-6} \times L^{2.11}$  (Koehler et al. 1969)

Mass of capelin =  $2.7 \times 10^{-5} \times L^{2.76}$  (Lambert and Bernier 1989)

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# Concordance of seabird population parameters: analytical methods and interpretation

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## Abstract

In an ecological context, concordance may be defined as the tendency for paired values of some parameter, such as the annual productivity of bird species, to show similar directions and magnitudes of deviation from the mean. Where concordance among populations is high, there is an implied similarity of the ecological factors affecting performance. Conversely, if populations behave discordantly, dissimilarity of underlying ecological factors is likely. In evaluating birds as indicators of the marine environment, the biologist typically is confronted with a three-dimensional array of observations (species, areas, and years) in which there are more missing values than filled cells. This frustrates attempts to analyze concordance using existing methods (e.g., Kendall's coefficient, or correlation combined with cluster analysis), which are either impossible to apply to incomplete data sets or potentially misleading when applied to incomplete data sets. I suggest an alternative method for analyzing concordance that makes maximal use of available data. For a given data set partitioned into the smallest units containing information about concordance, one computes an index of concordance using a regression approach and tests for significance using randomization methods. This procedure would seem to have wide application to ecological studies generally and to seabird monitoring in particular.

## Résumé

En écologie, on peut définir la concordance comme le fait, pour des valeurs appariées relatives à des paramètres tels que la productivité annuelle chez certaines espèces d'oiseaux, d'indiquer une tendance et une ampleur similaires sur le plan des écarts par rapport à la moyenne. Une concordance marquée entre les valeurs visant diverses populations laisse croire qu'il existe une similarité des facteurs écologiques ayant une incidence sur la performance. En revanche, si les valeurs enregistrées accusent une disparité, il est très probable que les facteurs sous-jacents ne soient pas similaires. En règle générale, lorsque les biologistes évaluent les oiseaux marins en tant qu'indicateurs de l'état du milieu marin, leur évaluation porte sur trois valeurs observées (espèce, région et année), pour lesquelles il y a davantage de

données manquantes que de données disponibles. Cette situation complique l'analyse de la concordance à l'aide des méthodes actuelles (par exemple, le coefficient de Kendall, ou corrélation des rangs, conjugué à l'analyse typologique), qui ne peuvent être appliquées à des données incomplètes ou qui, lorsqu'appliquées à de telles données, peuvent induire les chercheurs en erreur. Nous proposons comme solution de remplacement une méthode d'analyse de la concordance qui permet une utilisation optimale des données disponibles. À partir d'un ensemble de données réparties en fonction des plus petites unités contenant de l'information sur la concordance, on calcule un indice de concordance au moyen d'une analyse de régression et de tests de signification effectués sur une base aléatoire. Cette façon de procéder pourrait trouver une application étendue dans le cadre des études relatives à l'écologie et plus particulièrement en ce qui concerne la surveillance des oiseaux marins.

## 1. Introduction

Because seabirds nest in mixed colonies and are easy to observe, population studies often yield concurrent information on numbers, productivity, phenology, or other parameters for several species. The aim of monitoring is to document annual and longer-term variation in population parameters, and it is pertinent to inquire whether variation between species, or between colonies of the same species, is concordant. In this context, concordance refers to the tendency for paired values of some parameter, such as the annual productivity of bird species, to show similar directions and magnitudes of deviation from the long-term mean. If two or more populations are strongly concordant, then the key ecological factors affecting their performance are probably the same. Conversely, if populations show a lack of concordance or behave discordantly, then dissimilarity of underlying ecological factors is implied.

Among high-latitude seabirds, examples of discordance arise frequently. In 1983, I made a late-season visit to the Semidi Islands, Alaska, and noted that Black-legged Kittiwakes *Rissa tridactyla* had completely failed to raise young. However, other piscivorous birds, including Thick-billed Murres *Uria lomvia*, Common Murres *Uria aalge*, and Horned Puffins *Fratercula corniculata*, were having good success. In fact, Horned

Puffins, which eat much the same food in summer as do kittiwakes at the Semidi Islands, were raising more young than they had in any of the five previous years in which they had been studied.

Surveys in Alaska's Prince William Sound present another interesting example involving kittiwakes. D.B. Irons (pers. commun.) has noted that some kittiwake colonies in the Sound consistently produce young in substantial numbers, whereas others just a few kilometres away have total breeding failures.

In many cases, patterns of concordance suggest testable hypotheses about ecological factors. For example, is the contrast between surface-feeding kittiwakes and diving alcids explained by the failure of shared prey to come to the surface in some years? Is the productivity of kittiwakes in Prince William Sound influenced by the distance to tidewater glaciers and the availability of ice-associated prey?

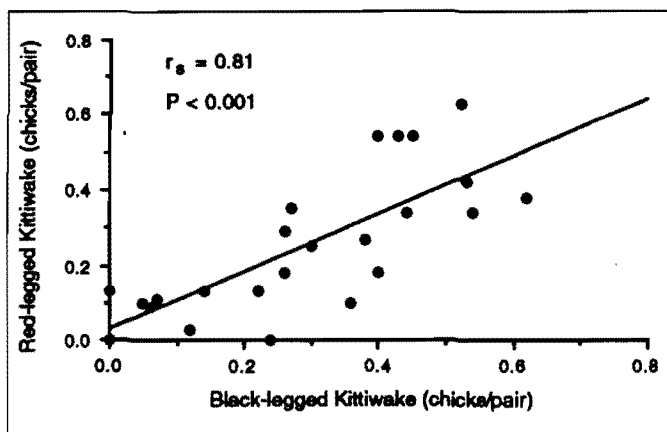
The investigation of these and similar questions requires first that we quantify and test the observed patterns on which our hypotheses are based. The aim of this paper is to introduce some new techniques for quantifying and testing the statistical significance of concordance in ecological data sets. I begin by illustrating the use of existing methods with some further examples from seabird monitoring in Alaska.

## 2. Concordance in seabird monitoring — approaches and problems

To quantify concordance in a single pairwise comparison, where an adequate number of paired observations are available, simple correlation analysis (Spearman's rank-order correlation or Pearson's product-moment correlation) is appropriate. An example is shown in Figure 1, in which annual productivities (young produced per pair) are plotted for Black-legged Kittiwakes and Red-legged Kittiwakes *Rissa brevirostris* in Alaska. The data set consists of 24 measurements of productivity in these species, obtained in the same locations and years. A high degree of concordance between the two is evident.

When three or more sets of observations are available for analysis, it may be of interest to assess concordance relationships for the data set as a whole. For example, Hatch and Hatch (1990) measured productivities in various subsets of a group of seven species during several years on the Semidi Islands. Their preliminary analysis (Fig. 2) attempted to identify, graphically, "good" and "bad" years for seabirds, by looking for instances in which all or most species varied in one direction or the other from their respective mean productivities. A serious problem is that all species were not observed in all years, and missing data can give rise to misleading interpretations. For example, the plotted values for Common and Thick-billed murres suggest that productivities were fairly concordant in 1979 and 1981 but discordant in 1980 (Fig. 2). In fact, all three years were relatively good years for murres, and therefore small deviations from mean productivity tend to be exaggerated relative to other species in the diagram. If comparable data were available for 1976 and 1978, when qualitative observations suggested that murres had much lower

**Figure 1**  
Correlation of annual productivity in Red-legged and Black-legged kittiwakes in 24 colony-years of observation in the Bering Sea



success, mean productivities would have been correspondingly lower, and the deviations in Figure 2 might have changed in magnitude, if not direction.

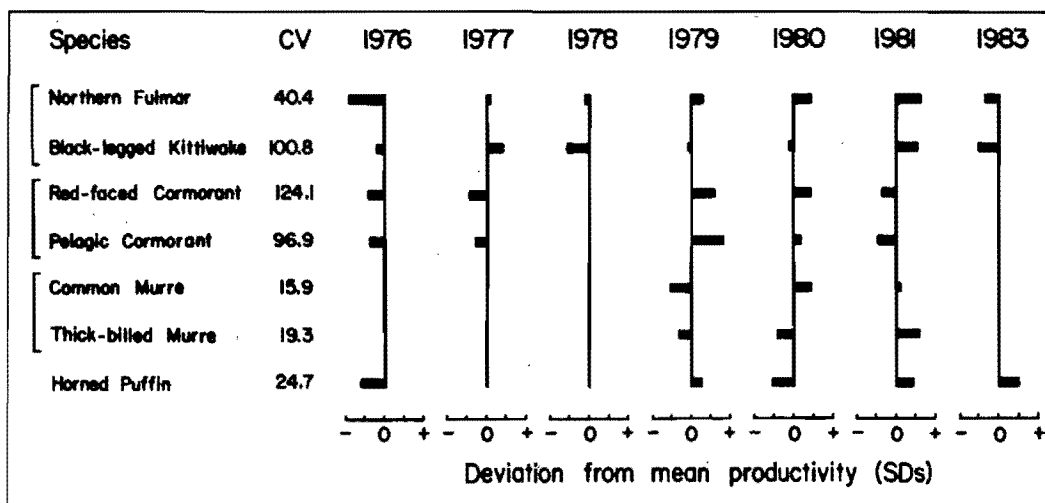
To address the problem of missing values, Hatch and Hatch (1990) recalculated means and standard deviations for a reduced data set in which all seven species were observed in three years (Fig. 3). For this array, it is possible to compute Kendall's coefficient of concordance ( $W$ ) and a significance level based on the chi-square distribution. Kendall's coefficient is a non-parametric statistic that measures overall agreement among the ranked values of three or more variables (Sokal and Rohlf 1981). There can be no missing values in any of the series included in the analysis. For the species and years depicted in Figure 3,  $W$  is low (0.082) and non-significant ( $P = 0.565$ ). This agrees with visual inspection of the data — at least two species occurred on low and high sides of the means in all three years.

Taking the analysis of these data a step further, Hatch and Hatch (1990) prepared a cluster diagram of pairwise correlations in productivity between species (Fig. 4). All available estimates of productivity were used to construct the matrix of similarity values (Pearson correlation coefficients), so the sample sizes were 3–7 years, depending on the species compared. Values were linked by an algorithm described in Lehner (1979). The resulting dendrogram is in essence a working hypothesis about the relative similarity of factors affecting the productivity of different species. In this instance, the two cormorant species seemed highly concordant with each other but distant from the rest of the seabird community with respect to annual productivity.

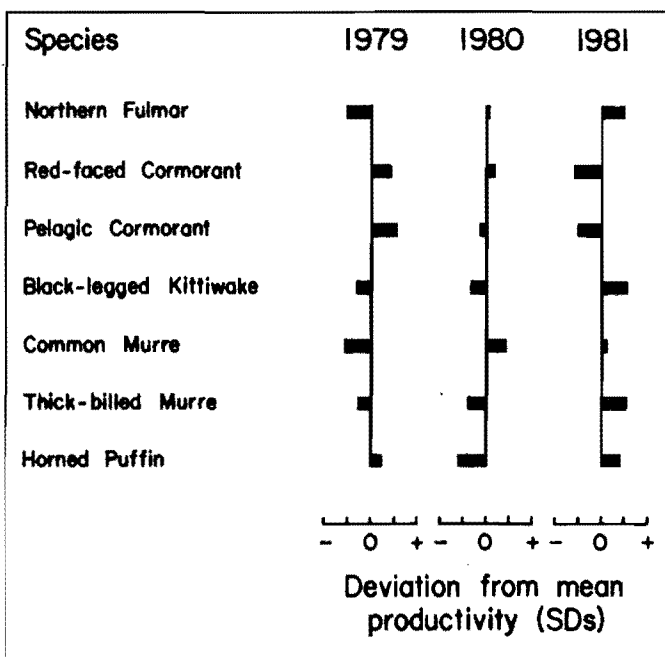
Cluster analysis of similarity values is a potentially powerful technique for quantifying concordance. It is limited, of course, to data sets in which all the categories compared have at least three observations in common (e.g., seven species observed in three years, 1979–1981, as in Figs. 2 and 3). The inclusion of additional observations for some pairs of species effectively treats the year effect as a random factor (cf. Sokal and Rohlf 1981:202–207 for a pertinent discussion of random and fixed effects). Relationships will be strengthened or modified by the accumulation of new data; in the present example, it is likely that some of the implied similarities

**Figure 2**

Annual deviations from the mean productivities of seven species breeding on the Semidi Islands, Alaska. No flag to the left or right of a midline indicates no estimate available for that species and year. Because of missing values, comparisons are strictly valid only for species with matching sets of observations (as bracketed on the left). CV is the coefficient of variation in productivity among years (from Hatch and Hatch 1990)

**Figure 3**

Annual deviations from mean productivity calculated over three years for seven species breeding on the Semidi Islands (from Hatch and Hatch 1990)

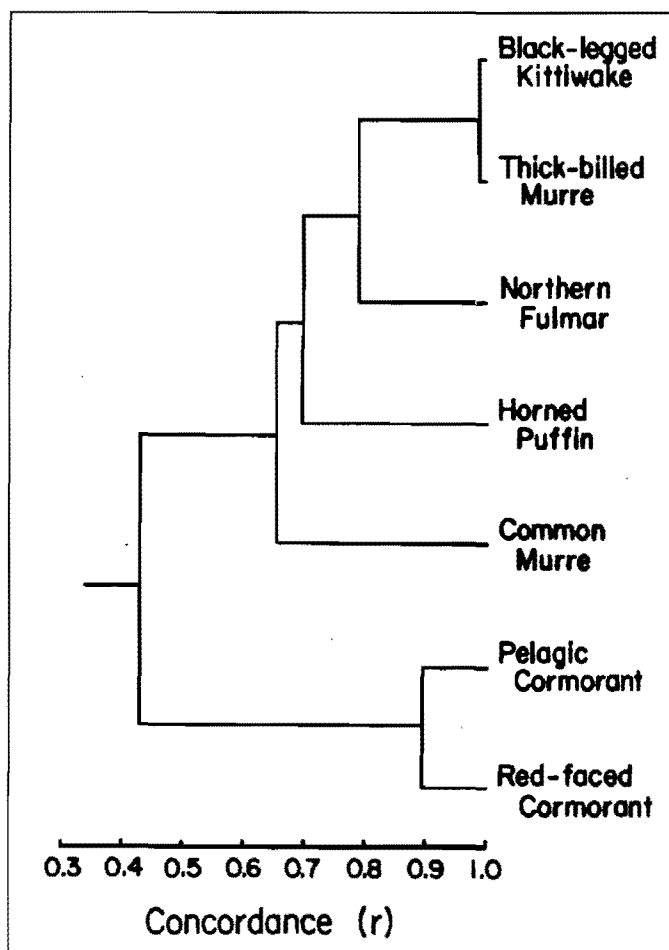


and differences were exaggerated by small sample sizes and missing values.

As a final example, consider some patterns of breeding success in Black-legged Kittiwake colonies throughout Alaska (Fig. 5). These data (Hatch et al. 1993) suggest regional differences between the Gulf of Alaska and waters to the north. In 1978, for instance, most colonies failed in the Gulf of Alaska, whereas those observed in the Bering and Chukchi seas were relatively productive. The opposite was true in 1984. Hatch et al. (1993) made no attempt to quantify this apparent geographic concordance — any analysis would again be hampered by the problem of missing values.

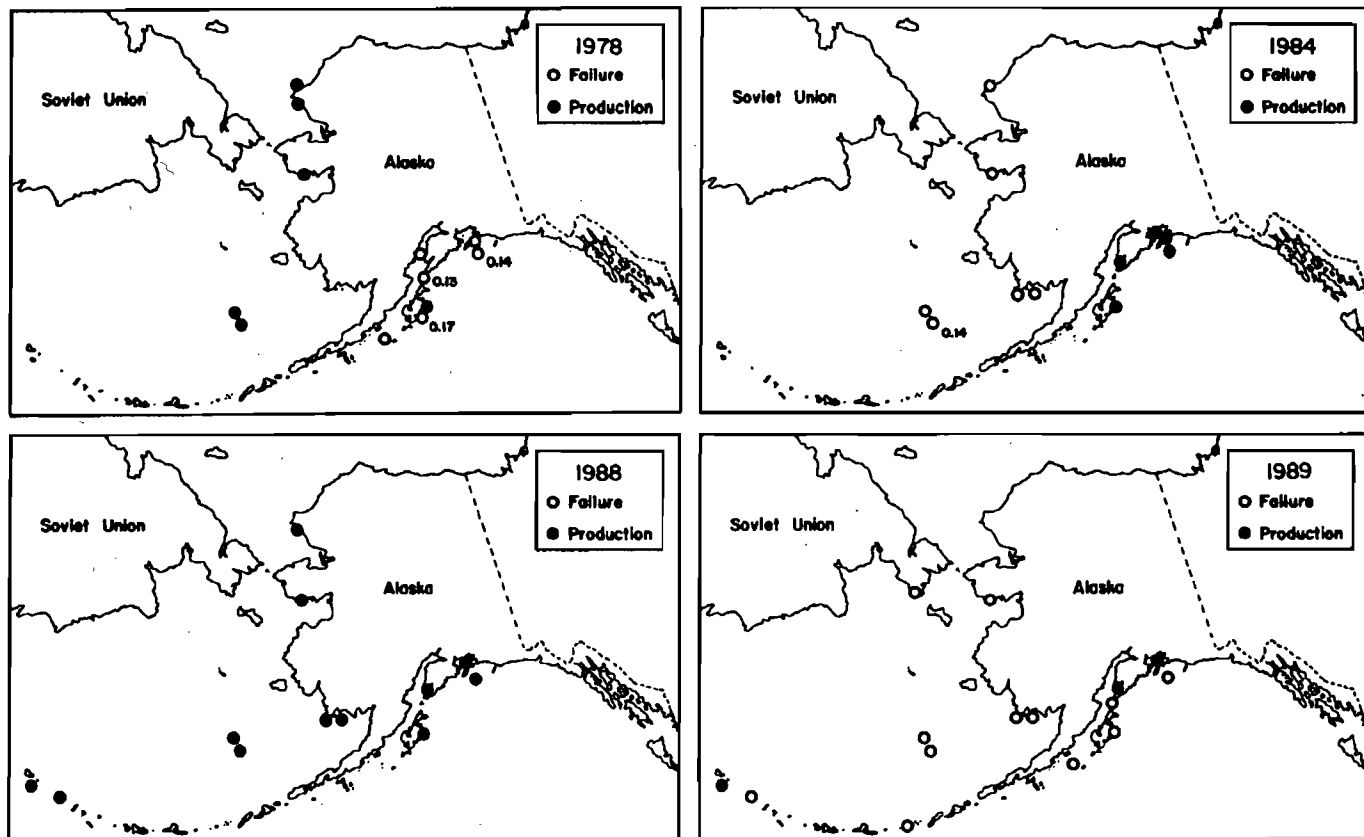
**Figure 4**

Cluster analysis of concordance relationships among seven species breeding on the Semidi Islands. Concordance is measured as Pearson correlation coefficients between species or groups with respect to annual breeding productivity (from Hatch and Hatch 1990)



**Figure 5**

Geographic concordance of breeding failure and success of Black-legged Kittiwakes in North Pacific colonies. Failure is defined as an instance in which productivity was  $\leq 0.1$  chicks/pair (with minor exceptions, as indicated) (from Hatch et al. 1993)



### 3. Generalization of the problem

The previous examples dealt with concordance relationships in two-dimensional arrays of data — different species observed over several years in a single area, or one species observed over several years in different areas. Monitoring programs, however, typically generate three-dimensional arrays of observations (various species observed in selected areas over a number of years). It is important to recognize that the questions illustrated thus far are drawn from a larger set of ecologically meaningful questions about concordance that can be asked of such a data set. The possibilities are represented schematically in Figures 6, 7, and 8. The basic strategy for partitioning the data remains the same — we analyze each plane of a three-way data set as a two-dimensional array, while controlling for the third dimension. Each layout gives rise to a pair of complementary questions.

In the first instance (Fig. 6), one might have productivity estimates from a single study site for a number of species in several years. It is reasonable to ask (1) whether some years are uniformly more productive across species than others (i.e., within areas, do we find concordance of species across years?) and (2) whether some species are consistently more productive than others. (This latter question is problematic. Controlling for area, the question is really asking whether one species is consistently more productive than another in that area, *relative* to the mean productivities of the same species in a

larger region. A somewhat different approach from what I present may be necessary to handle that question.)

A second analysis (Fig. 7) would control for year and pose the following questions: (1) Are some areas consistently more productive than others for all species studied? This approach could lead to a classification of areas in terms of those that seem especially favourable for breeding seabirds and those that are less productive. (2) Are some species consistently more productive than others in all areas? (Here again, because different species have varying levels of potential productivity, this question requires at least a calibration step before the data can be meaningfully analyzed.)

Finally, controlling for species (Fig. 8), we may ask (1) whether some years are better than others for this species across all areas and (2) whether some areas are consistently better at producing this species than others.

The purpose of a concordance analysis is to provide quantitative answers to such questions. Working with real data, however, one finds that standard analyses are limited if data sets contain missing values. Data can be split into arrays of various dimensions that have no missing cells, but this leads only to multiple, possibly contradictory, answers to the questions at hand.

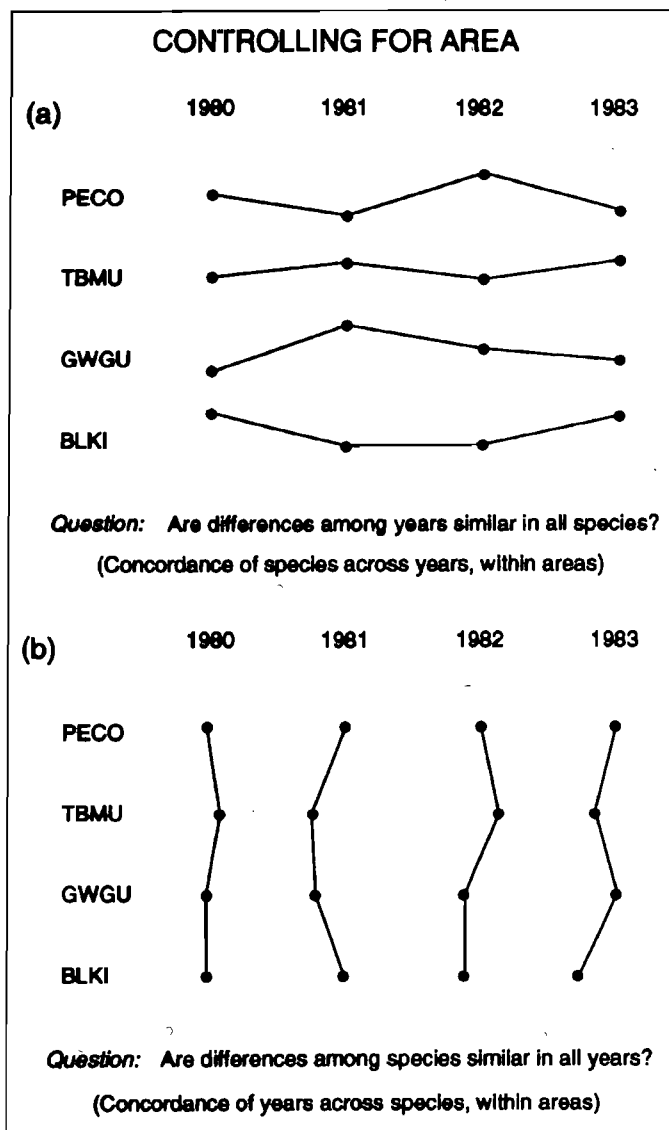
### 4. Numerical methods

An alternative approach is based on the recognition that  $2 \times 2$  arrays are the fundamental units of concordance.



**Figure 6**

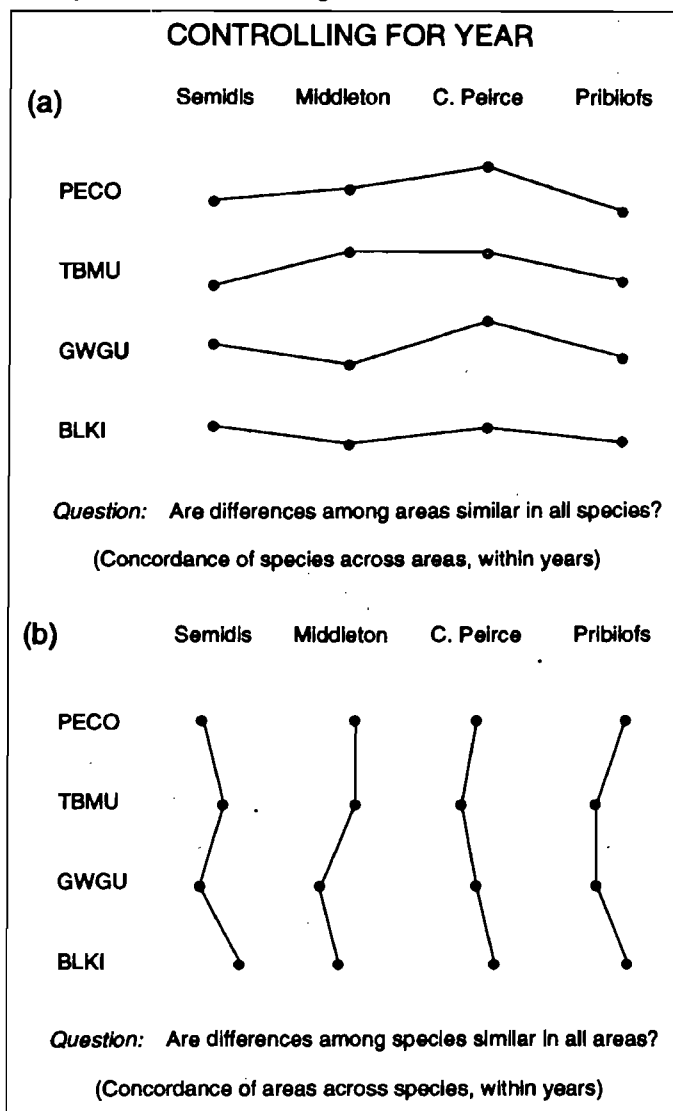
Alternative views of a three-dimensional data set of seabird productivity, controlling for area. Species, years, and magnitudes of change have been chosen arbitrarily for illustration. PECO, Pelagic Cormorant; TBMU, Thick-billed Murre; GWGU, Glaucous-winged Gull; BLKI, Black-legged Kittiwake



A  $2 \times 2$  array exists if two species are observed in two years in the same area, if two species are observed in two areas in the same year, or if the same species is observed in two areas in two years. Such an array has no missing values and is logically the smallest unit of data that contains information about concordance. The strategy in the numerical approach is to partition a given data set into all possible  $2 \times 2$  arrays, to derive from these an index of concordance based on regression analysis, and to test the significance of this index using randomization methods (Manly 1991; Potvin and Roff 1993). Partitioning may generate a large number of  $2 \times 2$  arrays. For instance, a  $5 \times 7$  array with no missing values contains 210 such subarrays. A complete  $6 \times 8$  parent array contains 420 subarrays, and a  $12 \times 12$  parent contains 4356. Typically, this number is greatly reduced by missing data. The randomization step also entails extensive computation,

**Figure 7**

Alternative views of a three-dimensional data set of seabird productivity, controlling for year. Species, areas, and magnitudes of change have been chosen arbitrarily for illustration. Acronyms are defined as in Figure 6

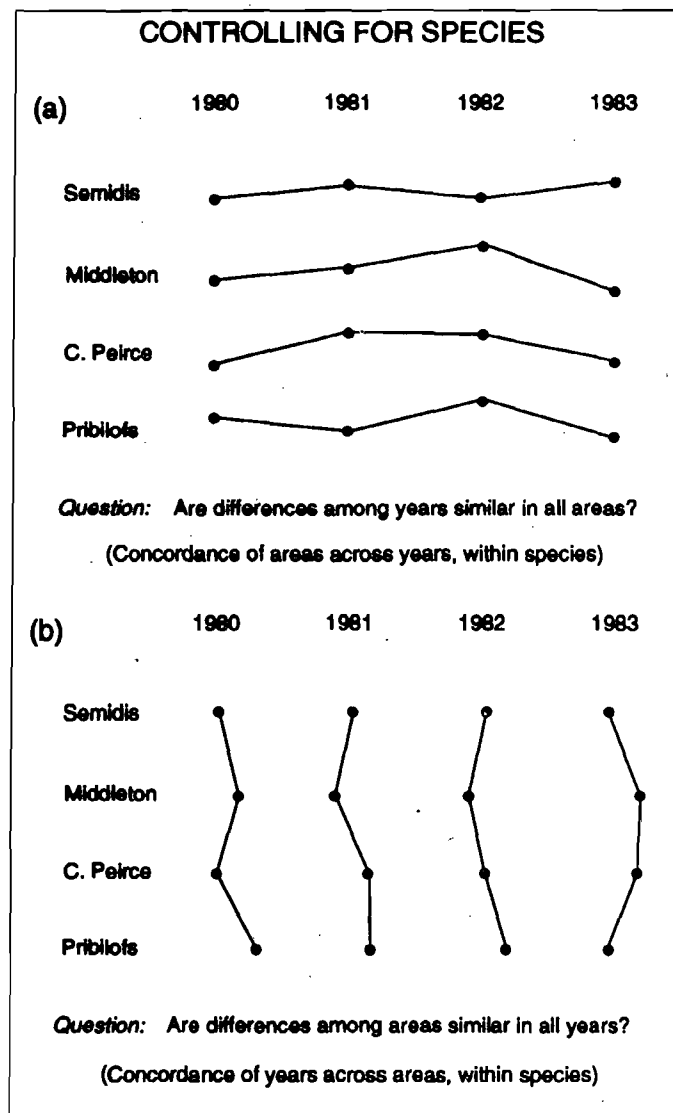


however, and a computer program is the only practical way to handle real data.

The magnitude of change between two observations in a  $2 \times 2$  array can be represented by a line segment with a slope equal to the difference between measurements (Fig. 9a). Each  $2 \times 2$  array contains a pair of line segments corresponding to the horizontal view of the array and another pair corresponding to the vertical view (as in examples a and b, Figs. 6–8). Perfectly parallel line segments would indicate perfect concordance (identical magnitudes and directions of change between observations) for the limited comparison embodied in a  $2 \times 2$  array. Conversely, line segments at right angles would represent perfect discordance.

Conceptually, we seek an index that expresses the average degree of parallelism in all possible pairs of line segments in our original array. One method of doing this is illustrated in Figure 9b. If, for every  $2 \times 2$  array generated, the slope of line segment 1 ( $Y_1$ ) is plotted against the slope of line segment 2 ( $Y_2$ ), the resulting plot will be a scatter of points whose slope approaches unity as

**Figure 8**  
Alternative views of a three-dimensional data set of seabird productivity, controlling for species. Areas, years, and magnitudes of change have been chosen arbitrarily for illustration



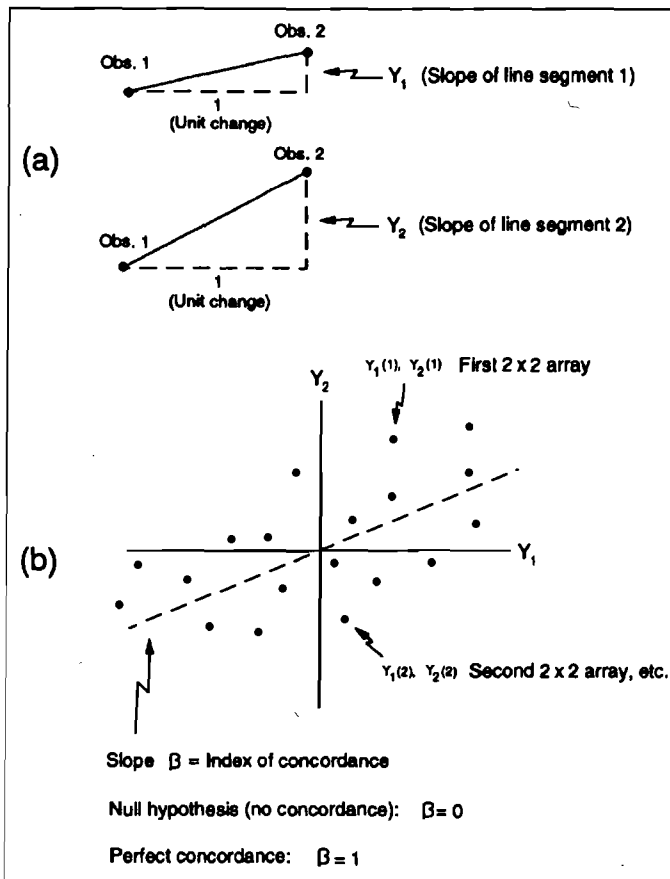
the average parallelism among the pairs of line segments increases. This slope is an index of concordance for the entire array. Computationally, the value is obtained in the same manner as a nonstandardized slope in regression analysis:

$$\text{Concordance } (\beta) = [\Sigma (Y_1 - \bar{Y}_1) (Y_2 - \bar{Y}_2)] / \Sigma (Y_1 - \bar{Y}_1)^2$$

All available observations contribute to the index, the precision of which will increase with additional data. The filling in of missing cells, however, will not affect the slopes or parallelism of line segments already present.

Our concordance index ( $\beta$ ) takes a value of unity in the case of perfect concordance throughout an array and a value of zero when there is no evidence of any relation between slopes in the  $2 \times 2$  comparisons. In principle, it is possible for  $\beta$  to be less than zero (indicating negative concordance, or discordance) and to test the significance of such an outcome (see below). The index cannot reach negative unity, however, because it is impossible for all

**Figure 9**  
Schematic diagram illustrating the computation of  $\beta$ , an index of concordance for data sets with missing values. (a) Changes between pairs of observations in a  $2 \times 2$  array are measured as slopes. Change along the horizontal axis (representing the contrast of two years) is arbitrarily assigned a value of unity; therefore, each of the slopes,  $Y_1$  and  $Y_2$ , is simply equal to the difference between two paired observations. (b) Paired values,  $Y_1(i)$  and  $Y_2(i)$ , are plotted in a coordinate system. The slope of the resulting scattergram is  $\beta$ , an index of concordance for the parent array



slopes of line segments in an array to be at right angles to all others simultaneously.

Consider an array with several colonies arranged in a vertical list and observations of a species' productivity in several years arranged horizontally. We desire to know whether this species' productivity varies concordantly among colonies across years. Because of asymmetry in the regression used to estimate  $\beta$  (the slopes of  $Y_1$  regressed on  $Y_2$  and of  $Y_2$  regressed on  $Y_1$  are different), the value of  $\beta$  varies with the particular sequence in which colonies are placed in the vertical list. This sequence is arbitrary, however, and must not be permitted to influence the value of  $\beta$ . This problem is addressed by randomizing the row sequence a large number of times and computing a new  $\beta$  at each iteration. The mean of those values is a measure of concordance along the horizontal dimension, irrespective of the ordering of colonies in the vertical list. References to any observed  $\beta$  hereafter pertain to a mean value thus calculated.

The significance test for an observed  $\beta$  is based on further randomizations of the data. In addition to randomizing the row sequence of an array, one allows the order of values within rows to vary and computes  $\beta$  for

each of a large number of such randomizations. This yields a distribution of  $\beta$  based on the null hypothesis of no concordance. The mean of this randomized  $\beta$  should approximate zero. The only constraint in performing these randomizations is that values within rows must remain linked. If values were randomized across colonies, the analysis of concordance would be confounded by the likelihood of differences among colonies in their mean productivities. Thus, the row sequence is randomized, as are the positions of values within rows, but observations cannot move independently among rows. Within rows, of course, values are swapped randomly among filled cell positions (i.e., empty cells remain empty). The significance of the observed  $\beta$  is determined by computing the percentage of values in the randomized distribution that are more extreme than the observed outcome. This analysis, then, essentially answers the question, "Is there anything special (significantly improbable) about the particular sequences of low and high productivities observed, or could the given series have arisen purely by chance?"

This general approach can be used to perform contrasts and significance tests of at least three kinds:

- (1) *Significance of an observed  $\beta$ .* As above, the observed  $\beta$  is compared with a null distribution generated by randomizing both the row sequence and the order of values within rows of the original array. The decision whether to use a one-tailed or two-tailed test of significance depends on the existence of an a priori hypothesis about concordance. If positive concordance is a reasonable prediction, then a one-tailed test is appropriate.
- (2) *Significance of the difference between two  $\beta$ 's.* Given two arrays of comparable data, it may be of interest to know whether concordance in one array is greater than concordance in the other. The observed difference is simply the difference between the two observed  $\beta$ 's. This value is compared with a null distribution of the difference, which is generated by repeatedly and randomly selecting a value from the randomized distribution of  $\beta$  for the first array, subtracting a randomly selected value from the randomized distribution of  $\beta$  for the second array, and plotting the distribution of these differences. An observed difference between  $\beta$ 's that is greater than 5% of the possible differences generated randomly is significant at the 0.05 level. A two-tailed test is appropriate in the absence of any a priori prediction about the relative levels of concordance in the two arrays.
- (3) *Tests for group cohesion.* In many situations, a subset of categories along one dimension of an array constitutes a hypothetically cohesive group. For example, if six of 20 colonies studied share common oceanographic features, one may wish to test whether recognition of those six as a distinct group is warranted. The test is performed by randomly selecting groups of six colonies from

the list of 20 and computing the observed  $\beta$  for each artificial group. The distribution of those values is the randomized one under the null hypothesis of no group effect. (As a matter of computational efficiency, it is unnecessary to randomize repeatedly the row sequences of the artificial groups if their initial row sequences are random — the replication in choosing a large number of possible groups suffices to produce the appropriate distribution.) The observed concordance in the proposed group of six colonies is compared with this randomized distribution of  $\beta$ 's to see if it is sufficiently deviant. Because this test would normally involve an a priori hypothesis, a one-tailed test is appropriate.

## 5. Application to Pacific kittiwakes

In Alaska, the productivity of Black-legged Kittiwakes is better documented than that of any other seabird species. Hatch et al. (1993) assembled data available through the 1989 breeding season. The resulting array (Table 1) provides a suitable data set for application of the methods described above. Twenty-four colonies were studied over 14 years, but 190 of 336 potential observations are missing. Only one colony (St. George Island) was studied in all 14 years. Two colonies studied in one year only (Chiswell Islands and Cape Stoletiya) make no contribution to the analysis of concordance. Data are grouped according to colony location: Gulf of Alaska (68 observations) and the Bering and Chukchi seas (78 observations). Each of the following examples addresses a question about concordance of kittiwake productivity among colonies across years (as in Fig. 8a).

The analysis for the whole array is illustrated in Figure 10. The array contains 146 filled cells and 1662  $2 \times 2$  subarrays (of a possible 25 116 subarrays if the parent array were completely filled). The observed  $\beta$ , computed as the mean index after 1000 randomizations of the row (colony) sequence in Table 1, is 0.302. This value is highly significant ( $P < 0.001$ ) when compared with the null distribution of  $\beta$ , also based on 1000 randomizations (of observations within colonies). Thus, there is strong evidence of concordant annual variation in the productivity of kittiwake colonies throughout the northeastern Pacific.

The analysis of colonies in the Gulf of Alaska (a  $14 \times 14$  parent array) has 233 of a possible 8281 subarrays available, whereas data from the Bering and Chukchi seas offer 563 subarrays (of 4095 possible for that area). Observed  $\beta$ 's are 0.573 in the Gulf and 0.438 in the Bering and Chukchi seas. Both values are higher than the overall index for Alaskan colonies and highly significant when compared with their null distributions (Figs. 11 and 12). To test whether concordance is higher in the Gulf than in the Bering and Chukchi seas, I tabulated 1000 differences among randomly selected values from the null distributions of  $\beta$  in the two areas (Fig. 13). The observed difference between areas (0.135) is not significant by either a one-tailed test ( $P = 0.162$ ) or a two-tailed test ( $P = 0.324$ ). (Because the null distribution is fairly symmetrical, the two-tailed probability is approximately double the one-tailed probability. The actual critical

**Table 1**  
Productivity of Black-legged Kittiwakes in Alaskan colonies, 1976–1989 (data from Hatch et al. 1993)

Location	Productivity (no. of young/nest)															n (years)
	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	Mean	
<b>Gulf of Alaska</b>																
Middleton I.	—	—	0.14	—	—	≤0.47	0.30	0.03	0.76	0.04	0.05	0	0.21	0.02	0.20	10
Hinchinbrook I.	≤0.03	≤0.51	≤0.04	—	—	—	—	—	0.28	—	—	—	—	—	0.22	4
Wooded Is.	0.33	0.63	—	—	—	—	—	—	—	—	—	—	—	—	0.48	2
Prince Wm. Sound	—	—	—	—	—	—	—	—	0.35	0.25	0.31	0.34	0.33	0.34	0.32	6
Chiswell Is.	—	—	—	—	—	—	—	—	—	—	—	0	—	—	0	1
Kachemak Bay	—	—	—	—	—	—	—	—	0.78	0.22	0.55	0.02	0.61	0.29	0.41	6
Chisik I.	—	—	0.01	0.32	—	—	—	0	—	—	0.25	0	—	—	0.12	5
Barren Is.	—	0.90	0.13	0.13	—	—	—	—	—	0	—	—	—	0	0.23	5
Chiniak Bay	—	1.23	0.77	—	—	—	—	0	0.42	0	0	0	0.26	0.09	0.31	9
Cathedral I.	—	0.74	0.17	—	—	—	—	—	—	—	—	—	—	—	0.46	2
Ugaiushak I.	0.07	0.77	—	—	—	—	—	—	—	—	—	—	—	—	0.42	2
Semidi Is.	0.29	0.62	0	0.36	0.30	1.04	—	0	—	0	0	0	—	0	0.24	11
Shumagin Is.	0.19	—	—	—	—	—	—	—	—	0	0.18	—	—	—	0.12	3
Midun I.	—	—	—	—	—	—	—	—	—	—	0	0.26	—	—	0.13	2
<b>Bering/Chukchi seas</b>																
Round I.	—	—	—	—	—	—	0	0	0	0	0	0.08	0.54	0.08	0.09	8
Cape Peirce	0.16	0	—	—	—	0.16	—	—	0.01	0.01	0	0.02	0.16	0.06	0.06	9
St. George I.	0.62	0.45	0.22	0.40	0.38	0.07	0.01	0.01	0.14	0.12	0.26	0	0.40	0	0.22	14
St. Paul I.	0.52	0.43	0.36	0.54	—	—	—	—	0.06	0.27	0.31	0.24	0.53	0.04	0.33	10
St. Matthew I.	—	—	—	—	—	—	0	0	—	0.19	0.19	—	—	—	0.10	4
St. Lawrence I.	0	—	—	—	—	0.86	—	—	—	—	—	0.09	—	—	0.32	3
Bluff	0.04	0.11	0.82	1.07	≤0.94	≤0.70	—	0.27	0	0	≤0.38	0.65	0.61	0	0.43	13
Cape Thompson	0	0.64	0.50	1.10	1.15	—	—	—	—	—	—	—	0.15	—	0.59	6
Cape Lisburne	0.14	0.61	0.78	1.70	1.53	1.36	—	0.61	0	0.20	0.90	—	—	—	0.78	10
Cape Stoletiya	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0	1
Mean	0.20	0.59	0.33	0.70	0.86	0.67	0.08	0.10	0.26	0.09	0.23	0.12	0.38	0.08	0.30	
n (colonies)	12	13	12	8	5	7	4	9	11	14	15	14	10	12		146

values for significance at 0.05 are –0.292 and 0.315 in this instance.)

Is there an ecological justification for grouping the observations by geographic region (Gulf of Alaska versus Bering and Chukchi seas)? The tests for group cohesion are depicted in Figures 14 and 15. Relative to the expected concordance within any randomly chosen group of 14 Alaskan colonies, the observed concordance in the Gulf (0.573) is significant ( $P = 0.016$ ; one-tailed probability). In the Bering and Chukchi seas, however, the observed concordance (0.438) is not significant when compared with the distribution of values for randomly chosen groups of 10 colonies ( $P = 0.174$ ; one-tailed probability). These results lend support to the general conclusion suggested above (Fig. 5) that factors affecting the productivity of kittiwake colonies in the Gulf of Alaska are partially decoupled from those at work in waters to the north.

## 6. Discussion

In designing or analyzing the results of ecological monitoring studies, there is no substitute for thorough sampling effort or complete data sets. A well-designed sampling scheme with no data gaps brings more information to bear on any given question about concordance, and it allows the use of well-established methods of statistical analysis. In conducting field studies, however, data gaps are all but inevitable. The techniques described here are intended to make the best of this common situation. An index of concordance based on partitioning the data into  $2 \times 2$  arrays makes maximal use of the information available, and the associated

significance tests address several questions that often arise in comparative studies.

Throughout this paper, the focus has been on seabird productivity, which provides many familiar examples and problems in data analysis. However, numerical techniques could easily be applied to other parameters, such as population size, phenology, or survival, and obviously they are not limited in application to marine birds. The procedures offer a general approach to ecological hypothesis testing wherever questions about concordance are involved. They have practical application in the process of choosing and evaluating species and study sites as environmental indicators. In the realm of seabird biology and conservation, the need for such quantitative tools becomes ever greater as we accumulate data on species, sites, and years in different ocean systems and as seabirds gain acceptance as indicators of the marine environment.

## Acknowledgements

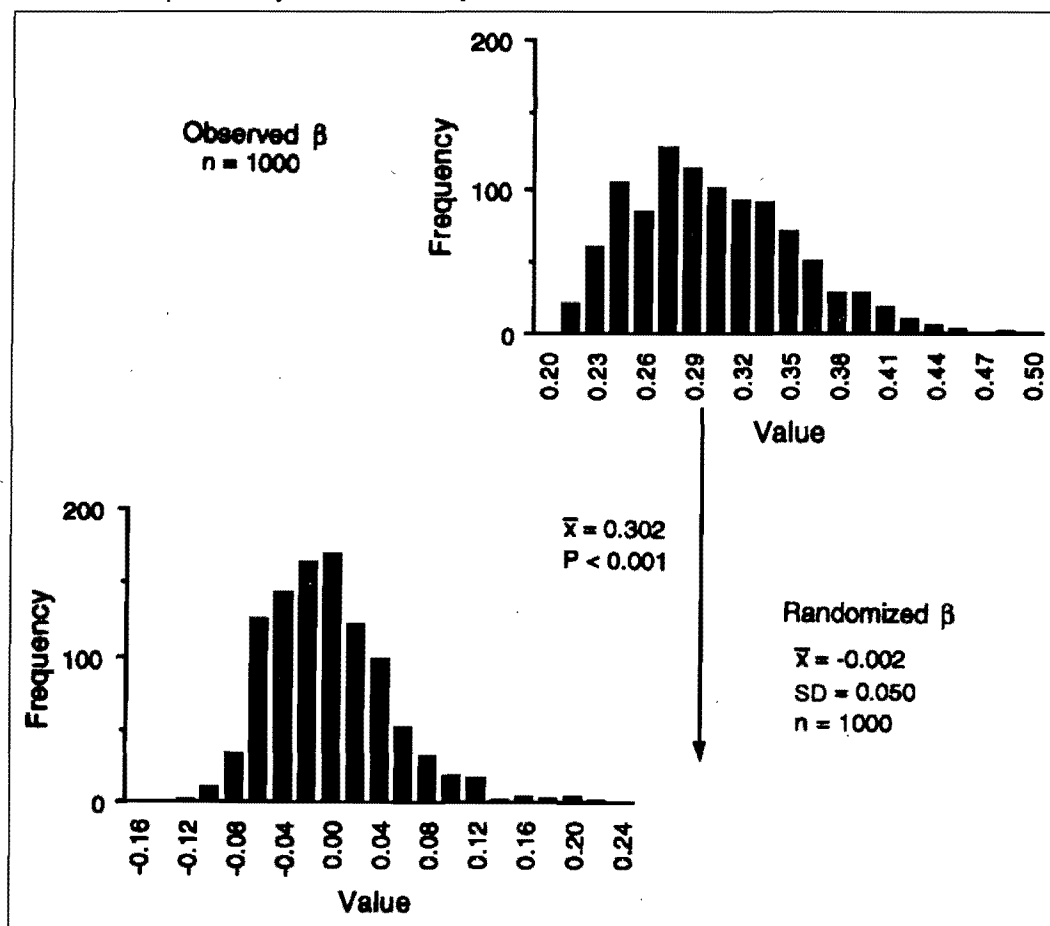
Information presented in Table 1 reflects the collective effort of many people, to all of whom I am grateful for their contributions. I thank G.V. Byrd, D.C. Duffy, D.B. Irons, R.A. Myers, J.F. Piatt, M.S. Udevitz, and two anonymous reviewers for comments on the manuscript.

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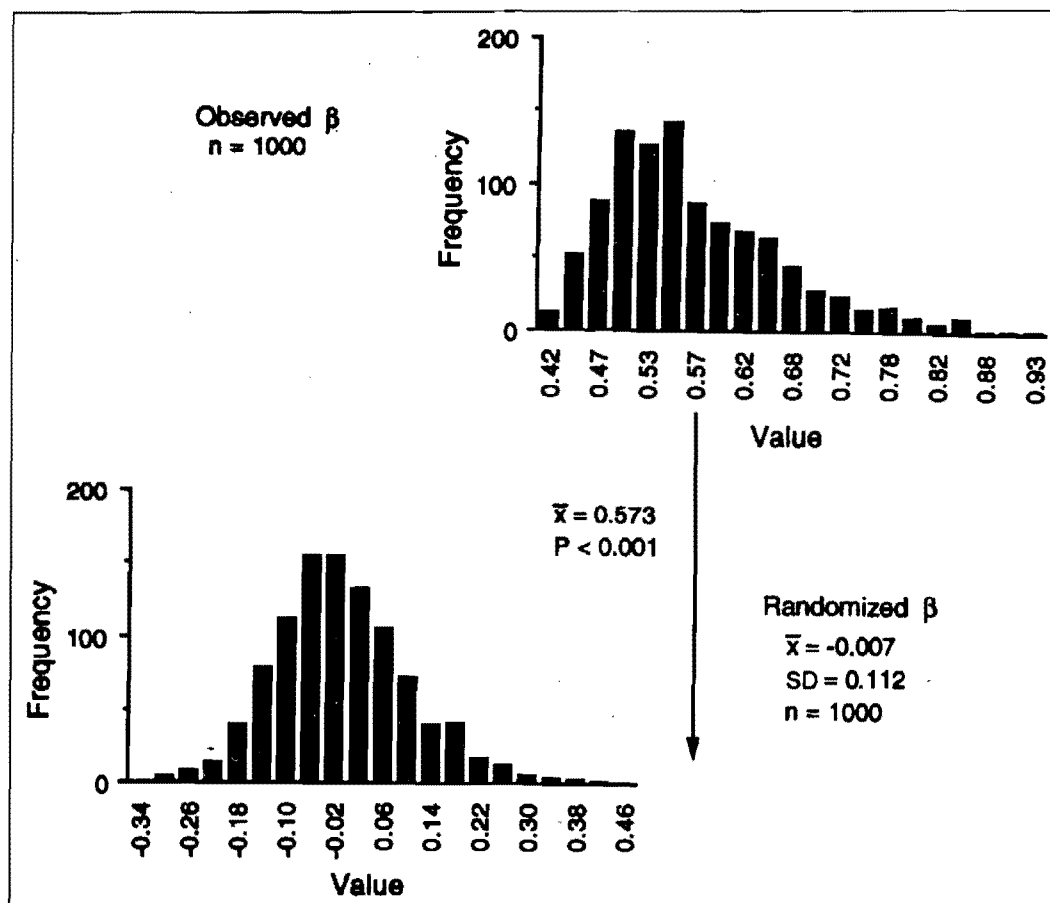
**Figure 10**

Index of concordance and test of significance for Black-legged Kittiwake productivity in 24 colonies over 14 years (data from Table 1). Concordance is computed as the mean value for 1000 arrays with randomized row (colony) sequences. Significance is indicated by the position of the observed  $\beta$  in the distribution of  $\beta$  for a fully randomized array



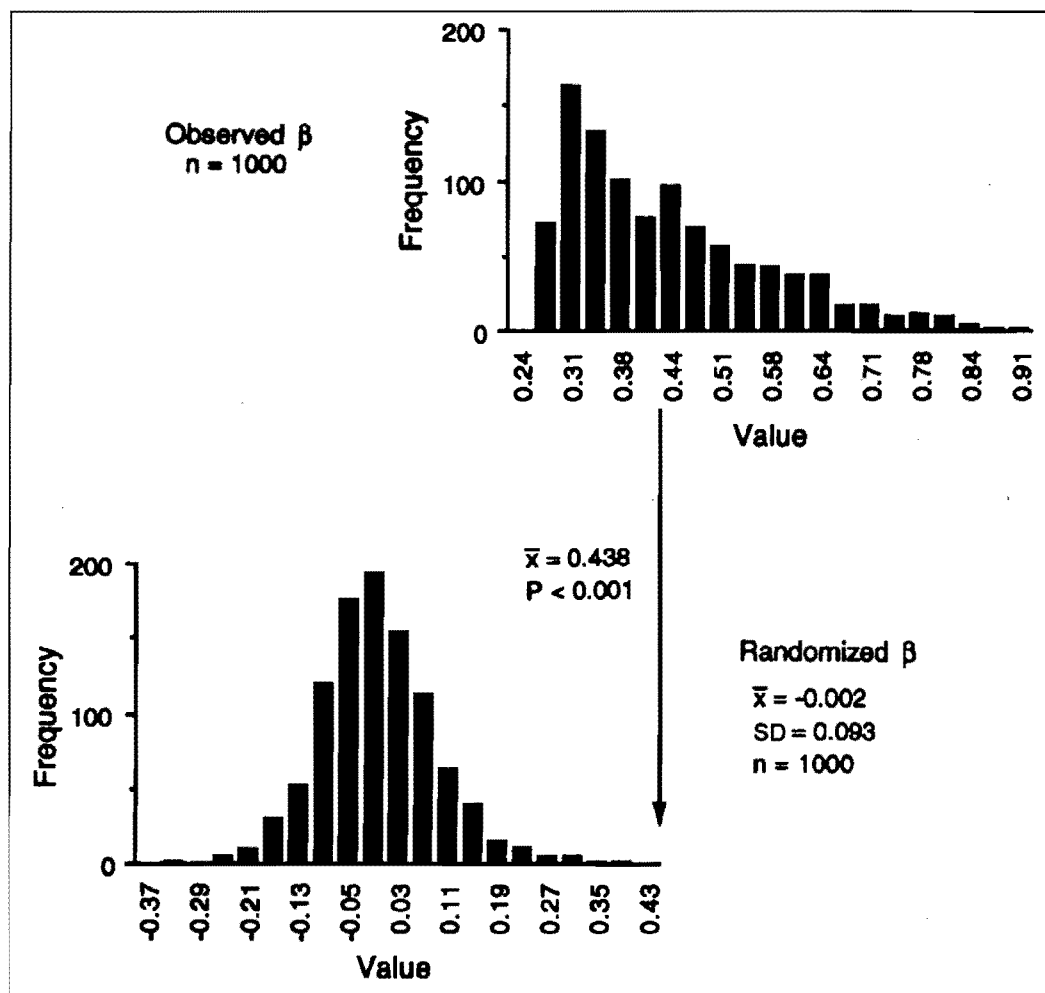
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**Figure 11**  
Index of concordance and test of significance in 14 colonies of Black-legged Kittiwakes in the Gulf of Alaska over 14 years (data from Table 1). See Figure 10 and text for explanation



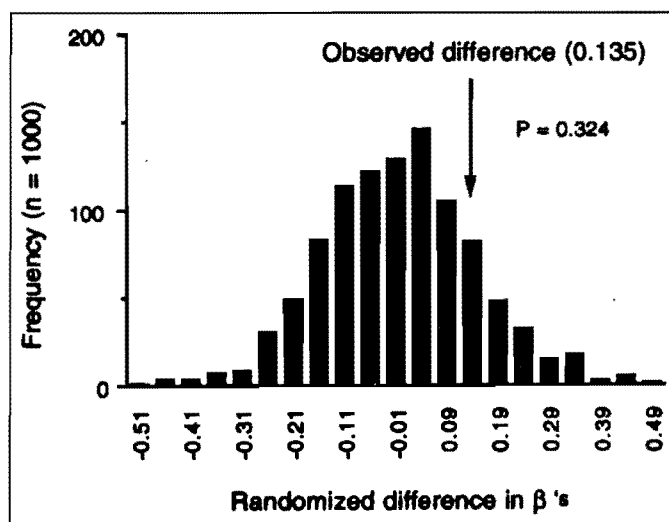
**Figure 12**

Index of concordance and test of significance in 10 colonies of Black-legged Kittiwakes in the Bering and Chukchi seas over 14 years (data from Table 1). See Figure 10 and text for explanation



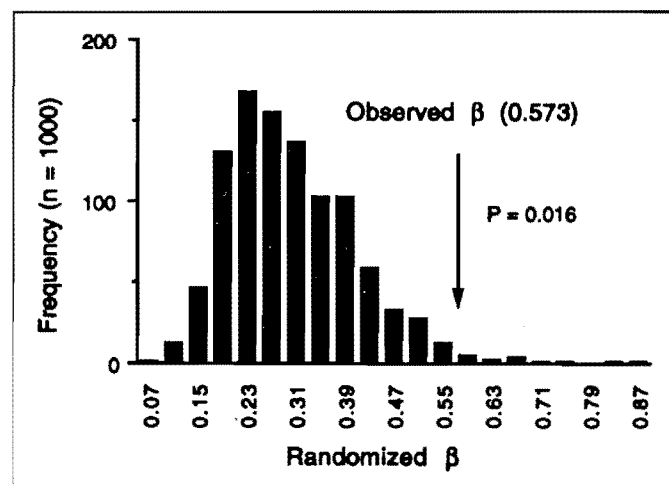
**Figure 13**

Observed difference between  $\beta$ 's (kittiwake productivity in the Gulf of Alaska and Bering/Chukchi seas) compared with the randomized distribution of the difference

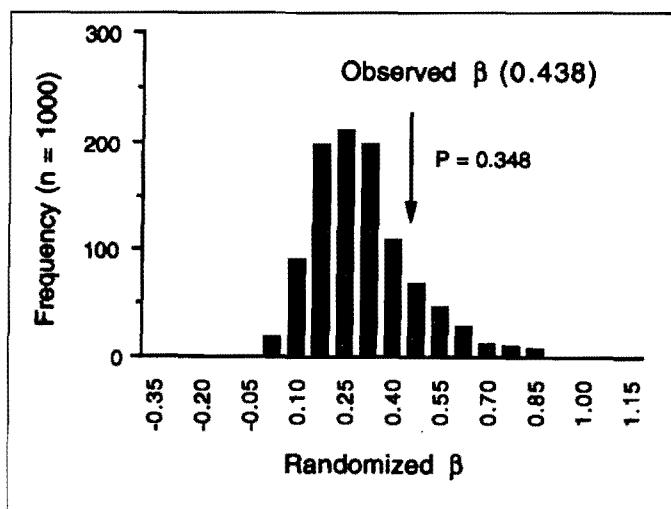


**Figure 14**

Observed  $\beta$  for kittiwake productivity at 14 colonies in the Gulf of Alaska compared with the distribution of  $\beta$ 's for randomly chosen groups of 14 Alaskan colonies



**Figure 15**  
Observed  $\beta$  for kittiwake productivity at 10 colonies in the Bering and Chukchi seas compared with the distribution of  $\beta$ 's for randomly chosen groups of 10 Alaskan colonies





# Energy expenditure of breeding Common Murres

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## Abstract

The doubly labelled water method was used to measure carbon dioxide ( $\text{CO}_2$ ) production and food consumption in Common Murres *Uria aalge* (mean body mass  $1025 \pm 53$  g) throughout the chick-rearing period (three- to 20-day-old chicks) on Hornøya in northern Norway. The field metabolic rate (FMR) of foraging birds averaged  $3.34 \text{ mL CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ , or a daily energy expenditure of  $2200 \text{ kJ} \cdot \text{d}^{-1}$ . This is 3.8 times the resting metabolic rate (RMR), measured for lying birds in the laboratory to be  $0.88 \text{ mL CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ , or  $580 \text{ kJ} \cdot \text{d}^{-1}$ . FMRs of breeding Common Murres varied widely among individuals and among days (range  $959\text{--}3954 \text{ kJ} \cdot \text{d}^{-1}$ ). This is equivalent to a variation in the FMR/RMR ratio from 1.7 to 6.8, which suggests that breeding Common Murres have a flexible energy budget and that they can adjust their foraging behaviour in response to changes in food abundance. There was a significant positive correlation ( $P < 0.005$ ) between FMR and the time at sea. The high and variable FMR is probably associated with a high cost of flying and diving in Common Murres.

The mean daily change in body mass of each bird studied was  $38 \pm 21$  g. Assuming that body fat is the main energy resource (minimum 17 g and maximum 59 g) and based on a minimum FMR of  $959 \text{ kJ} \cdot \text{d}^{-1}$ , breeding Common Murres may rely on these resources for an average of 1.5 days (minimum 16 hours and maximum 2.4 days) without feeding. The average rate of food consumption by adult Common Murres, calculated on the basis of the chemical composition and digestibility of capelin *Mallotus villosus* and sand lance (*Ammodytes* sp.), was 440 g fresh matter per bird every day. This food consumption is equal to 43% of body mass per day. The water influx rate was highly positively correlated with changes in body mass ( $P < 0.0001$ ), indicating that Common Murres digest as much food as possible at sea before returning to the colony. The population of 1400 pairs of Common Murres on Hornøya is estimated to consume a total of 27 580 kg of prey during 20 days of chick rearing.

## Résumé

Nous avons utilisé la méthode de l'eau à deux isotopes pour mesurer la production de dioxyde de

carbone ( $\text{CO}_2$ ) et la consommation d'aliments chez la Marmette de Troil *Uria aalge* (masse corporelle moyenne de  $1025 \pm 53$  g) durant toute la période d'élevage (poussins âgés de trois à vingt jours) sur la Hornøya, en Norvège septentrionale. Le taux métabolique en activité (TMA) chez les individus en quête de nourriture correspondait en moyenne à  $\text{CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ , soit une dépense énergétique quotidienne de  $2\,200 \text{ kJ} \cdot \text{d}^{-1}$ . Ce taux représente 3,8 fois le taux métabolique au repos (TMR) qui, mesuré en laboratoire chez des oiseaux au repos, équivalait à  $0,88 \text{ mL CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ , ou  $580 \text{ kJ} \cdot \text{d}^{-1}$ . Le TMA des individus reproducteurs chez la Marmette de Troil variait grandement selon l'oiseau et selon le jour (variation de  $959$  à  $3954 \text{ kJ} \cdot \text{d}^{-1}$ ). Ces résultats correspondent à une variation fluctuant entre 1,7 et 6,8 dans le rapport TMA/TMR, ce qui laisse supposer que les individus reproducteurs de cette espèce ont un bilan énergétique variable et qu'ils peuvent, lorsqu'ils sont en quête de nourriture, modifier leur comportement en fonction de l'abondance de cette dernière. On a noté une corrélation positive significative ( $P < 0,005$ ) entre le TMA et le temps passé en mer. Le caractère élevé et variable du TMA est probablement lié au coût énergétique important du vol et de la plongée chez la Marmette de Troil.

Chez les oiseaux étudiés, la variation moyenne quotidienne de la masse corporelle était de  $38 \pm 21$  g. En partant de la prémisse que la graisse constitue la principale réserve d'énergie (minimum de 17 g et maximum de 59 g) et en supposant un TMA minimal de  $959 \text{ kJ} \cdot \text{d}^{-1}$ , on peut conclure que les Marmettes de Troil reproductrices pourraient subsister en moyenne 1,5 jour (minimum de 16 heures et maximum de 2,4 jours) sans se nourrir en puisant dans cette réserve. Chez les adultes, le taux moyen de consommation d'aliments, calculé d'après la composition chimique et la digestibilité du capelan *Mallotus villosus* et du lançon (*Ammodytes* sp.), représentait quotidiennement 440 g de matière fraîche par oiseau. Cette consommation équivaut à 43 % de la masse corporelle par jour. Par ailleurs, le taux d'absorption d'eau montrait une corrélation positive marquée avec les variations de la masse corporelle ( $P < 0,0001$ ), ce qui indique que la Marmette de Troil digère le plus de nourriture possible pendant qu'elle est en mer avant de rejoindre sa colonie. On estime à 27 580 kg de proies pour 20 jours d'élevage la consommation totale de nourriture des 1 400 couples de Marmettes de Troil sur la Hornøya.

## 1. Introduction

The seabird breeding populations in the Barents Sea and the northern parts of the Norwegian Sea are among the largest in the world (Anker-Nilssen and Barrett 1991), and Common Murres *Uria aalge* are an important species in the seabird communities in this region. They breed colonially in groups of hundreds to thousands of birds along the coast of northern Norway.

In order to determine the energy flow through seabird populations or communities, it is important to determine the energy requirements of individuals. The resting metabolic rate (RMR) and field metabolic rate (FMR) of seabirds breeding in the north are high compared with those of tropical and temperate species (Roby and Ricklefs 1986; Obst et al. 1987; Gabrielsen et al. 1987, 1988, 1991).

Cairns et al. (1987) hypothesized that breeding Common Murres have flexible time budgets that are adjusted to changes in fish availability. Burger and Piatt (1990) found that breeding Common Murres spent more time at sea in response to poor feeding conditions. This change in feeding behaviour resulted in a constant provisioning and did not affect growth and survival of the chicks. Monaghan et al. (1994), studying the foraging behaviour of breeding Common Murres in two years of radically different levels of food abundance, also found that birds spent more time at sea — five times as much, in fact — in a poor year than in a good year. According to their calculation, the energy expenditure of the breeding birds was twice as high in the poor year as in the good year. Breeding Common Murres seem to have flexible time budgets, but whether they also have flexible energy budgets was one of the main questions addressed in the present study.

Energy demands upon parent birds are thought to be at a maximum during the chick-rearing period (Drent and Daan 1980; Ricklefs 1983). In seabirds, free-living parents use energy at 3–6 times their basal metabolic rate (BMR) or RMR during the breeding period (Birt-Friesen et al. 1989). Based on doubly labelled water (DLW) studies on seabirds, among others, several researchers have hypothesized a daily maximum sustained working level of  $4 \times \text{RMR}$  during the chick-rearing period (Drent and Daan 1980; Ellis 1984). Although some DLW studies support such a hypothesis (Roby and Ricklefs 1986; Gabrielsen et al. 1987, 1991; Mehlum et al. 1993), other studies have shown that some seabirds exceed this level (Birt-Friesen et al. 1989; Cairns et al. 1990; Obst and Nagy 1992). In the present study, this hypothesis was tested by comparing RMR and FMR measured at the same locality during the same breeding period.

FMRs in seabirds are generally presented as an average throughout the chick-rearing period. Only two studies in which the DLW method was used have investigated the relationship between adult FMR and age of chicks (Roby and Ricklefs 1986; Gabrielsen et al. 1991). In both these studies, adult FMR was independent of the chicks' age. One would expect adult energy expenditure to increase with the age of the chick to meet the increasing energetic demands of the growing chick (Coulson and Pearson 1985). Common Murres as well as Thick-billed Murres *Uria lomvia* have a very high wing loading (Greenewalt 1962) and probably use more energy

per unit distance flying than other seabirds (Pennycuik 1987; Croll et al. 1991). One consequence of this high wing loading is that the murres are able to transport only those chick meals that are less than 1.5% of their body mass (Gaston and Nettleship 1981). In this study, FMR was measured at different chick ages to determine if adult murres are able to adjust their energy budgets as a result of the increased energy demands of their chicks.

## 2. Material and methods

### 2.1 Birds

Common Murres breeding on Hornøya in Finnmark (70°22'N, 31°10'E) were studied on 7–13 July 1990, when approximately 1400 pairs (Anker-Nilssen and Barrett 1991) of Common Murres bred on the island. The chicks were between three and 20 days old when we performed our DLW study, with one or both parents ( $n = 11$ ) making foraging trips.

### 2.2 Weather

Local weather conditions were measured at Hornøya Fyr (lighthouse), 300 m from the colony. During the study period, the weather was mild, with no precipitation and little wind. The mean ( $\pm$  SD) air temperature was  $13.1 \pm 2.0^\circ\text{C}$ , and mean wind speed was  $4.1 \pm 1.8 \text{ m}\cdot\text{s}^{-1}$ . The ocean surface temperature was  $9.5 \pm 1.0^\circ\text{C}$ . There was continuous (24 h·d<sup>-1</sup>) daylight.

### 2.3 Resting metabolic rate

RMRs of 11 adult Common Murres were measured in a field laboratory near the colony. RMR measurements were made during both the day and "night" using the apparatus described by Gabrielsen et al. (1988). A metabolic chamber was placed outside in an open-top wooden box (in which the bird could see only the sky). Metabolism was measured at ambient chamber temperatures, which ranged between 10 and 20°C.

We measured air flow ( $3.5\text{--}4.0 \text{ L}\cdot\text{min}^{-1}$ ) with a mass flow meter (Model F-201C-FA, Hi-Tec) connected to a readout (Model 5611-EA, Hi-Tec). Oxygen ( $\text{O}_2$ ) consumption was measured with an Applied Electrochemistry  $\text{O}_2$  analyzer (S-3A), and  $\text{CO}_2$  production was measured with a Leybold-Heraeus (BINOS 1)  $\text{CO}_2$  analyzer. Temperature in the metabolic chamber was measured with thermocouples connected to a Fluke thermometer. Body temperatures were not measured during metabolism trials but were measured separately after each experiment, using a small thermocouple inserted 2–3 cm into the cloaca. Birds were habituated to the metabolic chamber by being introduced into it three times before the first measurements were made 12 hours after their capture in the colony. Each bird was measured two times. At each ambient temperature, recordings were measured for at least three hours. Metabolism was measured under full light conditions while the bird was resting. Oxygen consumption ( $\text{mL O}_2\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ ),  $\text{CO}_2$  production ( $\text{mL CO}_2\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ ), respiratory quotient (RQ), and energy expenditure ( $\text{kJ}\cdot\text{d}^{-1}$ ) were calculated at standard temperature and pressure (STP,  $0^\circ\text{C}$ , 760

mmHg). To calculate energy expenditure from  $O_2$  consumption, a conversion coefficient of  $20.08 \text{ kJ} \cdot \text{L}^{-1} O_2$  was used (Schmidt-Nielsen 1975).

## 2.4 Doubly labelled water

Field metabolic rates (FMRs, as  $CO_2$  production) and water influx rates (WIR) were measured using the DLW method (Lifson and McClintock 1966; Nagy 1980; Nagy and Costa 1980), using the same procedure as described by Gabrielsen et al. (1987), in 11 adult Common Murres caught on the nest. These consisted of three pairs and five individuals. Each bird was placed in a nylon bag and carried to the field laboratory.

Birds were injected with  $2.5\text{--}3.0 \text{ mL } H_2^{18}O$ , containing 97.11 atom % oxygen-18 and 0.4 mCi tritium, into the pectoral muscle. The birds were held in a wooden box for 1.0–1.5 hours while the isotopes mixed thoroughly in body fluids (Degen et al. 1981; Williams and Nagy 1984). Birds were weighed to the nearest 5 g using a Pesola spring balance. Wing, head, and bill lengths were measured to the nearest 1 mm in an attempt to differentiate the sexes in all pairs. Each bird was banded and marked with individual patterns on the breast using felt-tipped pens. Blood samples ( $5 \times 70 \mu\text{L}$ ) were taken from a wing vein. All birds were released in the colony, and they returned to nest sites within 30 minutes. Over the next six days, they were recaptured, weighed, and sampled, some two and three times. The nest sites were not disturbed, but the birds were monitored from a hide continuously for six hours each day (randomly during both the day and "night") and thereafter visited every three hours to check if the birds were present. This check frequency was assumed to give representative samples of activity based on previous studies of murres (Furness and Barrett 1985; Burger and Piatt 1990). Two background samples were taken from control birds at the start and at the end of the experimental period. The background was 0.2023 atom % for oxygen-18 and 35 cpm for tritium. Measurements of FMR by DLW become unreliable when the final level of oxygen-18 approaches background. One sample was excluded, as the final oxygen-18 enrichment was within 5% of background.

Blood samples were stored in flame-sealed, heparinized microhematocrit capillary tubes and vacuum-distilled to obtain pure water. Isotope levels in water were measured by liquid scintillation spectrometry (for tritium) and proton activation analysis (for oxygen-18) (Wood et al. 1975) by K.A. Nagy (University of California, Los Angeles, California, U.S.A.). Rates of  $CO_2$  production were calculated with equation 2 in Nagy (1980), and WIRs from equation 4 in Nagy and Costa (1980). Body water volumes at recapture were calculated as the initial fractional water content multiplied by body mass at recapture. Validation studies in the laboratory have shown that DLW measurements of  $CO_2$  production are accurate to within 7% (Nagy 1989).

## 2.5 Food consumption

Food samples were collected from adult Common Murres feeding their chicks. For the purpose of initial considerations, it was assumed that the food given to the

chicks was the same as what the adults ate themselves. During the study, Common Murres fed chicks primarily on capelin *Mallotus villosus* (53%), sand lance (*Ammodytes* sp.) (39%), and herring *Clupea harengus* (8%) (M. Asheim, pers. commun.). The conversion factors for these diet items should be within 5% of that for capelin, owing to similarities in the conversion factors for protein and fat (Schmidt-Nielsen 1975). FMRs were converted from units of  $CO_2$  production to units of energy (J) by using the factor  $26.1 \text{ J} \cdot \text{mL}^{-1} CO_2$ . This factor was calculated from the chemical composition of capelin (76.2% water, 6.6% fat, 15.2% protein, 1.9% ash) and sand lance (70.7% water, 6.7% fat, 15.0% protein) (Barrett et al. 1987; R.T. Barrett, unpubl. data). Energy equivalents for fat and protein were from Schmidt-Nielsen (1975). In this calculation, it was assumed that the proportions of dietary fat and protein assimilated were the same as their proportions in the diet and that Common Murres ate only capelin and sand lance during our study. The amount of food an adult Common Murre would have to consume to satisfy its daily energy requirements (as measured with DLW) was calculated from the energy content of food samples and the energy assimilation efficiency for capelin and sand lance. Capelin and sand lance contain  $26.25 \text{ kJ} \cdot \text{g}^{-1}$  and  $21.35 \text{ kJ} \cdot \text{g}^{-1}$  dry matter, respectively. Based on feeding experiments in which kittiwakes and Thick-billed Murres ate capelin with a fat content of 7%, an assimilation efficiency of 80% was used (Brekke and Gabrielsen 1994). Thus, with a water content of 76% for capelin and 71% for sand lance, the food contains  $6.25 \text{ kJ} \cdot \text{g}^{-1}$  wet mass, or  $5.0 \text{ kJ}$  metabolizable energy per gram of fresh matter.

## 2.6 Statistics

Two-tailed t-tests were used to compare means. Results are reported as means  $\pm$  SD unless noted otherwise. Analysis of covariance (ANCOVA) (SAS Institute, Inc. 1988) was used to simultaneously relate FMR and WIR to the age of chick, time at sea, body mass change, and individual variation. In order to test the effect of individuals, I first excluded all data from individuals from which only one measurement was collected (1, 5, and 6). When no such effect of individuals was found, all data were included in further calculations. Body mass change ( $\% \cdot \text{d}^{-1}$ ) was arcsine-transformed for analysis.

## 3. Results

### 3.1 Resting metabolic rate

The mean temperature in the metabolic chamber during metabolic trials was  $16.1 \pm 2.7^\circ\text{C}$ . Based on measurements of six species of seabirds in the high Arctic (Gabrielsen et al. 1988), this should be well within the murres' thermoneutral zone. The body mass of each individual was used when calculating the mass-specific metabolic rate. The mean body mass during the metabolic measurements was  $913 \pm 53 \text{ g}$ . Standing birds ( $1.31 \pm 0.04 \text{ mL } O_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ;  $n = 9$ ) had a significantly higher mass-specific RMR value than lying birds ( $1.20 \pm 0.03 \text{ mL } O_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ;  $t = 7.22$ ,  $n = 12$ ;  $P < 0.05$ ), or a 9% difference in RMR level between standing and lying birds. The  $CO_2$

production of a resting, lying bird was  $0.88 \text{ mL CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ , or  $580 \text{ kJ} \cdot \text{d}^{-1}$ . The mean RQ, within the thermoneutral zone, was  $0.73 \pm 0.01$ . The mean body temperature of resting, lying birds was  $39.7 \pm 0.05^\circ\text{C}$  ( $n = 7$ ).

### 3.2 Body mass

Owing to large variations in body size in Common Murres, it was not possible to separate males from females based on measurements of wing, head, and bill lengths (M. Asheim and R.T. Barrett, unpubl. data). The mean body mass of birds included in the DLW experiment was  $1025 \pm 53 \text{ g}$  ( $n = 22$  measurements). This value was used in subsequent calculations. Throughout the experimental period (1–3 days for each bird studied), all Common Murres maintained their body mass (the arithmetic average of mass changes) to within  $0.25 \pm 2.99\% \cdot \text{d}^{-1}$  (Table 1). Body mass change for each bird averaged  $38 \pm 21 \text{ g} \cdot \text{d}^{-1}$  (11 birds).

### 3.3 Field metabolic rate

Of 11 birds used in the DLW experiment, one FMR sample was obtained from three birds, two samples from five birds, and three from three birds. As there was no effect of individuals, all data were included in further calculations. FMRs of free-ranging birds averaged  $3.34 \text{ mL CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ , or  $2200 \text{ kJ} \cdot \text{d}^{-1}$  (Table 1). This gives an average FMR/RMR ratio (based on whole body rates of metabolism) of 3.8. There was much variation in body mass, FMR, and WIR among individuals and among days (Table 1). When FMR ( $\text{mL CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ) was related to the age of the chick and time at sea, there was a significant positive correlation between FMR and time at sea ( $r^2 = 0.36$ ;  $P < 0.005$ ) (Fig. 1):

$$\text{FMR} = 1.65 + 0.14 T \quad (1)$$

where FMR =  $\text{mL CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$  and  $T$  = time at sea in  $\text{h} \cdot \text{d}^{-1}$ . The average time at sea was  $12.95 \pm 3.43 \text{ h} \cdot \text{d}^{-1}$ . FMR of adults was weakly positively correlated with age of the chick ( $r^2 = 0.44$ ;  $P = 0.12$ ). When age of the chick was used as a covariate in a multiple regression model, the explained variance increased from  $r^2 = 0.36$  to  $r^2 = 0.44$ . This may indicate that adults with older chicks spend slightly more time at sea than adults with small chicks.

### 3.4 Water influx

WIR in Common Murres was  $352 \pm 138 \text{ mL} \cdot \text{d}^{-1}$  ( $n = 22$  measurements) (Table 1). When WIR ( $\text{mL} \cdot \text{d}^{-1}$ ) was related to body mass change, age of the chick, and time at sea, there was a significant positive correlation between WIR and body mass change ( $r^2 = 0.59$ ;  $P < 0.0001$ ) (Fig. 2):

$$\text{WIR} = 342.7 + 61.5 \text{ BMC} \quad (2)$$

where WIR = water influx rate ( $\text{mL} \cdot \text{d}^{-1}$ ) and BMC = body mass change ( $\% \cdot \text{d}^{-1}$ ). When the time at sea and the age of the chick were used as covariates in a multiple regression model, the explained variance decreased from  $r^2 = 0.59$  to

$r^2 = 0.48$ . This indicates no significant correlation between WIR and age of chick. This is probably due to the large daily variation in WIR. When the mean WIR value was used for each bird, water (food) consumption tended to increase ( $P < 0.067$ ) as the chick grew. However, more samples are needed to show such a relationship.

Body water content during the experimental period averaged  $68.5 \pm 3.1\%$  of body mass ( $n = 9$ ).

### 3.5 Food consumption

FMR in free-ranging Common Murres averaged  $2198 \pm 576 \text{ kJ} \cdot \text{d}^{-1}$  (Table 1). At a metabolizable energy yield of  $5.0 \text{ kJ} \cdot \text{g}^{-1}$  fresh food, Common Murres consumed  $440 \text{ g}$  of fresh food, or approximately 43% of their body mass daily. This estimate of feeding rate was checked by calculating the associated WIR and comparing it with the actual influx measured with tritiated water. A mass of  $440 \text{ g}$  of fresh fish —  $220 \text{ g}$  of capelin (76.2% water) and  $220 \text{ g}$  of sand lance (70.7% water) — contains  $323.2 \text{ mL}$  of water. Metabolic water production from oxidation of assimilated proteins and lipids would provide an additional  $0.122 \text{ mL}$  water per gram fresh food (conversion factors from Schmidt-Nielsen 1975), or  $53.7 \text{ mL}$  water. This yields a total of  $376.9 \text{ mL}$  water for consumption of  $440 \text{ g}$  of food, which is about 7% higher than the measured water influx of  $351.5 \text{ mL}$  per bird (Table 1). This comparison from energy expenditure is reasonable and indicates that Common Murres drank little or no seawater while foraging.

## 4. Discussion

### 4.1 Resting metabolic rate

The RMR value in the present study was obtained while birds were at rest (both standing and lying), in a postabsorptive state, and within the thermoneutral zone. I do not claim to have measured true BMR, but these metabolic measurements are comparable to values termed BMR in the literature, as they were made in a similar manner.

In the present study, the mass-specific RMR of lying Common Murres was 9% lower than that of standing birds. The mass-specific RMR value was equivalent to RMR values for Common Murres measured at St. Paul Island in Alaska (Gabrielsen et al. 1996) (Table 2). Johnson and West (1975), in a metabolic study of captive Common and Thick-billed murres at Fairbanks, Alaska, obtained RMR values that were 7% and 5% higher, respectively, than those of lying Common Murres measured at Hornøya and at St. Paul Island (Table 2). The mass-specific RMR value of Thick-billed Murres measured at St. Paul Island, Alaska, was similar to that measured on Svalbard (Table 2). These mass-specific RMRs of murres in Alaska, Svalbard, and northern Norway are considerably higher (56–61%) than those reported by Cairns et al. (1990) (Table 2) for Common Murres in Newfoundland. Cairns et al. (1990) used a closed respirometry method, described by Ricklefs et al. (1984). The same system was also used on Northern Gannets *Sula bassana* in Newfoundland (Birt-Friesen et al. 1989); the BMR value obtained in this study was 85%

**Table 1**

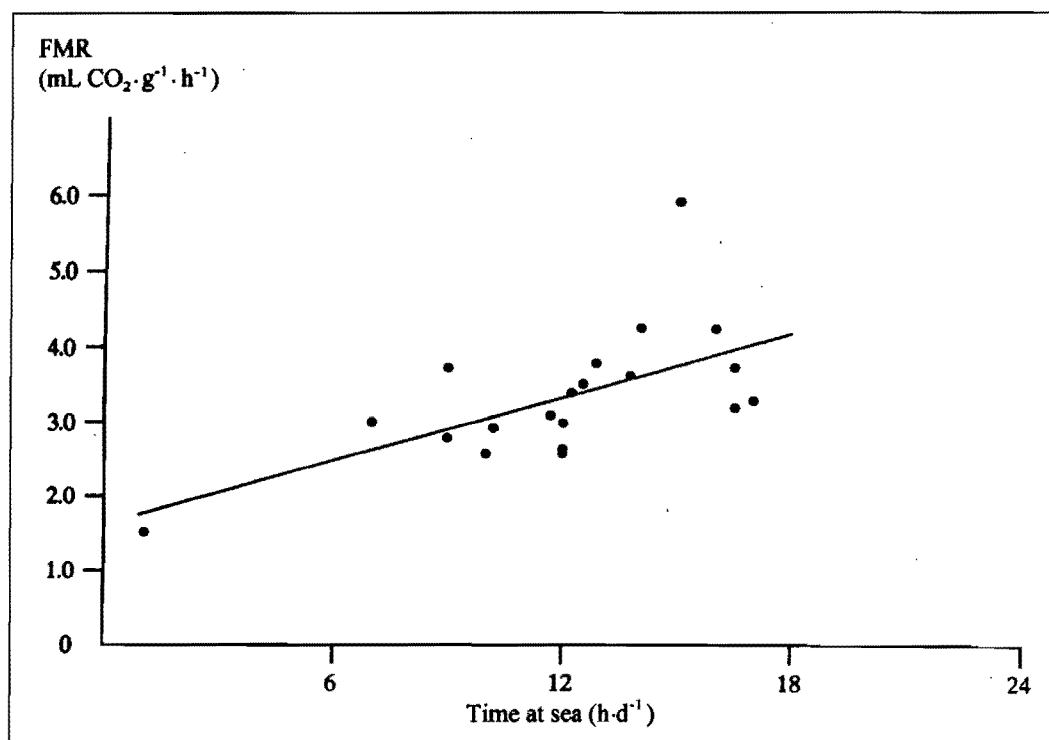
Field metabolic rate, water influx rate, body mass (mean, change, and arcsine-transformed), and time at sea of adult Common Murres on Hornøya, 7–13 July 1990

Bird no. <sup>a</sup>	Age of chick (d)	Body mass			Field metabolic rate		Water influx rate (mL·d <sup>-1</sup> )	Time at sea (h·d <sup>-1</sup> )	Measurement period (d)
		Mean (g)	Change (%·d <sup>-1</sup> )	Arcsine trans.	mL CO <sub>2</sub> ·g <sup>-1</sup> ·h <sup>-1</sup>	kJ·d <sup>-1</sup>			
C-1	18	1026.0	5.90	3.38	3.00	1975	413	12.00	1.03
C-2	4	945.5	-1.95	-1.12	3.11	1890	249	11.46	1.03
C-2	5	939.5	0.67	0.38	3.51	2122	460	12.29	1.12
C-3A	5	1089.5	1.00	0.58	3.23	2260	308	17.20	1.01
C-3	7	1085.0	-1.87	-1.07	2.64	1844	273	12.00	0.99
C-4B	13	1010.0	-0.58	-0.33	2.57	1666	240	9.50	1.02
C-4	14	1007.5	0.10	0.05	3.64	2357	469	13.41	1.00
C-5	3	977.5	-2.53	-1.44	1.53	959	150	1.00	1.66
C-6	15	937.0	1.08	0.61	3.19	1923	340	16.34	1.97
C-7C	9	1074.5	0.95	0.54	3.76	2597	333	16.34	1.08
C-7	10	1056.5	-4.45	-2.55	3.73	2534	201	9.07	1.00
C-7	11	1044.0	2.11	1.20	2.92	1959	360	10.19	1.00
C-8B	16	1016.5	4.60	2.64	4.22	2757	588	15.50	1.13
C-8	17	1035.5	-1.36	-0.77	5.94	3954	351	14.53	1.06
C-8	18	1015.5	-2.71	-1.55	—	—	300	13.55	0.91
C-9	6	1064.0	0.93	0.53	2.80	1911	271	9.07	1.02
C-9	7	1076.5	0.67	0.38	3.77	2611	368	12.43	2.08
C-10A	8	1081.5	-6.55	-3.76	2.65	1839	183	12.00	1.03
C-10	9	1059.0	2.53	1.44	3.39	2306	349	12.14	1.05
C-10	10	1087.0	2.45	1.40	3.12	2180	530	12.14	1.09
C-11C	9	945.5	-0.51	-0.29	3.06	1861	273	6.58	1.03
C-11	10	966.0	5.09	2.91	4.26	2642	729	14.30	0.94
Mean		1024.5	0.25	0.14	3.34	2198	352	12.57	1.15
SD		52.6	2.99	1.71	0.86	576	138	3.26	0.32

<sup>a</sup> Pairs marked with a common letter.

**Figure 1**

The relationship between field metabolic rate (FMR) and time (T) at sea (h·d<sup>-1</sup>) in breeding Common Murres (FMR = 1.65 + 0.14 T, r<sup>2</sup> = 0.36, P < 0.005)



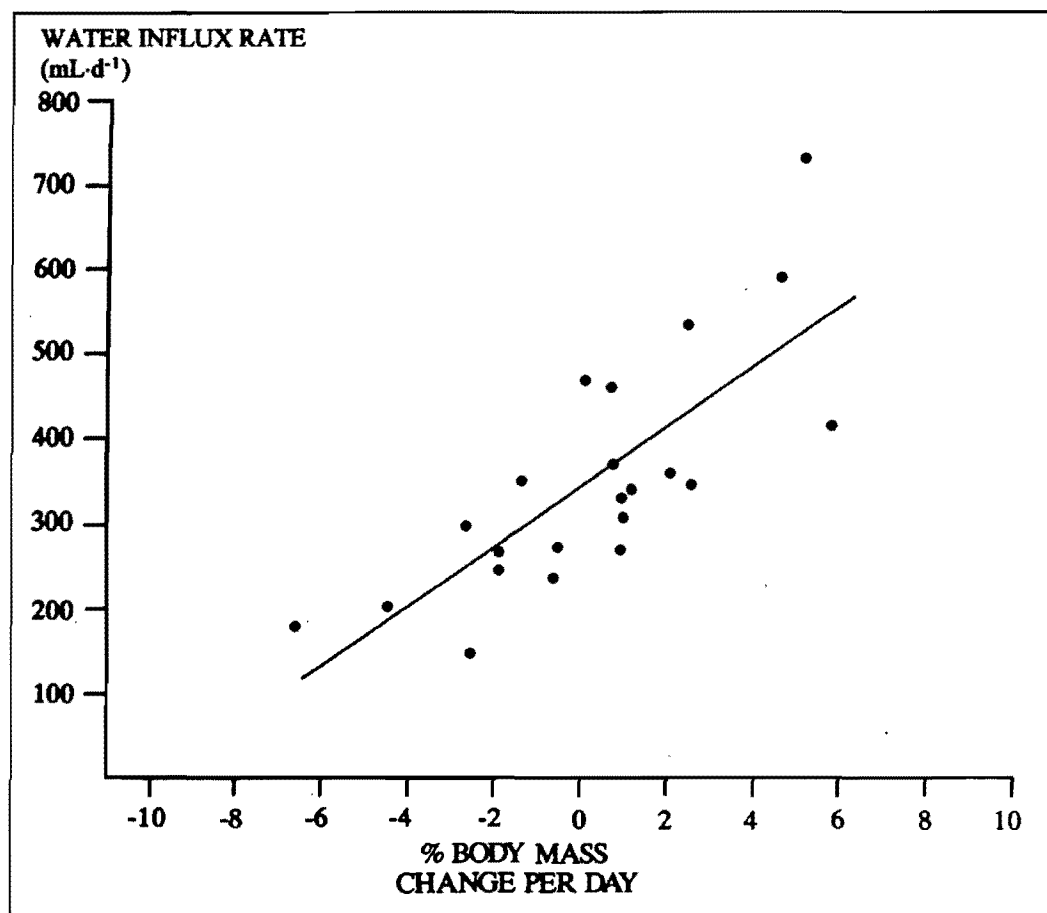
lower than the BMR value obtained on the same species in Scotland using an open respirometry system (D.M. Bryant and R.W. Furness, unpubl. data). To test the validity of these BMR or RMR values, it will be necessary to carry out a controlled comparison of the open system used in

this study with the closed respirometry technique used by Cairns et al. (1990) and Birt-Friesen et al. (1989).

The mass-specific RMR value in Common Murres exceeds allometric predictions made for nonpasserines by 143–189% (Lasiewski and Dawson 1967; Aschoff and

**Figure 2**

The relationship between water influx rate (WIR) and body mass change (BMC) (%·d<sup>-1</sup>, based on arcsine-transformed data) in breeding Common Murres (WIR = 342.7 + 61.5 BMC,  $r^2 = 0.59$ ,  $P < 0.0001$ )

**Table 2**

Resting metabolic rate (RMR) of Common Murres (CM) and Thick-billed Murres (TBM) measured at different localities

Species	Body mass (g, $\pm$ SD)	No. of birds	RMR (mL O <sub>2</sub> ·g <sup>-1</sup> ·h <sup>-1</sup> , $\pm$ SD)	Location	Source
CM	956 $\pm$ 12	5	1.28	Fairbanks, Alaska, U.S.A. <sup>a</sup>	Johnson and West 1975
CM	803 $\pm$ 52	10	1.19 $\pm$ 0.05	St. Paul Island, Alaska, U.S.A.	Gabrielsen et al. 1996
CM	972 $\pm$ 24	3	0.77 $\pm$ 0.15	Great Island, Newfoundland, Canada	Cairns et al. 1990
CM	913 $\pm$ 53	11	1.20 $\pm$ 0.03	Hornøya Island, Norway	This study
TBM	989 $\pm$ 10	5	1.23	Fairbanks, Alaska, U.S.A. <sup>a</sup>	Johnson and West 1975
TBM	1090 $\pm$ 59	11	1.17 $\pm$ 0.05	St. Paul Island, Alaska, U.S.A.	Gabrielsen et al. 1996
TBM	819 $\pm$ 73	11	1.11 $\pm$ 0.12	Ny-Ålesund (Svalbard), Norway	Gabrielsen et al. 1988

<sup>a</sup> Birds captured in the colony at St. Lawrence Island, Alaska.

Pohl 1970), birds in general (Bennett and Harvey 1987), and seabirds (Ellis 1984; Gabrielsen et al. 1996). However, the RMR value is very similar to that predicted from the latitude-corrected equation of Ellis (1984). This equation is based on a percentage increment (% BMR = 2.02 lat. + 52.3) relative to predictions made from the Lasiewski and Dawson (1967) equation.

The RMR values obtained in this study and earlier BMR or RMR studies of northern seabird species (Scholander et al. 1950; Johnson and West 1975; Gabrielsen et al. 1987, 1988, 1991, 1996; Gabrielsen and Mehlum 1989) confirm findings that seabirds breeding at high latitude have a higher RMR (or BMR) than similar species at low latitudes. The high RMR is consistent with Weathers' (1979) observations that the RMR (or BMR) of

high-latitude bird species generally exceeds those of warm-climate species.

The high RMR value may also indicate a difference in the adaptation to cold by different seabird species. Whereas Common Murres measured both on Hornøya (70°N) and at St. Paul Island, Alaska (57°N) (Gabrielsen et al. 1996), show no latitudinal trend in mass-specific RMR, there is a strong latitudinal trend in RMR in Black-legged Kittiwakes measured at Svalbard (79°N) (Gabrielsen et al. 1988), Hornøya (G.W. Gabrielsen, unpubl. data), and St. Paul Island (Gabrielsen et al. 1996). This may be related to their foraging mode, in which Common Murres are better cold adapted than kittiwakes. Common Murres are divers and are thus more exposed to a low seawater temperature than are surface-feeding



**Table 3**  
Field metabolic rate (FMR) of Common Murres (CM) and Thick-billed Murres (TBM) measured at different localities

Species	Body mass (g, $\pm$ SD)	No. of birds	FMR (mL CO <sub>2</sub> g <sup>-1</sup> h <sup>-1</sup> , $\pm$ SD)	Location	Source
CM	940 $\pm$ 34	4	3.18 $\pm$ 0.53	Gull Island, Newfoundland, Canada	Cairns et al. 1990
CM	1025 $\pm$ 53	11	3.34 $\pm$ 0.86	Hornøya Island, Norway	This study
TBM	936	3	2.37	Digges Island, N.W.T., Canada	Gaston 1985b
TBM	820	8	2.89	St. Paul Island, Alaska, U.S.A.	E. Flint (unpubl. data)

kittiwakes. However, murres may be exposed to less variation in temperature, as seawater temperatures vary less than air temperatures. Although the RMR is the same at different latitudes, the thermal conductance is lower (i.e., they are better insulated) in murres studied in the high Arctic (Johnson and West 1975; Gabrielsen et al. 1988, 1996). Murres therefore appear to have reduced their insulation as the ambient air and seawater temperatures increase with decreasing latitude (Gabrielsen et al. 1996).

#### 4.2 Field metabolic rate

Prior to this study, energetic studies of free-living murres have been characterized by small sample sizes (3–4 individuals) and have not taken chick age into account. In this study, the number of measurements has been increased. However, in order to show relationships between FMR and the different ecological parameters, the sample size should be increased even further.

The mean mass-specific FMR value (3.34 mL CO<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>) obtained for adults during the chick-rearing period on Hornøya was 8% higher than the mean value (3.18 mL CO<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>) of Common Murres (four individuals) measured during the same period at Gull Island, Newfoundland (Cairns et al. 1990) (Table 3). Both these FMR values are 10–40% higher than the FMR values obtained for Thick-billed Murres in the Pribilofs (2.89 mL CO<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>; E. Flint, unpubl. data) and in the eastern Canadian Arctic (2.37 mL CO<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>; three individuals; Gaston 1985b) (Table 3). Because Thick-billed Murres live in colder environments and are better insulated than Common Murres (Johnson and West 1975; Gabrielsen et al. 1988), these findings are consistent with the suggestion that the high FMR in Common Murres is associated with cold stress.

The FMR of Common Murres was 23–134% above the allometric equations made for birds in general (Kendeigh et al. 1977; Walsberg 1983) and for seabirds (Nagy 1987; Birt-Friesen et al. 1989; Nagy and Obst 1991). Birt-Friesen et al.'s (1989) equation for birds breeding in cold water and using flapping flight gave the best prediction for Common Murres.

The high FMR in high-latitude seabirds is explained by the cost of thermoregulation in cold environments and by foraging mode (flying or diving), which is especially expensive in murres. Ellis (1984) proposed a close linkage between RMR and the maximum power output, whereas Roby and Ricklefs (1986) and Gabrielsen et al. (1988) suggested that the birds' physical activity may influence the RMR. According to Birt-Friesen et al. (1989), auks and diving petrels have an elevated FMR compared with other seabirds because they

use their wings both for flying and for diving. This contrasts with the situation in penguins, in which wing morphology is optimized for swimming, and that in such seabirds as fulmars and larids, whose wing morphology is optimized for flying. As the optimum design for wings differs for flyers and divers, one would expect that an intermediate stage would be less effective both in water and in air. According to Greenewalt (1962), the wing loading of auks falls within the upper extreme of the range for all flying birds. Of three auk species measured, Common Murres had the highest wing loading (body mass 950 g, wing area 544 cm<sup>2</sup>, wing loading 1.75 g cm<sup>-2</sup>; Pennycuick 1987). Using Pennycuick's (1989) Program 1 to calculate flight cost, the values for Common Murres, based on body measurements of individuals included in the DLW experiment, were related to the measurements of FMR, and no correlation was found. In this study, it was not known how much time is spent foraging at sea or how far the birds flew when foraging at sea. However, as there is a good correlation between FMR and time at sea (Fig. 1), the high and variable FMR might be associated with a high cost of flying and diving in Common Murres.

#### 4.3 Flexible energy budget

Several recent studies have shown that Common Murres are able to change their foraging behaviour in response to changes in food availability. For instance, Monaghan et al. (1994) found an increase in diving time in years with low food abundance. The increase in foraging effort (increased diving time) resulted in an estimated doubling of energy expenditure. In the present study, times spent flying and diving are unknown, so it is impossible to calculate respective costs. However, based on preliminary heart rate recordings of free-ranging Common Murres foraging from Hornøya, using a data logger system (P.J. Butler, T. Woakes, and G.W. Gabrielsen, unpubl. data), there are indications that the energy cost of diving is high. According to Croxall and Briggs (1991), 80–95% of the total daily energy budget is incurred at sea. The diving behaviour data from Common Murres (Cairns et al. 1990; Monaghan et al. 1994; P.J. Butler, T. Woakes, and G.W. Gabrielsen, unpubl. data) and my energetics data show that Common Murres are able to increase their FMR to 2–7 times their RMR during the breeding period. This clearly suggests that breeding Common Murres may be able to adjust their FMR in response to changes in food abundance.

Although Common Murres show great flexibility in time and energy budgets, their ability to change their work rate while foraging at sea does not seem to affect breeding success (Monaghan et al. 1994; Uttley et al. 1994). For Common Murres during situations of moderate food

abundance, this may indicate that factors such as provisioning rate, chick growth, and breeding success, which are monitored in the colony, may not reflect food availability in the area (Burger and Piatt 1990). Similarly, although there was a good correlation between FMR and time at sea, the latter does not necessarily reflect the parents' foraging effort (see Cairns 1987, 1992).

#### 4.4 Parental energy demand

According to Ricklefs (1983), parental energy demands are at a maximum during the chick-rearing period. The working level during this time, described as "the maximum sustainable working level," was suggested to be about  $4 \times \text{BMR}$  (Drent and Daan 1980). This was later supported with DLW studies (Roby and Ricklefs 1986; Gabrielsen et al. 1987, 1991; Mehlum et al. 1993). However, studies show that some species exceed this sustainable working level during chick rearing (e.g., Birt-Friesen et al. 1989; Cairns et al. 1990; Obst and Nagy 1992). The FMR/RMR ratio in the present study ranges from 2 to 7, which corroborates the suggestion that Common Murres can exceed this metabolic ceiling.

Until now, DLW studies of seabirds have been presented as an average FMR throughout the chick-rearing period. In two species of diving petrels (Common Diving-Petrel *Pelecanoides urinatrix* and Georgian Diving-Petrel *P. georgicus*) (Roby and Ricklefs 1986) and in Dovekies *Alle alle* (Gabrielsen et al. 1991), there was no change in adult FMR with respect to chick age. In adult penguins, the highest energy cost was found at the end of chick growth (Gales and Green 1990). Burger and Piatt (1990) contend that there is a lack of consistent evidence for any increase in parental feeding effort as the chick grows. However, this seems unlikely, as the maintenance requirements of Common Murre chicks are thought to increase about sixfold while the chicks are in the colony (Coulson and Pearson 1985). In several studies of Common Murres, there was no apparent increase in provisioning rates with increasing chick age (Birkhead 1977; Harris and Wanless 1985). However, Birkhead and Nettleship (1987) found an increase in two seasons among Thick-billed Murres and in one season among Common Murres. As the growing chicks require more energy as they become older, it is expected that the parent bird must use more energy to catch and transport sufficient food to the colony. In the present study, a weak correlation ( $P = 0.12$ ) was found between FMR and chick age, suggesting that adults with older chicks might spend slightly more time at sea than adults with smaller chicks.

It is suggested that the energy requirements of the chick are small compared with the daily energy expenditure of adults. In Common Murres, at the peak of growth, the energy requirements of the chick are only 20% of those of the adults (G.W. Gabrielsen, unpubl. data). It may well be that adult Common Murres, with an average FMR/RMR ratio of 3.8, are working at a maximum during chick rearing and are unable to provide more food to secure further growth of their chicks. This would therefore support the hypothesis that murre chicks fledge at <30% of adult body mass owing to the inability of parents to provide sufficient food to older chicks at the colony (Sealy 1973; Birkhead 1977; Furness and Barrett

1985; Gaston 1985a; Ydenberg 1989; cf. Burger and Piatt 1990; Monaghan et al. 1994).

#### 4.5 Body mass change

Croll et al. (1991) found a decrease in body mass of adult Common Murres very soon after their chicks hatched, which was interpreted as an adaptation to reduce the energy cost of flight while foraging. It was estimated that the energy saved was equivalent to 25% of the RMR (or BMR) per day, or a 5–10% reduction in the mechanical power required for flight (Croll et al. 1991). Common and Thick-billed murres studied on Hornøya lost 100 g and 80 g, respectively, from the end of incubation to fledging (M. Asheim, pers. commun.). In this study, average body mass was stable throughout the chick-rearing period. However, there were large individual and daily variations in body mass decrease (mean  $38 \pm 21 \text{ g} \cdot \text{d}^{-1}$ ). Breeding Common Murres, working at a maximum during chick rearing, will, by processing food and storing excess energy at sea, be energetically more efficient when flying back to the colony than parents returning with full stomachs. Diurnal mass cycles associated with fat deposition have been shown in several species of tits (*Parus* spp.) (Haftorn 1992). In Common Murres, the daily variation in body mass must also be associated with storage and turnover of body fat. While the fat is processed and stored at sea, the reserves can be used for maintenance when the bird is not feeding. Breeding Common Murres with a minimum FMR of  $959 \text{ kJ} \cdot \text{d}^{-1}$  (Table 1) and utilizing body fat as the energy resource (losing an average of  $38 \text{ g} \cdot \text{d}^{-1}$ , with an energy equivalent of  $38.5 \text{ kJ} \cdot \text{g}^{-1}$ ) will be able to rely on these resources for an average of 1.5 days (minimum 16 hours and maximum 2.4 days) without feeding.

#### 4.6 Food consumption

Based on the estimate of food consumption, Common Murres were calculated to consume an average of 43% of their body mass per day during chick rearing. According to Diamond et al. (1986), a high food consumption rate in hummingbirds may cause physiological limitations owing to digestive bottlenecks. This means that high food consumption and digestion may also limit the Common Murres' time foraging at sea. In this study, WIR was correlated to body mass change. As WIR is a measure of the amount of food processed, this indicates that, while at sea, the murres probably spend time feeding themselves and processing the food. In murres, a full meal, based on stomach analyses of birds shot at sea just after foraging, weighs between 80 and 100 g (G.W. Gabrielsen, pers. obs.). If the amount of food ingested while foraging at sea is processed randomly in time before the bird is caught and weighed in the colony, one would not expect any correlation between WIR and body mass change. However, the high correlation between WIR and changes in body mass indicates that Common Murres digest as much as possible at sea before returning to the colony. Consistent with this hypothesis, birds collected at the colony rarely have any food material in the foregut (A.J. Gaston, unpubl. data).



If these birds have to consume an average of 440 g·d<sup>-1</sup> to cover their own requirements and the digestive process takes 1–2 hours for each meal (Brekke and Gabrielsen 1994), they need to spend 4–8 hours digesting their own food. In murre, the time spent at sea ranges between 47 and 96% of daylight time (Burger and Piatt 1990). On Hornøya, Common Murres spend 54% of their time at sea, which is similar to the 47% recorded for Thick-billed Murres at the same colony (Furness and Barrett 1985). While at sea, 70–85% of time is probably spent digesting food on the surface (Cairns et al. 1990; Monaghan et al. 1994).

Several factors influence the calculation of food consumption of breeding murre. Whereas the metabolic efficiency is determined by the fat content in the food (Brekke and Gabrielsen 1994), the energy density of the food has the greatest effect on the calculation of food consumption. Cairns et al.'s (1987) study of Common Murres in Newfoundland was based on capelin with a lower fat content than those caught around Hornøya, and there the daily average food consumption was 16% higher than in the present study. When presenting population energy requirements, it is therefore important to present energy values of different food items.

The Barents and Norwegian seas are very productive. Capelin, sand lance, and herring are three extremely important constituents of the diet of nearly all seabird species in the area. The diet of Common Murres breeding on Hornøya consists mainly of capelin and sand lance (Furness and Barrett 1985; Barrett and Furness 1990). However, herring is now becoming an important food item during the breeding period (M. Asheim and R.T. Barrett, pers. commun.). The present estimate of food consumption by all Common Murres was based on the assumption that adults eat nearly the same diet as the chicks and that they ate only capelin and sand lance. However, as the energy content of sand lance in this study was not significantly different from that of capelin, the calculation of the total amount of food needed would not be influenced by varying proportions of these prey.

During 20 days of chick rearing, each Common Murre consumed an average of 8.8 kg of food. This includes only the needs of the adult and excludes the foods given to the young. Based on the WIR of growing Common Murre chicks, water content of food, and the energy value of food, it was calculated that a 15-day-old chick consumed 105 g of fresh food each day (G.W. Gabrielsen, unpubl. data). The food requirements of two adults and one chick should total 19.7 kg during 20 days of chick rearing. The consumption by 1400 pairs of Common Murres on Hornøya would thus be 27 580 kg during chick rearing.

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# Ecological interactions between marine mammals, commercial fisheries, and their prey: unravelling the tangled web

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## Abstract

Much research has been done during the past 15 years ostensibly to address the subject of trophic interactions linking marine mammals with the rest of the marine food web. Numerous attempts have been made to evaluate the types and amounts of food eaten by particular marine mammals and the probable impacts of this consumption on food stocks, especially those that are "harvested" by humans. Some progress has been made on the former, much less on the latter. When it comes to questions about ecological interactions between marine mammals and commercial fisheries, the conclusion today — like that more than a decade ago — is that we cannot yet predict with any certainty the effects of increasing or decreasing marine mammal populations on both the abundance of their prey and the catches of commercial fisheries.

In this paper, I attempt to assess why progress has been so slow. It is due, in part, to the failure to recognize the limitations of existing techniques, such as the construction of energy budgets and analyses of stomach contents and feces, for evaluating the dynamic interactions between marine mammal populations and other components of marine trophic webs. Attempts to build "tactical" models of marine food webs have likewise added little to our understanding of the functioning of marine ecosystems. If more progress is to be made, we require better empirical data, but not just for marine mammals; we require it for all components of marine trophic webs. We also need a better theoretical framework for addressing trophic interactions, including predator-prey relationships and interspecific competition, in marine ecosystems. It is already clear that overly simple predator-prey or competition models are inadequate for the task. For this reason, some researchers are now working with more complex models, which concentrate on "important" components of individual ecosystems; others are beginning to investigate the application of food web theory to marine ecosystems. Although such approaches may eventually enhance our understanding of the functioning of marine ecosystems, we must, in the interim, accept that such systems are complex and poorly understood. Pretending otherwise — as some nonspecialists frequently do — is naive and potentially misleading.

## Résumé

Au cours des quinze dernières années, on a mené de nombreuses recherches visant expressément à examiner les interactions trophiques entre les mammifères marins et les autres éléments du réseau alimentaire marin. On a déployé bon nombre d'efforts pour évaluer, d'une part, les types et les quantités d'aliments ingérés par des espèces données de mammifères marins et, d'autre part, les répercussions éventuelles de cette consommation sur les ressources alimentaires, en particulier celles qui sont « exploitées » par l'homme. Certains progrès ont été accomplis en ce qui concerne le premier volet de l'évaluation, mais, pour ce qui est du deuxième, les travaux n'ont pas autant progressé. Au chapitre des interactions biotiques entre les mammifères marins et la pêche commerciale, on conclut aujourd'hui, comme il y a plus d'une décennie, qu'il est impossible à l'heure actuelle de prévoir avec certitude les conséquences des augmentations et des déclin des populations de mammifères marins sur l'abondance de leurs proies et sur les prises des pêcheurs commerciaux.

Dans le présent document, nous tentons de déterminer les raisons de la lenteur des progrès. Elle peut être attribuée en partie au fait qu'on n'a pas reconnu les limites des techniques existantes (telles que l'interprétation des bilans énergétiques, ainsi que l'analyse du contenu de l'estomac et des matières fécales), lorsqu'il s'agit d'évaluer les relations dynamiques entre les mammifères marins et les autres éléments des réseaux trophiques marins. De la même façon, les tentatives visant à créer des modèles « stratégiques » relatifs à ces réseaux n'ont pas permis de mieux comprendre le fonctionnement des écosystèmes marins. Des données empiriques plus fiables sont nécessaires si l'on souhaite que les connaissances dans le domaine avancent, non seulement au sujet des mammifères marins, mais également par rapport à toutes les composantes des réseaux trophiques marins. En outre, on doit disposer d'un meilleur cadre théorique pour pouvoir se pencher sur les interactions trophiques, notamment le rapport prédateur-proie et la concurrence entre les espèces, au sein des écosystèmes marins. Il appert d'ores et déjà clairement que des modèles trop simples pour ces deux phénomènes ne suffisent pas à la tâche. Certains chercheurs travaillent donc à établir des modèles plus complexes centrés sur les

éléments « importants » de chaque écosystème. D'autres commencent à faire des recherches sur l'application possible de la théorie des réseaux alimentaires aux écosystèmes marins. Bien que de telles approches soient susceptibles de nous éclairer quant au fonctionnement de ces écosystèmes, nous devons pour le moment accepter le fait qu'il s'agit d'écosystèmes complexes et que nous saisissons mal les lois qui les régissent. Se refuser à l'admettre, comme certains spécialistes le font, équivaut à faire preuve de naïveté et pourrait aboutir à des résultats faussés.

## 1. Introduction

In the late 1970s, the depletion of important fish stocks and the development of new fisheries raised concerns about potential conflicts between marine mammals and fisheries (e.g., FAO 1978). Some people worried that marine mammals were competing with commercial fisheries for dwindling marine resources; others believed that changing fishing patterns, such as the rapid development of the capelin *Mallotus villosus* fishery in the Northwest Atlantic during the 1970s, posed an "insidious" threat to marine mammal populations (FAO 1979:78).

It was because of such concerns that the International Union for the Conservation of Nature and Natural Resources (IUCN) held a workshop in early 1981 to examine the problems arising from actual or perceived conflicts between marine mammals and fisheries around the world (Anon. 1981a; Lavigne 1982a; Beddington et al. 1985). Since then, numerous other workshops and symposia have been held to examine case studies involving particular marine mammals and fisheries (e.g., Anon. 1981b, 1991a, 1991b, 1993; Lavigne 1991a).

In reviewing the reports of the various meetings and the available literature, what is particularly striking is that the scientific understanding of interactions between marine mammals and fisheries, arising from the predatory activities of both and the potential for interspecific competition (see Anon. 1981a; Lavigne 1991a), has not improved greatly since the 1981 IUCN meeting. We continue to neglect, for the most part, the possible effects of commercial fisheries on marine mammals. As well, we continue to conclude (e.g., Bowen 1992), as we did more than a decade ago (e.g., Anon. 1981a, 1981b), that we cannot predict reliably the effects of increasing or decreasing marine mammal populations on both the abundance of their prey and the catches of commercial fisheries. This lack of progress does nothing to resolve disputes, which continue to arise from "perceived" conflicts between marine mammals and fisheries.

Traditionally, questions about potential ecological interactions between marine mammals and fisheries have been approached in three ways: through studies of energy flow in individual marine mammals and their populations (i.e., bioenergetics), through studies of marine mammal feeding habits using analyses of stomach contents and feces, and through the use of models.

My objective here is to review briefly what we have learned from each approach and to attempt to assess why progress has been so slow. I then address the question: Where do we go from here?

## 2. Bioenergetics

Perceptions about the potential impacts of marine mammals on fisheries are often biased by the belief that marine mammals have elevated metabolic rates — an adaptation for living in cold water (reviewed in Lavigne et al. 1986a). The view that marine mammals have higher metabolic rates than other mammals, together with the suggestion that they are "inefficient converters of fish flesh" (Sergeant 1973), leads logically (but incorrectly) to the conclusion that marine mammals have "voracious" appetites (e.g., Power and Grégoire 1978) and, as a consequence, that they have a disproportionate impact on the ecosystems they inhabit.

Although such antiquated views persist in the literature (e.g., Ridgway and Harrison 1986; Wunder 1986; Bennett and Harvey 1987; Elgar and Harvey 1987; Lindstedt and Swain 1988; Kasting et al. 1989; Ridgway 1990), research over the last 15 years has found that metabolic rates of marine mammals are not significantly different from those of other mammals when measurements are made under similar conditions (Nordøy and Blix 1985; Lavigne et al. 1986a, 1986b; Folkow and Blix 1987; Innes et al. 1987; Innes and Lavigne 1991). Similarly, where ecological efficiencies have been estimated, there is nothing to indicate that marine mammals have lower production/ingestion efficiencies or production/assimilation efficiencies (i.e., production efficiencies; see Lavigne 1982b) than other mammals (Lavigne et al. 1982, 1985).

Consistently, estimates of the average daily food consumption of individual marine mammals suggest that they are not the "gluttons" that Slijper (1979) and others presumed them to be (see Innes et al. 1987). For their size, "maintenance" rates of energy ingestion (*sensu* National Research Council 1981) by adult marine mammals are not significantly different from those of terrestrial mammals, and feeding rates of growing marine mammals are consistently similar to those of growing terrestrial mammals (Innes et al. 1987). If any generality is beginning to emerge from more recent studies, it is that the average annual energy requirements of marine mammals may be even lower than we have presumed in recent years (e.g., Renouf et al. 1991, 1993; also see Section 5.1).

Regardless, on an *annual* basis, average daily metabolic rates ( $\text{ADMR}$ ,  $\text{kcal} \cdot \text{d}^{-1} = 0.04843 \text{ W} = 0.04843 \text{ J} \cdot \text{s}^{-1} = 4.184 \text{ kJ} \cdot \text{d}^{-1}$ ) of individual marine mammals, like those of terrestrial mammals, can be approximated, for now, by:

$$\text{ADMR} = \beta (70 M_i)^{0.75} \quad (1)$$

where  $M$  is mean body mass in kg,  $70 M_i^{0.75}$  provides an estimate of basal metabolic rate (BMR,  $\text{kcal} \cdot \text{d}^{-1}$ ) (Kleiber 1975; see also Lavigne et al. 1986a), and  $\beta$  typically has a value somewhere between 1.0 and 3.0, depending on such things as the age, sex, reproductive condition, activity, and species involved (McNab 1984; Innes et al. 1987; Murie and Lavigne 1991).

Equation 1 suggests that ADMR, which should approximate *average* "field metabolic rate" (FMR) (see Nagy 1987; Costa et al. 1989), is a simple multiple of BMR. This "assumption" has recently been questioned by

Koteja (1991), who noted that such a relationship "does not have a strong backing in the experimental data." Observed differences in the slopes of *interspecific* relationships between FMR and BMR and body mass and, hence, the lack of a strong correlation between FMR and BMR (Koteja 1991) are to be expected, however, because FMRs for various species are rarely measured under standardized conditions. As even Koteja agrees that such "criticism is fully justified and difficult to reject," I will continue.

Estimates of individual energy requirements provide a basis for estimating the energy requirements of entire populations. In theory, this should be easily accomplished, as long as estimates of population size and, ideally, age structure, together with a growth curve describing changes in body mass of individuals with age, are available. Given our present understanding, an average annual energy budget (expressed in kcal·d<sup>-1</sup>) for any marine mammal population can be approximated by:

$$\text{ADMR}_{\text{pop}} = \sum_{i=0}^w N_i (\beta_i) (70 M_i^{0.75}) \quad (2)$$

where  $M_i$  and  $\beta_i$  are mean values for each cohort,  $N_i$  gives the number of individuals in each cohort, and  $w$  is the last age class represented in the population.

For most populations, the greatest uncertainty rests not with our ability to estimate energy requirements of individuals, but rather with the estimates of population size ( $N$ ), age structure ( $N_i$ ), and size at age ( $M_i$ ). As well, although there will always be room to refine population energy budgets estimated in this way, such refinement will not overcome the fundamental limitations associated with this approach for examining ecological interactions, such as predator-prey relationships and interspecific competition between marine mammal populations, commercial fisheries, and their prey. Most importantly, bioenergetics alone does not even begin to address the question of *interactions*, nor does it tell us anything about the prey species eaten by marine mammals. The latter deficiency can be addressed, however, using analyses of stomach contents or of feces.

### 3. Feeding habits

Feeding habits of marine mammals have been traditionally studied using stomach content analyses (Jobling and Breiby 1986; Murie 1987). More recently, attempts have also been made to use fecal analyses to evaluate the feeding habits of certain marine mammals, an approach that is similar to the scat analyses of terrestrial biologists (Prime and Hammond 1987). Using such approaches, it is relatively easy to get *some* description of various prey consumed by marine mammals at specific times and places (e.g., Fig. 1).

Such descriptions of the diet are, however, almost always biased in a number of ways. There is the age-old problem of obtaining a random sample of a wild population of animals; there are biases associated with the precise time and place of sampling; there are also problems associated with the differential rates at which different types and sizes of prey are digested (Bigg and Fawcett 1985; da Silva and Neilson 1985; Murie and Lavigne 1986; Markussen and Øritsland 1992).

There are additional problems related to standardization (or lack thereof) in both the collection and reporting (e.g., units) of data. A cursory examination of the literature indicates, for example, that data from stomach content analyses have been expressed in at least 10 different ways (e.g., Bigg and Perez 1985; Murie and Lavigne 1992). Confusion frequently arises because each method yields a figure — usually a percentage — that describes the relative contribution of a particular prey species to the diet. It is frequently forgotten, however, that the percentage values obtained from each method are not directly comparable.

Consider the partial results of a stomach content analysis of grey seals *Halichoerus grypus*, summarized in Table 1 (from Murie and Lavigne 1992). In this example, four methods of expressing the results are given. Clearly, the estimated contribution to the diet of each prey species, A, B, and C, varies widely, depending on the underlying units of measurement (compare across rows). Furthermore, ranking the importance of each prey to the diet depends entirely on the measurement used (compare columns). If prevalence (the percentage of stomachs sampled containing a given prey species) is the method of choice, then species B is the most important component of the diet. If numbers are used, then C seems most important; if biomass, then B. But the most important prey item, measured in the units that are most vital to grey seals, namely energy (Lavigne et al. 1982), is prey item A.

Some of the differences outlined above relate to the size of the prey consumed and their energy density. Such considerations are not even taken into account by the two measures of frequency of occurrence (prevalence and numbers); consequently, these measures actually tell us little more than the fact that a given prey item was consumed. Such information is useful for producing checklists of prey species, but it does not allow for any meaningful partitioning of the diet. Partitioning the diet, which is a prerequisite for any investigation of potential interactions between marine mammals, fisheries, and their prey, can only be accomplished using measures of stomach contents based on the volume or mass of each prey species consumed and, ideally, on the amount of energy contributed by each prey species to the diet.

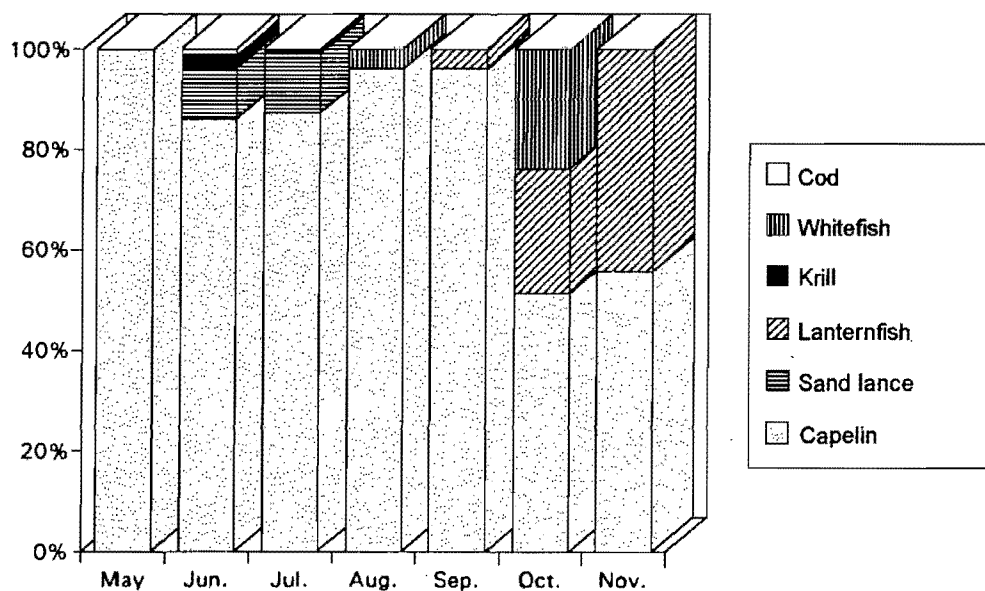
Such problems aside, if analyses of stomach contents or feces are done properly, they can, within limits, tell us what species are being consumed at a particular time and place, and in what proportions (e.g., McConnell et al. 1984; Benoit and Bowen 1990a, 1990b; Murie and Lavigne 1991, 1992). Such analyses alone, however, cannot usually provide adequate estimates of how much a marine mammal eats over time, because most feeding studies do not tell us how frequently the animals eat (Murie and Lavigne 1992). For an individual population, this problem can be circumvented, at least in principle, by combining information on its diet composition with its estimated energy requirements.

Although the feeding habits of most marine mammals are not yet known in sufficient detail to warrant such calculations, the methodology is outlined in Lavigne et al. (1985, Table 19.7). In that example, the energy requirements for Northwest Atlantic harp seals *Phoca groenlandica*, estimated as either metabolizable energy or gross energy (see Lavigne et al. 1982), generated by a detailed annual population energy budget, were simply



**Figure 1**

Percent occurrence of prey species in the stomachs of fin whales *Balaenoptera physalus* from Dildo, Newfoundland, 1970–1972 (redrawn from Mitchell 1974).

**Table 1**

Partial diet composition in grey seals feeding in the St. Lawrence estuary (from Murie and Lavigne 1992)

Prey	Prevalence (%)	Numbers (%)	Wet mass (%)	Energy (%)
A	20	8	26	42
B	41	17	36	22
C	24	36	10	12

partitioned into two components: fish with an energy density of  $2.6 \text{ kcal} \cdot \text{kg}^{-1}$  (wet mass) and invertebrates with an energy density of  $1.2 \text{ kcal} \cdot \text{kg}^{-1}$  (wet mass). Generally, biomass of each prey consumed ( $B_i$ ) can be calculated by:

$$B_i = \frac{p_i \cdot ME}{m_{e_i} \cdot d_i} = \frac{p_i \cdot GE}{d_i}$$

where  $p_i$  is the proportion of the diet (in energy terms) composed of prey  $i$ ,  $ME$  is the estimated energy requirement of the population measured as metabolizable energy,  $m_{e_i}$  is the metabolizable energy coefficient — the proportion of energy ingested (gross energy,  $GE$ ) that ends up as metabolizable energy ( $ME + m_{e_i} = GE$ ) — and  $d_i$  is the energy density of the prey. Such calculations reinforce the point that the biomass of prey consumed by a marine mammal to meet its energy requirements can vary by a factor of three, depending entirely on the energy density of the prey (Lavigne et al. 1985, Table 19.7; Montevecchi and Piatt 1984, Table 4; see also Bowen 1985).

Even if there were enough information to estimate the biomass of various prey species consumed by a marine mammal population using the above methodology, we would still have the problem that studies on food habits do not directly address the question of *interactions*, even when combined with bioenergetics data (as in equation 3). Although an estimate of the biomass of species A consumed by a marine mammal may be indicative of the

potential for interaction between a marine mammal and a fishery, the value itself tells us absolutely nothing about whether such an interaction is actually occurring (e.g., Murie and Lavigne 1992).

Data obtained from studies of bioenergetics and diet composition are, nonetheless, an essential starting point, insofar as they provide inputs for models, some of which can address questions about interactions between marine mammals, commercial fisheries, and their prey.

#### 4. Models

A variety of modelling approaches have been used to study (or describe) various aspects of marine mammal feeding ecology. These range from detailed "tactical" models (*sensu* Holling 1966) of specific ecosystems to simple "strategic" models, which sacrifice detail for generality.

##### 4.1 Tactical models

Several attempts have been made to construct detailed models of marine ecosystems that include marine mammals and their prey (e.g., Iverson 1977; FAO 1978; Davis et al. 1980; Welch et al. 1990; Field et al. 1991; Moloney and Wickens 1991). It is difficult, however, to find examples in which the energy flows have actually balanced; usually it appears as if there are not enough prey in the system to satisfy the energy requirements of the predators. Given this limitation, it is not surprising that this approach has yet to contribute much in the way of new understanding, either about the role that marine mammals play in such systems or, more specifically, about potential interactions between marine mammals and fisheries. This conclusion is consistent with the wider

view that tactical models rarely contribute new ecological insights (Yodzis 1989).

#### 4.2 Strategic models

A few attempts have also been made to apply simple models to investigate general questions about interactions between marine mammals and fisheries (e.g., May et al. 1979; Butterworth et al. 1988; Flaaten 1988; McCann and Yodzis 1992; see also Harwood 1983; Beverton 1985). Such attempts have essentially told us two things. First, the predicted behaviours of such systems are, not surprisingly, model dependent (e.g., compare Flaaten 1988 with McCann and Yodzis 1992). Secondly, they suggest that the reduction of a marine mammal population could be either beneficial or detrimental to a fishery, depending on the nature of the trophic relationships involved (Butterworth et al. 1988; see also Yodzis 1994).

So, although such modelling approaches have provided some qualitative insights into the range of possible outcomes of interactions between marine mammals, fisheries, and their prey, it has recently been concluded that the simple strategic models examined thus far, which involve only two or three components of a marine trophic web, are not adequate for evaluating conflicts between marine mammals and fisheries in the real world (for a recent discussion, see Anon. 1991b).

### 5. Where do we go from here?

#### 5.1 Bioenergetics

There is a general perception that we still require additional information on the energy budgets of individual marine mammals and their populations (e.g., Harris 1990a, 1990b). Much work is currently being done to document the details of individual energy budgets and how these vary with age, sex, season, reproductive condition, and activity (e.g., Renouf et al. 1993). As noted previously, much of this work suggests that the annual energy requirements of marine mammals may be even lower than previously thought.

Empirical research indicates, for example, that the cost of locomotion — until recently, a weak link in marine mammal energy budgets — in both seals (e.g., Innes 1984; LeBoeuf et al. 1988, 1989) and whales (e.g., Williams et al. 1992) is remarkably low in comparison to the energy cost of locomotion for mammals on land (see also Lavigne et al. 1982). As better time-activity budgets become available, it seems likely that estimates of annual energy requirements will be further reduced. Many pinnipeds, for example, spend much of their time sleeping, and energy consumption at such times is usually below basal levels (e.g., Worthy 1987; Boily 1991). Similarly, moulting seals may have reduced metabolic rates (Ashwell-Erickson et al. 1986).

Seals and whales also undergo regular periods of fasting. In mammals generally, fasting is accompanied by metabolic depression (Kleiber 1975; Markussen and Øritsland 1986; Rea and Costa 1992). This also seems to be the case in marine mammals (e.g., Worthy 1987; Øritsland and Markussen 1990; Markussen et al. 1992),

and, at least in the case of grey seals, metabolic depression occurs almost immediately following the onset of fasting (Nordøy et al. 1991). Energy budgets that do not take into account, implicitly or explicitly, the reduced energy requirements and, hence, reduced food consumption of marine mammals during regular periods of fasting will continue to overestimate their annual energy intake.

Recent longitudinal studies of the oxygen consumption of individual, captive harp seals suggest further that their average annual energy requirements may be lower than estimated in the past (e.g., Renouf et al. 1991, 1993). Undoubtedly, there are seasonal differences in oxygen consumption and in feeding habits of marine mammals throughout the year (e.g., Fedak et al. 1980; Lavigne et al. 1985; Ryg and Øritsland 1992). Such differences are associated with changes in activity levels, changes in appetite, and, possibly, changes in digestive efficiencies. They are also related to seasonal variation in condition and, hence, in the cost of thermoregulation (see Øritsland and Markussen 1990) and to the changes in metabolic rate associated with sleeping, fasting, and moulting noted above, or, as Renouf et al. (1993) have speculated, to seasonal changes in BMR.

Continuing work on marine mammal bioenergetics undoubtedly will refine existing energy budgets and provide better inputs into population and ecosystem models. An important question, however, is how much more do we really need to know about the energy requirements of individual marine mammals to address questions related to potential interactions between marine mammals and fisheries. It is my own opinion, given the lack of precision in other parameters (e.g., estimates of population size) and the even greater uncertainty associated with other ecosystem components (e.g., fish, invertebrates, and phytoplankton), that further advances in marine mammal bioenergetics will not, in the foreseeable future, contribute to any great change in the scientific advice proffered to management authorities on questions related to ecological interactions between marine mammals and fisheries.

#### 5.2 Feeding habits

Whenever a perceived conflict between a marine mammal and a fishery enters the public arena, it is always noted that we need more information on the feeding habits of the marine mammal. Even in cases where feeding habits are relatively well known, critics still claim that there are too few samples or that those that do exist are badly dated and not relevant to the current situation (which invariably corresponds with a decline in one or more fish stocks). The recent example of harp seals and the crisis in the northern cod *Gadus morhua* fishery off Newfoundland is a case in point. Responding to such criticism, it must be acknowledged that studies of feeding habits of a particular marine mammal will always refer to an earlier time. So, if such criticism were valid, it would be pointless, perhaps, to initiate further studies of feeding habits.

Many marine mammals are migratory, and their feeding habits change with season and location. Ideally, attempts should be made to obtain a consistent time series

of diet composition data for marine mammals in relation to prey abundance. In many cases, however, such as the Northwest Atlantic harp seal, which migrates some 3000+ km annually, it is virtually impossible to sample the population throughout a single year. So again, if there were any merit to the above criticisms, additional feeding studies would be a waste of time, because scientists will never be able to satisfy the critics' requirements for useful and relevant data.

I am not convinced, however, that such criticisms are very constructive. Regardless, research funds permitting, scientists will undoubtedly continue to refine their analyses of stomach contents and feces. In the future, however, more care should be given to the problems of sampling wild populations, and the results must be reported using appropriate and consistent standards (see Section 3). Field collections of marine mammal stomachs and feces should also be supplemented by carefully designed experiments that will improve the accuracy and precision of the results. Some progress has already been made in this area (see, for example, Bigg and Fawcett 1985; Murie and Lavigne 1985; Prime and Hammond 1987).

Recently, some researchers have used stable isotope ratios to infer predator-prey relationships in marine ecosystems (e.g., Hobson and Welch 1992). Although such techniques seem well suited for confirming the relative trophic position of components in marine ecosystems, it seems unlikely that they will ever provide precise information about the absolute amounts of various prey species consumed by a marine mammal (or other predator) population.

At the IUCN meeting on marine mammal fishery interactions in 1981, it was noted that in order to evaluate interactions between marine mammals and fisheries, data on the size distribution of common prey species taken both by the marine mammals and by the fisheries were also required. Some such data have emerged in recent years (e.g., Benoit and Bowen 1990a, 1990b; Murie and Lavigne 1991, 1992), but obviously more are needed. Such information should become a requisite part of the information collected both for marine mammals and other components of marine ecosystems and for the commercial fisheries with which they may potentially interact.

Similarly, in order to evaluate the extent of any competition between a marine mammal and a fishery, it is necessary to know how much of the feeding effort of the marine mammal and the fishing effort of the fishery are directed at the same prey populations (Harwood and Croxall 1988). Such information is needed at a variety of scales, depending on the nature of the specific question being addressed. In order to partition the annual energy requirements of Northwest Atlantic harp seals in a meaningful and relevant way, for example, it is necessary to know their seasonal distribution and movements in relation to those of their prey populations and of commercial fisheries throughout the entire Northwest Atlantic (e.g., Lavigne et al. 1985; see also Harwood and Croxall 1988). During those times of the year when the distributions of harp seals and commercial fisheries overlap spatially and temporally, it would also be useful to know specifically where the seals are feeding (and on what) in relation to the location and catches of the fishing boats (see Lavigne 1991a).

Although information on marine mammal diets obtained from proper stomach content and fecal analyses will provide useful inputs into ecosystem models, we must eventually go further. To date, we usually assume that marine mammals, particularly seals, are opportunistic predators, consuming those prey that happen to be most abundant in a particular place at a particular time. This perception leads to the belief that when a particular prey becomes less abundant, it will have little effect, because the marine mammal predator will simply switch to another, more available prey. This is not always the case. When capelin abundance declined in the Northwest Atlantic during the 1970s, for example, the condition of harp seals also declined significantly, suggesting that the seals did not simply switch to an alternative food source (Stewart and Lavigne 1984; but see McLaren and Smith 1985). Consistently, when the Barents Sea capelin stock collapsed in the mid-1980s, tens of thousands of harp seals, some in poor condition (K.I. Ugland, pers. commun.), moved beyond their usual range and invaded the coastal waters of northern Norway (Haug et al. 1991), possibly in search of food.

The conclusion that seals are opportunistic predators is, in reality, simply a convenient way of saying we do not know very much about prey selection by marine mammals. We need to know more, therefore, about the choices that marine mammals make when faced with alternative food resources in the real world (see, for example, Markussen and Øritsland 1992). This is clearly a difficult undertaking, but one potentially useful line of research might involve studies on marine mammals, paralleling those on other animals, which test some of the predictions of foraging theory (Stephens and Krebs 1986). Although marine mammals do not readily lend themselves to such research, a few researchers (e.g., G. Boyle, pers. commun.) are already attempting to design experiments with captive animals that may provide some indication of whether or not marine mammals "have actually read the foraging literature." Such insights would be extremely useful when attempting to model possible predator-prey scenarios in the marine environment.

Other researchers have made even more ambitious suggestions. McLaren and Smith (1985) suggested introducing harbour seals *Phoca vitulina* into "well-chosen lakes" to learn more about the role of pinnipeds in aquatic ecosystems. Alternatively, Markussen and Øritsland (1992) recommended using marine areas such as enclosed skerries, where selection and handling of live prey (of known species, sizes, and energy densities) by semicaptive marine mammals could be observed directly and repeatedly using underwater cameras or observation platforms. At first glance, such suggestions may seem fanciful. Upon reflection, however, approaches such as these may be the only way to obtain empirical data to address fundamental questions about the role of marine mammals in aquatic ecosystems and, specifically, about potential interactions between marine mammals and their prey.

### 5.3 Models

If any progress is to be made in addressing the very real and practical problems associated with the interaction



between marine mammals and fisheries, it must involve both qualitative and quantitative assessments of interactions among components in marine trophic webs. Towards this end, a number of recent initiatives are worth mentioning.

Guidelines for a tactical management model to investigate interactions between Cape fur seals *Arctocephalus pusillus pusillus*, hake (*Merluccius* spp.), and other predatory fish in the Benguela ecosystem were developed at a recent workshop in South Africa (Anon. 1991b). The aim of this exercise was to formulate the simplest "realistic" model that could give "qualitative insight" into the effect of a change in the size of the fur seal population on the yield of hake (Fig. 2). Evaluation of this approach is currently in progress.

A second approach that holds promise emerges from the work of Yodzis and Innes (1992), using "plausible" consumer-resource models. These models fit somewhere on the continuum between tactical and strategic models, incorporating both "energetic reasoning and allometric empiricism." Like the South African model, these models attempt to gain "maximum realism from minimum data." Testing such models on specific marine food chains has yet to be attempted.

A third approach, which remains to be examined in detail, involves the application of food web theory (reviewed in Pimm 1982) to marine ecosystems. Such work is currently in progress (P. Yodzis, pers. commun.), and it will be some time before an evaluation of its promise can be made.

These and other modelling approaches will be considered and possibly developed further during a series of ongoing workshops organized by the Scientific Advisory Committee to the United Nations Environment Programme's (UNEP) Marine Mammal Action Plan (Anon. 1992a, 1992b).

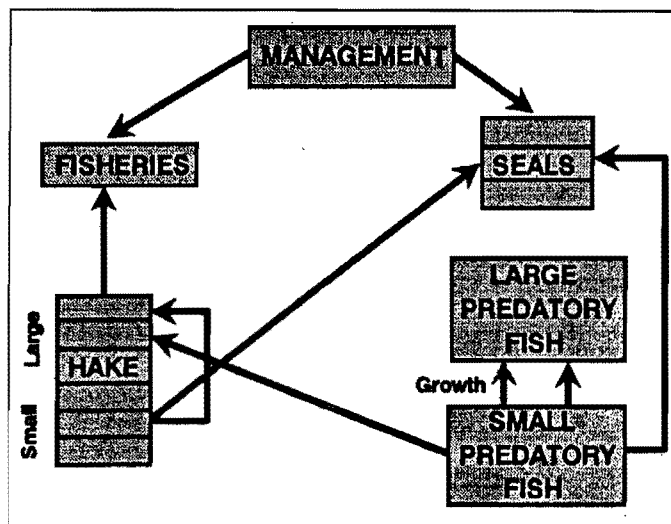
#### 5.4 Public education

In recent years, there have been numerous incidents in which it has been claimed that marine mammals must be culled to protect the interests of fisheries (reviewed in Anon. 1992b). Examples include harp seals throughout the North Atlantic (Lavigne 1991b), grey seals, both in Canada (Malouf 1986; but see Lavigne 1987) and in the United Kingdom (Lavigne 1992), Cape fur seals in southern Africa (Hanks 1990; Wickens 1991), and minke whales *Balaenoptera acutorostrata* in the Barents Sea off the coast of Norway (see, for example, Flaaten 1988).

There have also been a number of incidents in which the activities of fishermen were thought by some to be contributing to the decline of certain marine mammal populations, including Stellar's sea lions *Eumetopias jubatus*, harbour seals, and, possibly, North Pacific fur seals *Callorhinus ursinus*, all in the North Pacific Ocean off the coast of Alaska (Lowry and Frost 1988; Trites 1990, 1992; Anon. 1991a, 1993), and the South American sea lion *Otaria flavescens* (see Rodrigues and Bastida 1993) on the Falkland Islands in the South Atlantic (D. Thompson, pers. commun.).

Anyone who has followed the public debate surrounding any one of these perceived conflicts between a particular marine mammal and a commercial fishery will

**Figure 2**  
Proposed "base case" model for investigating management options for hake (*Merluccius* spp.) in the Benguela ecosystem (redrawn from Anon. 1991b)



know that, in addition to more "science," there is an urgent need for increased public education. Because the facts are not always self-evident, such debates provide virtually limitless opportunities for those so inclined to ignore or to distort the facts, or simply to create their own "reality," to gain support for their position. Such opportunities would be greatly reduced if the facts were readily available and well known. If they so chose, scientists could dissipate much unnecessary controversy, simply by taking a more active role in the public education process.

We might begin by making it widely known that unexploited marine mammal populations will not increase exponentially forever. We could remind people — including those who believe that exploitation is *necessary* to manage wild populations — that the very theory upon which the concept of "maximum sustainable yield" (which has been the foundation of fishery and marine mammal management for decades) is based is built on the presumption that populations are self-regulating. At some level, marine mammal populations will be limited by density-dependent factors such as the availability of food or breeding habitat. Even in the absence of "harvesting" or culling, marine mammal populations should, therefore, reach some dynamic equilibrium (which we call carrying capacity) with their environment.

We might also point out that unexploited marine mammal populations do not always behave in a manner predicted by "common sense." Certainly, some populations that were reduced to low levels by overexploitation (mostly in the last century) have, as a result of increased protection, shown remarkable recoveries that continue to this day. Northern elephant seals *Mirounga angustirostris* in the eastern Pacific and grey seals in eastern Canada are two good examples. Yet there are other marine mammal populations that have not increased measurably following protection. The classic example is the North Atlantic right whale *Eubalaena glacialis*, which appears to have maintained its numbers at about 350 animals since being protected in 1937 (Kraus and Brown 1992). There are still other instances in which

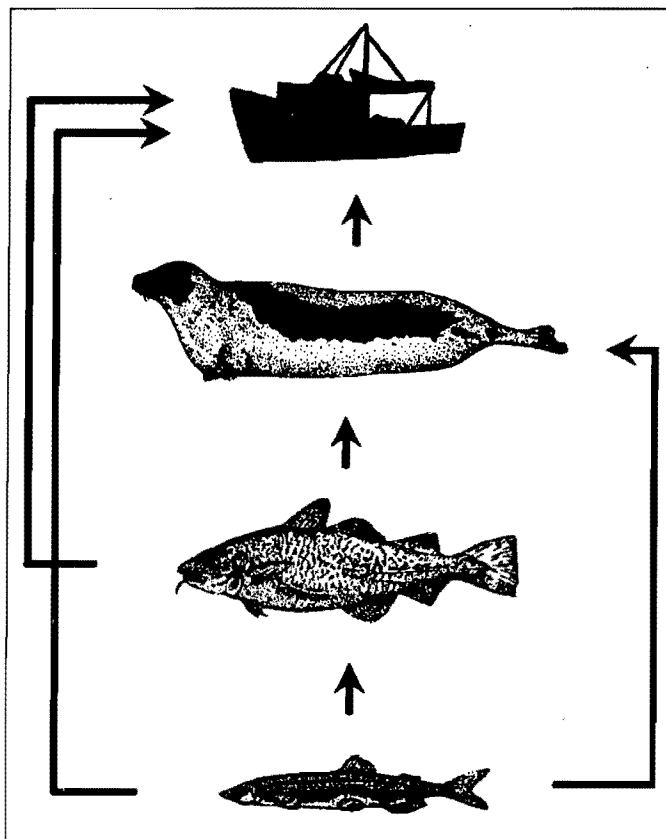
essentially unexploited marine mammal populations have actually declined. Two aforementioned examples are Stellar's sea lions in Alaska and South American sea lions on the Falkland Islands.

We must also convey more accurately the complexity of the ecosystems in which marine mammals and fisheries exist. In doing our analyses, there has been a tendency, for obvious convenience, to represent complex food webs as simple food chains (e.g., Fig. 3). Not surprisingly, others follow suit. As a result, "common sense" would seem to dictate that because they eat fish, fewer marine mammals will mean more fish for fisheries. However, if we inform people that marine systems are actually far more complex than simple food chain models suggest (see, for example, Fig. 4), then maybe some will begin to understand why "common sense" may lead to incorrect conclusions. Using the same logic as above, for example, one might remind people that in instances in which a marine mammal eats the predator of a commercially important fish, a reduction in the marine mammal population might actually mean fewer fish for fishermen — in other words, a cull of a marine mammal population might well be detrimental to the interests of a fishery.

Another popular misconception, which must be put to rest, arises from comparisons of the estimated amount of food eaten by a marine mammal with the amount of fish caught by a fishery (e.g., Harris 1990b). When the prey species of a marine mammal and a commercial fishery overlap, it is usually assumed that the two are in competition and, once again, that a reduction in the marine mammal population will result in larger catches for fishermen. Entirely neglected in such simple-minded arguments is the fact that dietary overlap alone is *not* a measure of ecological competition. Although the concept of "competition" seems deeply ingrained in the public psyche, its role in nature is not something that scientists understand very well; indeed, with the exception of simple laboratory experiments, it is often very difficult to demonstrate that interspecific competition is actually occurring in the real world (e.g., Wiens 1983). Consequently, the importance of competition, both as a driving force in evolution and in the structuring of ecological communities, remains the subject of considerable scientific debate. Consistently, there is not one single example that demonstrates that marine mammals are competing (in an ecological sense) with commercial fisheries (Anon. 1981a; Lavigne 1991a). Therefore, there is not one example of a situation in which a call for culling a marine mammal population has been supported by rigorous scientific evidence.

Widespread misconceptions about the so-called "balance of nature" also creep into discussions of interactions between marine mammals and fisheries (for a recent discussion of the "balance of nature," see Pimm 1991). It is frequently remarked that when we exploit fisheries, we disturb the balance of nature. This balance, the argument goes, can be restored simply by culling marine mammals. Such views are hopelessly naive. Natural ecosystems are not static, delicately balanced entities. Rather, they are dynamic, and they change over time. Most fish stocks, for example, naturally fluctuate widely from year to year (Campagna 1990). A particularly striking illustration was recently reported in the Barents

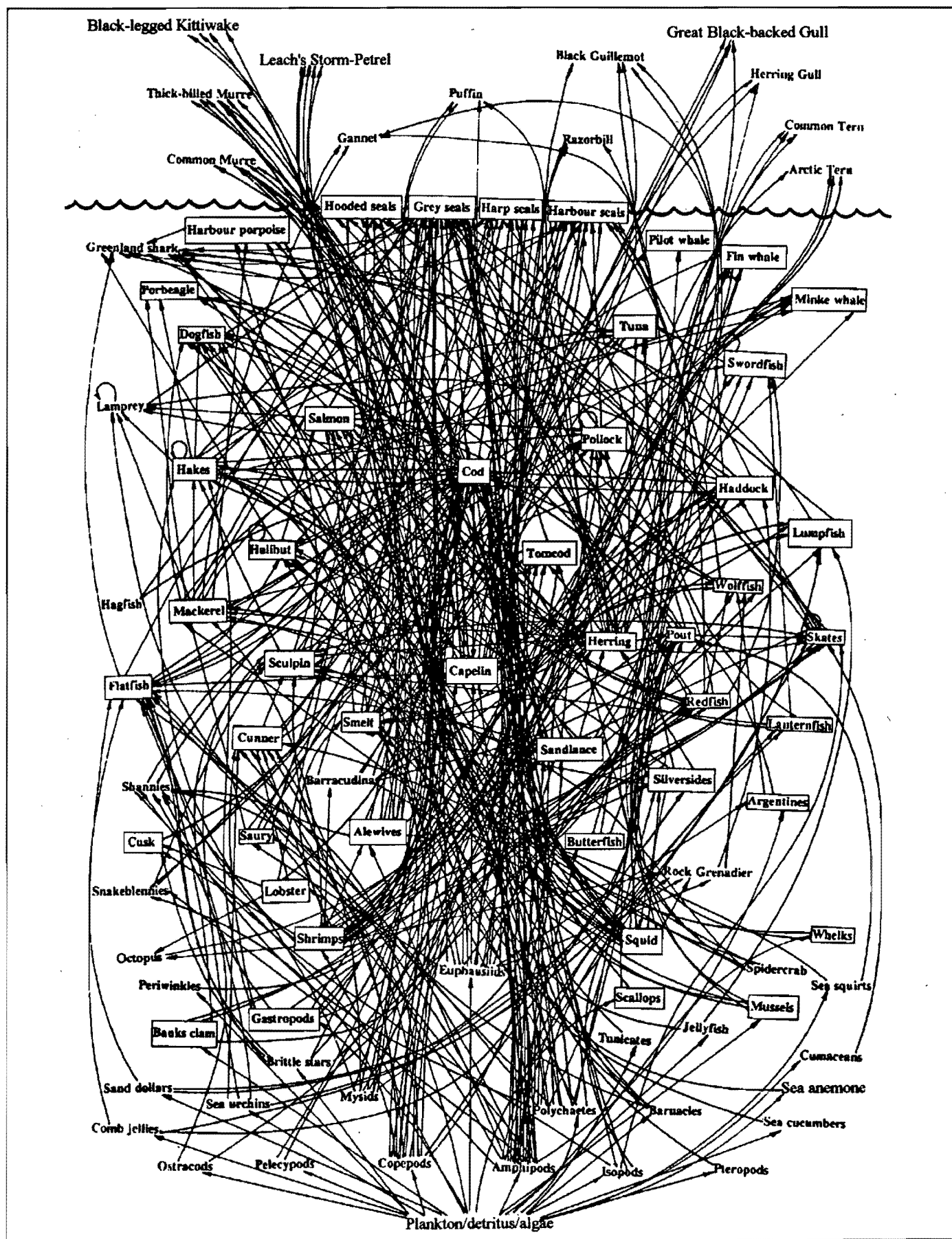
**Figure 3**  
Simple food chain representation of "trophic" interactions in the Northwest Atlantic. In this schematic, from top to bottom, humans (represented by a fishing vessel) hunt harp seals and fish for cod and capelin; harp seals eat both cod and capelin; and cod eat capelin (compare this representation with that outlined in Fig. 4)



Sea. Following a decline in the capelin biomass during the 1980s, the stock rebounded from an estimated 181 000 t in 1989 to some 2 620 000 t the following year (ICES 1990). To pretend that we know enough to "manage" such complex systems in order to achieve a "balance" that itself may be hypothetical is wishful thinking at best. Indeed, a recent workshop concluded that because the abundance of "stocks of fish and other prey are subject to considerable fluctuations . . . [a] comparison of fishery yields or stock levels before and after a seal cull would almost certainly not provide a reliable indication of its effect" (Anon. 1991b). Consistently, there are no well-documented examples of situations in which culling a marine mammal population has been shown to produce positive benefits for a fishery.

The fact is, we do not know how to manage ecosystems, and, in reality, we don't even try. What we do attempt to manage — and we haven't been very successful at this, either — is human activities. We grant licences to fishermen; we limit their catches with quotas or total allowable catches; or we limit the time (seasons) during which they are allowed to fish. The real object of management is not really to regulate wild populations of fish (or other wildlife) but rather to ensure that catches from them are sustainable into the future.

**Figure 4**  
 Partial food web for the Scotian Shelf (NAFO Fishing Areas 4VWX) in the Northwest Atlantic off eastern Canada. Species enclosed in rectangles are also exploited by humans. This web is incomplete, because the feeding habits of all components have not been fully described. Further, all species shown do not spend the entire year within the area (compiled from a variety of sources by D. Huyck)



## 6. Conclusions

Scientific understanding of the potential interactions between marine mammals and fisheries has not progressed very rapidly over the last 15 years. The reasons for this seem clear: biologists have spent far more time studying aspects of marine mammal energetics and their feeding habits than they have examining questions about ecological interactions.

We have only just begun to integrate information gleaned from bioenergetics and feeding studies with approaches designed to address the role that marine mammals play in marine ecosystems and, specifically, to investigate the potential impacts that they might have on commercial fisheries, and vice versa. It cannot be guaranteed, however, that when more research on interactions is completed, we will be able to provide answers to all the questions that arise about interactions between marine mammals and fisheries.

We must accept, therefore, that there will always be limits to our understanding of the natural world. Consistently, there are limits to what "science" can contribute to resolving current concerns about the potential impacts of marine mammals on commercial fisheries. As someone once remarked, prediction [in a stochastic world] is always difficult . . . especially when it involves the future.

We must also remember that perceived conflicts between marine mammals and fisheries tend to surface most often when commercial fish stocks are in a state of decline and when fishing interests seem threatened. Very often, the reasons for the decline in the fishery are clear — poor fishing practices and failures in fishery management. So, in addition to recommending more "science" as a solution to current fishery problems, we might also recommend some historical studies to examine the circumstances that frequently lead to the collapse of commercial fisheries: things like overcapitalization, overoptimistic quotas, excessive catches, and failures in enforcement. These are things we can do something about, which might not only ameliorate current fishery problems but also prevent them from recurring.

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