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SEABIRD/FISH INTERACTIONS, WITH PARTICULAR REFERENCE TO SEABIRDS IN THE NORTH SEA

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1 Seabird/fish interactions: an introduction

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The prey of seabirds consists in many cases of finfish or shellfish that are harvested by humans or which are the prey of species taken in commercial harvests. There is now a considerable body of literature investigating the trophic ecology of seabirds and the potential for interactions with fisheries (e.g., see reviews in Nettleship *et al.*, 1984; Croxall, 1987). Thus, in recent years growing attention has been paid to the inclusion of estimates of fish consumption by marine birds and mammals when multi-species models of fisheries interactions have been developed for assessing catch limits (Croxall, 1989; Anon., 1991; Rice, 1992). Several modelling efforts have shown that localized consumption of prey by seabirds has the potential to remove significant amounts of biomass (Weins and Scott, 1975; Furness, 1978; Furness and Cooper 1982; Duffy and Schneider, 1992), although when this impact is viewed over larger spatial scales, it represents only a small portion of the prey potentially available (e.g., Bailey, 1982; Duffy and Siegfried, 1987). If we assume that seabird populations are prey limited (Cairns, 1992b), then seabird consumption of prey taken by commercial harvests is of interest to marine scientists because of the potential for competition between seabirds and fisheries when local prey stocks become depleted (e.g., Schaefer, 1970; Furness, 1982; Furness and Monaghan, 1987; Montevecchi and Barrett, 1987; Croxall and Prince, 1987; Nehls, 1989; Croxall, 1989; Vader *et al.*, 1990a). In other instances, fisheries activities can increase the availability of prey to birds by removing predatory fish (Springer, 1992) or by generating offal and discards (e.g. Wahl and Heinemann, 1979; Hudson and Furness, 1988; Furness *et al.*, 1988; Garthe, 1993; Camphuysen *et al.*, 1993; Garthe *et al.*, 1996).

The trophic linkages of seabirds to fish stocks are also of interest as they provide an alternative approach for monitoring changes in the distribution, abundance and age class structure of prey populations. Recent attempts to use seabirds as indicators of aspects of prey stocks include Hislop and Harris (1985), Berruti (1985), Cairns 1987, 1992a), Croxall (1989), Monaghan *et al.* (1989), Barrett *et al.* (1990), Hatch and Sanger (1992) Klages *et al.* (1992), Montevecchi and Myres (1992), Montevecchi (1993), Decker *et al.* (1995); Hunt *et al.* (1996, In press), see also Lilly (1991). Indices of changes in prey stocks determined from seabirds complement more traditional

indices used in fisheries management and can provide information about age classes of fish and inshore populations and distributions frequently under sampled in conventional surveys (Barrett *et al.*, 1990; Barrett, 1991; Montevecchi and Berruti, 1991; Montevecchi and Myres, 1992). Implicit in this approach to monitoring prey stocks is the assumption that aspects of seabird behaviour and population biology are linked to prey stock size, but the reliability and nature of such links require documentation before such indices can be accepted (Cairns, 1987, 1992; Hunt *et al.*, 1991). Nevertheless, it is clear that prey abundance influences seabird population biology at the extremes of stock size variation. A full understanding of the nature of interactions between seabirds and fisheries can only be gained when the relationship between seabirds and their food organisms on the one hand, and between fisheries and fish populations on the other, are understood.

1.1 What seabirds eat

Seabird species take a wide variety of prey in a diversity of marine habitats. For instance, waders typically exploit infaunal invertebrates in littoral and sublittoral zones, and many nearshore-foraging sea ducks, cormorants, and shags take epibenthic prey in the neritic zone. Other marine birds include surface- and near-surface-foraging storm-petrels, fulmars *Fulmarus glacialis*, gannets *Morus bassanus*, gulls and terns, and subsurface pursuit-diving auks that forage in nearshore, and to a lesser extent, in offshore waters.

The primary foods of most seabirds worldwide are densely-schooling, small, lipid-rich pelagic fishes, crustaceans and cephalopods that occur in the upper- to mid-water column (e.g. Furness, 1978; Hunt *et al.*, 1981; Anderson and Gress, 1984; Croxall *et al.*, 1984; Piatt and Nettleship, 1985; Montevecchi *et al.*, 1992). Seabirds also consume demersal fishes (during pelagic egg, larval and juvenile stages (Barrett *et al.*, 1990), inshore benthic fishes (Birt *et al.*, 1987), shellfish (Goudie and Ankney, 1988) and fish offal and discards (Hudson and Furness, 1988). At high northern latitudes, sandeels *Ammodytes* spp., herring *Clupea harengus*, capelin *Mallotus villosus*, walleye pollock *Theragra chalcogramma* and Arctic cod *Boreogadus saida* dominate harvests of pelagic fishes by seabirds. Anchovies and sardines are primary prey for birds in temperate boundary currents (Rice, 1992). In the northern hemisphere cephalopods are mostly exploited by seabirds at mid- and low-latitudes (Furness, 1995); crustaceans can be important prey at any latitude. Because most seabirds eat small fish or the juvenile stages of large fish, in many cases it can be assumed that the period of highly variable fish mortality has passed, and that seabirds take prey after the size of the prey cohort has been set. Most seabirds show seasonal variation in diet and varying degrees of prey selectivity. Many species are opportunistic, taking whatever mix of prey species is available, although in multispecies communities, seabird species show distinct, consistent preferences for particular prey. Prey preferences may be constrained by forag-

ing behaviour and energy requirements. Energetic constraints include the costs of capturing and transporting food to chicks at colonies during breeding seasons, and the energy density of prey. The high metabolic demands of seabirds require frequent intake of energy-rich food.

Seabirds are migratory and exhibit seasonal changes in distribution and concentrations. Waders and most species of sea ducks migrate to high latitude tundra or freshwater habitats to nest and rear offspring. Seabirds aggregate at insular and coastal colonies that tend to be very large at high latitudes, with higher numbers of large and moderately sized colonies in temperate areas. Foraging ranges around breeding colonies are usually in the order of 10s of km, and for the most part less than 100 km, with the exception of pelagic seabirds such as some petrels. Once young birds of the year leave the colony, many species shift to more pelagic habitats, though most species of gulls and terns continue to forage in nearshore habitats throughout the year.

Most species of marine birds capture their food independently of human activities, though others have learned to exploit fisheries' offal and discards. Large-scale demersal trawler fisheries have provided massive quantities of artificial (naturally unavailable) food in the form of offal and discards (e.g., Wahl and Heinemann, 1979; Abrams, 1983; Tasker *et al.*, 1987; Hudson and Furness, 1988; Furness *et al.*, 1992; Camphuysen *et al.*, 1993; Garthe, 1993). This "new food" production may be responsible for increases in the numbers of many seabirds (e.g., Fisher, 1952; Burger and Cooper, 1984; Furness, 1992; Howes and Montevecchi, 1993).

1.2 How much seabirds eat

Seabirds consume substantial tonnages of fish and other marine organisms. The most widely used and comparative index of fish consumption by seabirds is the proportion or percentage of pelagic fish production consumed (Wiens and Scott, 1975). Ratios of consumption to production are more useful indices than ratios of consumption to biomass for small pelagic fish, crustaceans and cephalopods (Duffy and Schneider, 1992). When assessing potential influences of predation by seabirds on fish populations, it is informative to consider harvests in terms of yield-at-age analyses and number of individual prey harvested because birds often take juvenile fish that otherwise might have had a high probability of entering a fishery (Cairns, 1992a). To date, there are few examples of this approach (Barrett *et al.*, 1990; Anker-Nilssen, 1992).

Estimates of the pelagic production consumed by seabird communities are generally inversely related to ocean area included in the energetic model (Table 1.1), suggesting that competitive interactions with fisheries are more likely at the meso-scale (Furness, 1990; Bailey, 1991) than at larger scales. However, even in consideration of localized marine areas, these models miss the dynamics of pelagic prey movements through avian foraging ranges around colonies. Food supplies around colonies in highly dynamic regimes may depend more on the advection and in migration of prey than on its production locally (e.g. Cairns and Schneider, 1990; see also Springer *et al.*, 1987; Hunt, 1991). Low consumption rates by seabirds over large scales imply that seabirds are unlikely to compete with fisheries, but do not indicate that seabirds are unaffected by commercial fishing (Duffy and Schneider, 1992).

Table 1.1 Community energetics models of fish harvests by seabirds.

Location	Estimated % pelagic fish production consumed	Major consumers	Sources
Oregon coast	22	Shearwaters, Storm-petrel, Cormorant, Guillemot	Wiens & Scott, 1975
Foula	29	Fulmar, Guillemot, Shag, Puffin	Furness, 1978
North Sea	5–8	Fulmar, Gulls, Terns, Guillemot, Puffin	Bailey, 1986; Bailey <i>et al.</i> , 1991
North Sea	5–10	Fulmar, Gannet, Shag, Gulls, Kittiwake, Terns, Razorbill, Guillemot, Puffin	Tasker <i>et al.</i> , 1989
Saldanha Bay	29	Penguin, Gannet, Cormorant	Furness & Cooper, 1982
Benguela region	6	Gannet, Cormorant	Duffy <i>et al.</i> , 1987

1.3 Seabird life history characteristics and influences of fluctuations of prey stocks on seabird populations

The behavioural ecology and life-history traits of marine birds act to buffer seabird populations from fluctuations in food supply (Montevecchi and Berruti, 1991; Cairns, 1992a). Seabirds display the classic K-selected characters of high annual survivorship, great longevity, delayed sexual maturity, and low annual reproductive rate. All seabirds are K-selected in relation to typical birds and mammals of similar size, and the intensity of K-selectedness increases with increasing distance of foraging habitat from shore. Lack (1968) classified seabirds as inshore foragers, which seek prey within sight of land and which rear several young per year, or offshore foragers which search for prey across the width of continental shelves and beyond, and which raise one young per year. Survivorship, longevity, and age of sexual maturity are greater in the offshore than in the inshore foragers. One might add a third category; that of oceanic birds, which have exceptionally long lifespans and which may breed only in alternate years.

Fluctuations in fish stock recruitment are likely to affect the survival of adult seabirds and seabird reproduction differently. Except in extreme cases of a region-wide collapse of all available prey stocks, adult seabird survival is unlikely to be affected by the common interannual variability of prey stocks. This is because adults can shift to alternate prey or migrate to seek prey in other regions. In contrast, breeding birds are tied to their colonies, and local fluctuations in fish recruitment can have a dramatic effect on seabird reproduction. If food supplies are reduced below the amount needed to generate and incubate eggs, or the specific species and size of prey needed to feed chicks is unavailable, local reproduction by seabirds will fail. Seabird reproductive output can, therefore, be expected to vary with fish recruitment, and the degree of linkage will depend on the narrowness of the species-size requirements of chick feeding and the availability of alternate prey. Seabird populations will not directly track fluctuations in prey recruitment because seabird populations are typically composed of numerous year classes, and recruitment of a cohort of seabirds to breed occurs over a number of years. Over the long term, seabird populations will respond to fish recruitment fluctuations if recruitment is consistently good or bad for several years.

In typical situations where seabirds harvest young teleost fishes, populations of adult seabirds and of adult fish will be relatively stable and numbers of young fish and young birds will be relatively unstable. However, in situations where seabirds feed on fish subject to environmental changes sufficiently intense to kill adult fish, both seabird populations and seabird reproduction may fluctuate greatly. The El Niño Southern Oscillation (ENSO) is the classic example, where physical phenomena severely reduce fish populations to the point that adult seabirds may starve. In such a case, seabird population recovery can be expected to lag behind population recovery of the

fish, since the fish can reproduce much faster than the birds.

There are many demonstrations of positive associations between the reproductive performance of seabirds and independent estimates of prey abundance (Hunt and Butler, 1980; Anderson and Gress, 1984; Springer *et al.*, 1986; Monaghan *et al.*, 1989; see also Diamond, 1978; Gaston *et al.*, 1983; Furness and Birkhead, 1984; Birkhead and Furness, 1985; Hunt *et al.*, 1986; Birt *et al.*, 1987). There is also evidence for decreases in seabird populations in response to drastic changes in prey stocks (Lid, 1980; Duffy, 1983; Schreiber and Schreiber, 1989). Some of these food shortages are generated by megascale oceanographic events, such as ENSO warm water events. Surface-feeding seabirds are more vulnerable to thermal perturbations than are pursuit-divers that can access much more of the water column (Montevecchi, 1993; Decker *et al.*, 1995). The higher vulnerability of surface feeders compared to pursuit-divers is reflected in the higher reproductive variability of the former.

1.4 Fisheries and seabird interactions

Fisheries probably always have greater effects on seabirds than vice-versa. The most direct influences of human-induced changes of fish populations on seabirds occur when both the fishery and the birds exploit the same-sized prey of a particular species, usually small pelagic fishes. There are many examples of such interactions producing severe consequences for seabirds (Table 1.2; Montevecchi, 1993). Indirect, more complex trophic interactions can occur when fisheries are directed at larger prey than seabirds eat, i.e. when seabirds prey on fish of smaller size than are captured by the fishery. Because most large-scale fishery technologies (e.g. trawlers, gill nets) target large demersal fishes, most of the effects of these fisheries are indirect and positive. By cropping large piscivorous predators and cannibals, these fisheries benefit seabirds by increasing the abundances of small fish and crustaceans (e.g. Sherman *et al.*, 1981; Alverson, 1991; Springer, 1992; see also May *et al.*, 1979). However, if recruitment overfishing occurs, it may be harmful to seabirds because availability of juvenile stages of the predatory species may be reduced. From a seabird's point of view, the ideal situation is removal of a competing predator which is never itself a prey. Over-harvest of whales in the Southern Ocean has often been cited as being of benefit to penguins because of the removal of a competitor. The current depletion of many groundfish species in the Northwest Atlantic may provide a test of this notion. Seabirds, notably guillemots *Uria aalge*, eat some juvenile cod *Gadus morhua* but their main prey is capelin, a major prey of cod. If fisheries aid seabirds by removal of competitors, seabird reproductive rates should be higher than normal in the next several years in areas where groundfish stocks are low and limiting. When seabirds prey on smaller fish than the fishery captures, then seabirds have a greater probability of influencing prey availability for human harvests (Bailey *et al.*, 1991; Cairns, 1992a).

Table 1.2 Correspondence between collapses of fish stocks and breeding failures or population declines of seabirds.

Fish	Years	Location	Bird	Source
Herring	1964–1989	Norway	Atlantic puffin	Barrett <i>et al.</i> , 1987; Anker-Nilssen, 1987,1992
Capelin	1985–1987	Barents Sea	Common guillemot	Vader <i>et al.</i> , 1990a,b
Sandeel, herring	1986–1990	Shetland	Shag, Common guillemot, Great skua, Kittiwake, Arctic tern, Atlantic puffin	Monaghan <i>et al.</i> , 1989; Uttley <i>et al.</i> , 1989; Furness, 1990; Bailey <i>et al.</i> , 1991; Hamer <i>et al.</i> , 1991; Klomp and Furness, 1992
Capelin	1981	NW Atlantic	Atlantic puffin	Brown and Nettleship, 1984
Anchovy	1969–1980	S. California Bight	Brown pelican	Anderson <i>et al.</i> , 1982
Anchoveta	1950s–1970s	Humbolt Current	Peruvian brown pelican, Guanay cormorant, Peruvian booby	Duffy, 1983
Pilchard	1956–1980	Benguela	Jackass penguin, Cape gannet	Burger and Cooper, 1984; Crawford <i>et al.</i> , 1985

1.5 Focus of this report

The objective of this report is to evaluate the interactions that have been identified between seabirds and fish, and between seabirds and shellfish, in the North Sea and other nearby regions. Over 4 million marine birds breed on the islands and along the coast of the North Sea. In winter, similar numbers forage here, but species composition differs from that in summer due to seasonal migrations (Dunnet *et al.*, 1990). Additionally, particularly in autumn and winter, half a million seaducks forage in coastal waters and several million migrant waders forage in the intertidal zone. Chapter 2 of this report provides seasonal estimates of seabird consumption of prey, by prey species and by location for the North Sea. In Chapter 3, we extend the analysis of prey consumption by examining the size- or year classes of prey taken where data permit. In Chapter 4, we evaluate evidence that fisheries and seabirds in the North Sea compete for selected prey species. Our analysis is not comprehensive for pelagic birds in the North Sea. In Chapter 5, we include examples of studies detailing consumption of shellfish by seaducks but we do not consider consumption by shorebirds (waders) other than by oystercatchers. Our results provide a first step in developing the information necessary for including seabird prey demands in multispecies assessments for fisheries management, and for understanding the interaction between seabirds and fisheries.

Considerable data on interannual variation in the reproductive success of seabirds is available from the coasts of the North Sea. These data, when combined with information on colony specific food habits, have the potential of providing fisheries managers with additional insights as to the distribution and fluctuations of fish stocks. However, despite data from these colonies have not been drawn together to examine interannual variability, the spatial scales over which such variation correlates among colonies, and the biological and physical oceanographic factors that may force seabird responses. In approaching these analyses, we sought the council of fisheries biologists and oceanographers at the Marine Laboratory in Aberdeen. The task of assembling the multiplicity of data sets within and between disciplines has proven a greater task than originally envisaged, and the preliminary analyses presented in this report are intended as examples of the potential for a wider variety of investigations. The preliminary investigations of the available data reported in Chapter 6 have demonstrated that there exist adequate time series for meaningful analysis, that the initial results make biological sense, and that there is the potential for results of interest to a broad range of marine scientists. In Chapter 7, we examine the data from one set of tern colonies in the Wadden Sea as an example of what can be learned from studies of seabird reproductive ecology and food habits.

2 Estimation of food consumption by seabirds in the North Sea

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2.1 Introduction

It is important to know the consumption of prey by seabirds if their impact on fish stocks is to be adequately represented in the models of natural mortality used by fisheries managers. Likewise, if management schemes are to account for the needs of seabirds, there needs to be some estimate of these needs. To provide information of the consumption of prey by seabirds in the North Sea, the Study Group constructed a simple model. This model required the following information:

1. seabird numbers in sections of the North Sea for each month of the year,
2. energy requirements of these birds,
3. diet composition by mass,
4. energy content of foods,
5. food utilisation efficiency (assimilation efficiency).

In this section, the data requirements for estimation of fish consumption by North Sea seabirds are examined and estimates of consumption of prey are calculated using the best data currently available. Deficiencies in the data set are highlighted, since improvements to the estimates could clearly be made.

2.2 Seabird numbers

Seabird numbers were obtained by combining data on densities of seabirds at sea (numbers on or above a unit area of sea) throughout the year and from data on numbers of breeding and non-breeding individuals attending colonies around the North Sea in different months. The following two sub-sections detail these model inputs. These numbers and much of the rest of the model are based on the six ICES divisions of the North Sea (IVa west, IVa east, IVb west, IVb central, IVb east, IVc).

2.2.1 Seabirds at sea

Methods for counting birds at sea from ships in the North Sea are described by Tasker *et al.* (1984) and Webb and Durinck (1992). These methods, or slight variants, have

been used by seabird counters from many countries around the North Sea. The data collected by these observers have been assembled into one database (the European Seabirds at Sea (ESAS) database), managed by the Joint Nature Conservation Committee in Aberdeen, Scotland. The majority of the data within the North Sea were collected between 1980 and 1987, but some substantial new data for some areas in some months of the year are included in the present model. All available data have been used in this modelling effort, regardless of year. Temporal trends in seabird distribution have been ignored. Much of the information held on the database was published in 1987 (Tasker *et al.*, 1987). A further analysis is in progress which will include an analysis of any temporal trends (Webb *et al.*, in prep.).

Most observations were collected away from coasts due to the avoidance of nearshore waters by ships from which observations were made. This zone is used by a number of seabird species not considered in detail in this analysis. Survey effort farther offshore has not been uniform. In general, there has been a reasonable amount of survey in all areas in all months, with the exception of ICES Sub-Division IVa (east). Waters in this area have been surveyed adequately in July and August, but very poorly in January, March, October and December (Table 2.1). As a rough guide, every 1 km² surveyed takes about 10 minutes; thus there have been many hours spent in some areas. The higher the ratio of ICES rectangles to the number of rectangles in each area, the better the distribution of effort. Hunt (pers. comm.) estimates that between 500 and 1000 ten-minute counts are required in an area before the estimate of the mean number of birds in the area stabilizes satisfactorily.

Despite standardized observation procedures being used, different teams of observers produce some detectable variations between data sets. These variations have not been analyzed in depth; however, some data have been treated to minimize the effects of known variations and this will be described in detail in Webb *et al.* (in prep.). Estimates of the density of seabirds in the North Sea may change slightly once such analyses have been completed, and the outputs of the model constructed here may also change as a consequence.

Mean densities of each species in each ICES rectangle in each area were averaged to produce an average density of birds for each area for each month. The low survey effort in ICES Division IVa (east) in January and December produced anomalous mean densities (for kittiwake *Rissa tridactyla* and gannet) that were ignored, and a mean value interpolated between adjacent months' data was inserted. In addition, herring gull *Larus argentatus* densities in ICES Division IVc seemed anomalously high, and this density was reduced to one-fifth.

Table 2.1 Seabird distribution at sea in the North Sea. Data collected between 1980 and 1993. Survey effort (km²) covered in each month in each area and the number of ICES rectangles visited.

Month	Area											
	IVaW		IVaE		IVbW		IVbC		IVbE		IVc	
	km ²	rectangles	km ²	rectangles	km ²	rectangles	km ²	rectangles	km ²	rectangles	km ²	rectangles
Total in area	156,906	62	97,271	34	69,447	27	140,933	40	62,781	24	56,763	22
January	295	30	30	5	359	17	568	25	698	21	920	18
February	1,246	45	80	10	642	25	1,166	38	1,092	23	1,499	22
March	1,642	41	29	4	209	16	660	26	257	17	1,214	18
April	1,494	43	86	10	280	15	929	28	1,041	23	1,481	19
May	1,395	40	426	22	772	21	1,146	35	926	21	672	20
June	1,612	50	159	15	708	22	1,322	29	395	19	1,029	19
July	2,238	44	765	30	714	22	1,629	38	681	21	661	17
August	2,369	49	1,066	31	2,381	26	1,860	39	942	24	1,108	20
September	1,728	38	376	24	2,567	25	1,370	38	420	17	1,435	20
October	656	35	46	5	550	20	593	27	1,322	24	665	19
November	1,256	34	180	17	540	20	1,143	33	822	22	1,133	17
December	844	32	13	4	544	21	812	23	320	20	1,411	18
Total survey effort	16,775		3,253		10,266		13,198		8,916		13,228	

Table 2.2 Numbers of seabirds breeding on coasts of the five ICES areas considered.

Species	IVa (west)	IVa (east)	IVb (west)	IVb (east)	IVc	Census units
Northern fulmar	294,128	0	12,596	36	697	occupied sites
Gannet	21,648	0	22,130	0	0	pairs
Cormorant	1,483	18	703	0	18	"
Shag	13,486	1,755	4,563	0	0	"
Great skua	7,299	4	0	0	0	"
Black-headed gull	3,455	36,854	15,980	53,781	19,272	"
Common gull	15,770	43,240	80	6,452	7,790	"
Lesser black-backed gull	2,583	25,502	2,180	15,791	3,255	"
Herring gull	41,827	34,037	40,445	96,293	24,512	"
Great black-backed gull Kittiwake	9,924	14,480	31	1	0	"
Arctic tern	206,606	2,991	199,949	3,310	2,571	"
Common tern	55,951	8,634	5,349	4,712	83	"
Sandwich tern	1,157	39,815	1,730	14,407	4,378	"
Common guillemot	1,121	1,502	5,592	14,687	7,644	
Razorbill	507,487	438	167,609	4,900	0	individual at ledges
Black guillemot	54,537	302	18,260	16	0	"
Atlantic puffin	20,847	2,891	3	0	0	individuals in spring
	124,289	21,695	79,973	0	0	individuals, or burrows \times 2

2.2.2 Seabirds at colonies

Methods for counting birds at colonies vary with species. In general, surface nesting species have been counted by direct observation, while burrow nesting species have been censused by counting burrows, either as a total count or in a set of samples. Methods used in the UK in the 1980s are described by Lloyd *et al.* (1991). In general, these or similar methods have also been used elsewhere around the North Sea. Totals of these counts, mostly from the early to mid-1980s are given in Table 2.2. There have been few recent major changes in numbers in any area, but overall numbers of breeding sea-

birds are probably at or close to historical highs in most areas.

To calculate total numbers of birds feeding, the estimates of birds temporarily at colonies have to be added to those at sea. Table 2.3 indicates the proportion of the birds that breed at a colony that are likely to be present on land during each month. Because most cormorants *Phalacrocorax carbo* and shags *P. aristotelis* occur in the poorly surveyed near-shore zone, and because they are resident in areas, colony numbers (counted in pairs) were used for them throughout the model. Numbers of terns should also have been treated in this way, but due to an error were not. Their contribution to the overall model would be negligible even if their input numbers were doubled; thus this input error is not important overall.

Table 2.3 Factors used in converting seabird population colony census data to numbers of individuals at colonies in each month of the year. Proportion of census number that are present at colonies.

Species	Month											
	Jan	Feb	Mar	Apr	May	June	July	August	Sept	October	Nov	Dec
Fulmar	0.75	1.00	1.00	1.00	0.75	1.00	0.50	0.25	0.10	0.00	0.20	0.50
Gannet	0.00	0.00	0.25	0.75	1.00	1.00	1.00	1.00	0.50	0.10	0.00	0.00
Cormorant	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.80
Shag	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
Great skua	0.00	0.00	0.00	0.50	1.00	1.00	1.00	0.50	0.10	0.00	0.00	0.00
Black h. gull	0.00	0.00	0.25	0.50	1.00	1.00	1.00	0.50	0.10	0.00	0.00	0.00
Common gull	0.00	0.00	0.25	0.50	1.00	1.00	1.00	0.50	0.10	0.00	0.00	0.00
Lesser bb gull	0.00	0.00	0.00	0.50	1.00	1.00	1.00	0.50	0.10	0.00	0.00	0.00
Herring gull	0.00	0.10	0.50	0.75	1.00	1.00	1.00	0.50	0.10	0.00	0.00	0.00
Great bb gull	0.00	0.10	0.50	0.75	1.00	1.00	1.00	0.50	0.10	0.00	0.00	0.00
Kittiwake	0.10	0.25	0.50	1.00	1.00	1.00	1.00	0.50	0.10	0.00	0.00	0.00
Arctic tern	0.00	0.00	0.00	0.00	1.00	1.00	1.00	0.20	0.00	0.00	0.00	0.00
Common tern	0.00	0.00	0.00	0.00	1.00	1.00	1.00	0.20	0.00	0.00	0.00	0.00
Sandwich tern	0.00	0.00	0.00	0.00	1.00	1.00	1.00	0.20	0.00	0.00	0.00	0.00
Guillemot	0.10	0.25	0.50	1.00	1.00	1.00	0.50	0.00	0.00	0.00	0.00	0.00
Razorbill	0.10	0.25	0.50	1.00	1.00	1.00	0.50	0.00	0.00	0.00	0.00	0.00
Black guillemot	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Puffin	0.00	0.00	0.00	0.25	1.00	1.00	1.00	0.25	0.00	0.00	0.00	0.00

Table 2.4 Factors used to estimate the number of non-breeders at colonies in each month as a proportion of the colony census unit.

Species	Factors			
Fulmar	0.0	all months		
Gannet	0.2	(May, Jun, Jul)		
Cormorant	0.2	all months		
Shag	0.2	all months		
Great skua	0.2	(May, Jun)	0.1	(Jul)
Black h. gull	0.2	(May, Jun)	0.1	(Jul)
Common gull	0.2	(May, Jun)	0.1	(Jul)
Lesser -b. gull	0.2	(May, Jun)	0.1	(Jul)
Herring gull	0.2	(May, Jun)	0.1	(Jul)
Great -b. gull	0.2	(May, Jun)	0.1	(Jul)
Kittiwake	0.2	(May, Jun)		
Arctic tern	0.1	(May, Jun)		
Common tern	0.1	(May, Jun)		
Sandwich tern	0.1	(May, Jun)		
Guillemot	0.0	all months		
Razorbill	0.0	all months		
Black guillemot	0.0	all months		
Puffin	0.3	(May, Jun, Jul)		

In addition to breeding birds, colonies are also attended by non-breeding and pre-breeding birds. Table 2.4 lists the proportions of numbers counted at colonies that need to be added to account for these non-breeding birds. The timing of breeding activities, age at first breeding and adult survival rates needed for input of the above parameters have been reviewed by Dunnet *et al.* (1990).

Input to the model of numbers at colonies was thus a multiplication of numbers counted at colonies. The exact multiplier depended on species and time of year. These colony figures were added to estimates of numbers at sea before further energetic modelling.

It should be noted that new information on population levels at colonies in the south and east North Sea has become available since the review of Dunnet *et al.* (1990). This information documents considerable increases in the numbers of gulls breeding on these coasts; however such increases are not thought to have a great effect on the results of the model. Future model refinements should take account of such population changes.

2.3 Seabird energy requirements

The energy requirements of seabirds are very high relative to those of fish of the same mass. This is because, unlike fish, seabirds are endothermic and so use large

amounts of energy to maintain high body temperatures. This requires seabirds to burn more calories to offset heat loss. Metabolic rates in birds usually scale with body mass to a power of between 0.6 and 0.8, such that the metabolism per gram is considerably higher in smaller animals than in large ones. It is thus essential for metabolic rates of each group of predators to be taken into account (Furness, 1984).

Energy requirements of seabirds can be assessed in two independent ways. One involves the use of allometric equations (Croxall 1982; Adams and Brown, 1984; Ellis, 1984; Gavrilov, 1985; Bennett and Harvey, 1987; Gabrielsen *et al.*, 1988, 1993; Birt-Friesen *et al.*, 1989; Koteja, 1991; Bryant and Furness, 1995) or directly determined laboratory or captive metabolic rates extrapolated to the field situation by applying correction factors or by combining laboratory measurements of metabolic costs of activities with field studies of time-activity budgets (Wiens and Scott 1975; Furness, 1978, 1990; Croxall and Prince, 1982, 1987; Furness and Cooper, 1982; Croxall *et al.*, 1984, 1991; Abrams, 1985; Gaston, 1985; Bailey, 1986; Cairns *et al.*, 1986, 1991; Briggs and Chu, 1987; Duffy *et al.*, 1987; Brown, 1989; Bailey *et al.*, 1991; Crawford *et al.*, 1991; Diamond *et al.*, 1993).

The other method uses measurements of rates of turnover of isotopes (usually of hydrogen and oxygen; Nagy,

1980, 1987) in free-living seabirds in order to assess energy expenditure over the period between release of an injected individual and its recapture, usually a day or two later (Kooyman *et al.*, 1982, 1992; Davis *et al.*, 1983, 1989; Flint and Nagy, 1984; Nagy *et al.*, 1984; Adams *et al.*, 1986; Costa *et al.*, 1986; Ricklefs *et al.*, 1986; Roby and Ricklefs, 1986; Gabrielsen *et al.*, 1987, 1991; Obst *et al.*, 1987; Pettit *et al.*, 1988; Birt-Friesen *et al.*, 1989; Cairns *et al.*, 1990; Gales and Green, 1990; Green and Gales, 1990; Montevecchi *et al.*, 1992; Furness and Bryant, 1996).

2.3.1 Time-activity budget models

Many of the papers describing the energy requirements of seabird populations have used detailed species, time-activity budgets and estimates of the energy costs of incubation (Croxall, 1982; Grant and Whittow, 1983; Brown 1984; Brown and Adams, 1984; Pettit *et al.*, 1988), resting (Birt-Friesen *et al.*, 1989), walking (Ellis, 1984), flying (Ellis, 1984; Flint and Nagy, 1984; Birt-Friesen *et al.*, 1989), swimming (Ellis, 1984), diving (Kooyman *et al.*, 1982, 1992), or foraging (= 'at-sea metabolism') (Adams *et al.*, 1986; Costa and Prince, 1987; Birt-Friesen *et al.*, 1989; Cairns *et al.*, 1990); moulting (Croxall, 1982; Brown, 1985), chick growth (Brown, 1987) and other activities to produce a more detailed energy budget for seabirds (Furness, 1978; Burger, 1981). Such a procedure is possible only if detailed data exist for each species, and so is beyond the scope of this study. In particular, we lack information on the time-activity budgets of all North Sea seabirds outside the breeding season, and have little data for most species even during breeding. An alternative to this detailed time-budget approach is to use a direct measurement of energy expenditure as described in the next subsection.

2.3.2 Isotopic analyses of Daily Energy Expenditures (DEE)

The doubly-labelled water technique has recently been used widely on seabirds to measure field metabolic rates (FMRs) and hence average daily energy expenditures of free-living individuals. In some cases this has been combined with the use of devices to record time-activity budgets so that costs of components of the daily budget can be assessed. The technique is simple in principle, requiring birds captured and injected with deuterium (or tritium) and oxygen-18 to be recaptured, usually 24 or 48 hours after release, to obtain a second blood sample to measure the rate of turnover of each heavy isotope. The principles and limitations of analysis are reviewed by Nagy (1980) and Birt-Friesen *et al.*, (1989). In theory, this direct approach to the study of seabird energy demands seems optimal in that it avoids uncertainties in the reliability of complex models based on large numbers of inputs of uncertain accuracy. In practical terms the doubly labelled water method has limitations which may make it no better than the indirect modelling approach. In particular, the fieldwork is difficult and so sample sizes using labelled water tend to be small. Variances in meas-

urements obtained tend to be very large, giving mean estimates of energy expenditure with wide confidence intervals. Furthermore, the results may be biased. The method requires that the behaviour of the birds caught and injected is normal during the 24 or 48 hour study period. In practice, birds may not behave normally. Birt-Friesen *et al.* (1989) showed that injected gannets spent longer away from the nest than did control birds. The same result was obtained with gannets by Furness and Bryant (unpubl.), and they also found striking deviations from normal behaviour in fulmars (Furness and Bryant, 1996). Such effects are often not reported, and may not have been looked for. These results do not necessarily invalidate the procedure, but they do mean that the data produced need to be viewed with caution.

Only one study has examined the extent of agreement of results achieved by activity budget and by labelled water approaches. Nagy *et al.* (1984) obtained measurements of jackass penguin *Spheniscus demersus* FMRs only 3% higher than those produced by the bioenergetics model of Furness and Cooper (1982). Nagy *et al.* (1984) said that this close agreement lends confidence in both methods, which differ considerably in their approaches and assumptions. Kooyman *et al.* (1992) also compared results from labelled water estimation of the energy expenditure at sea with an estimate based on at sea activity budget data and model estimation from costs of resting and diving. Results from the two methods were within 7% of each other.

2.3.3 BMR multiples

Basal Metabolic Rate is the lowest rate of energy expenditure by a bird, in the thermoneutral zone, post-absorptive and at rest. Thus BMR is less than the 'Field Metabolic Rate' (FMR) (= DEE 'Daily Energy Expenditure', = AMR 'Active Metabolic Rate') which includes energy costs of thermoregulation, digestion, moult, reproduction and activity. Drent and Daan (1980) argued that birds and mammals are unable to sustain a work rate in excess of about 4.5 BMR, and most studies of the energy expenditure of birds and mammals using labelled water have found FMRs that are less than 4.5 BMR, though exceptions do exist (Birt-Friesen *et al.*, 1989). Thus it is reasonable to assume that for most seabirds FMR will fall within the range >1 BMR to 4.5 BMR.

Furness (1990) suggested that in cases where the data are not very precise and a simple model is to be preferred, it is best to take a multiple of BMR as a measure of the FMR, rather than to attempt a complex analysis of the energy costs of a time-activity budget. Similarly, Birt-Friesen *et al.* (1989) estimated that FMR of free-ranging breeding seabirds averaged 3.3 BMR (n=18). FMR can also be extrapolated from body mass in regressions calculated for birds of different foraging modes and in different oceanographic regions (Birt-Friesen *et al.*, 1989).

Bennett and Harvey (1987) showed that for the 47 species of birds for which estimates of FMR and BMR were available (but pooling breeding and nonbreeding period

data), the slope of FMR was significantly shallower (0.61) than the slope of BMR (0.68) in relation to body mass (log-log plots). Such a trend would make the use of a constant multiple of BMR invalid, but Koteja (1991) analysing a larger data set which included the data used by Bennett and Harvey (1987) found that for breeding birds as a whole ($n=23$) and for breeding seabirds ($n=12$) the slopes of BMR and FMR on body mass were equal. Furthermore, residuals of FMR and BMR from regression lines were significantly correlated for breeding birds ($r=0.48$, $n=23$, $p<0.02$), the subsample of breeding seabirds giving the same correlation ($n=12$, $r=0.51$). The implication is that species with high BMRs have high FMRs, the ratio of FMR to BMR being somewhat consistent among species, as predicted by the Drent and Daan (1980) model of maximum working capacity. These findings support the use of a single ratio of FMR to BMR. Bennett and Harvey (1987) found that birds had higher FMR to BMR ratios during breeding than at other stages of the annual cycle.

2.4 Diets of seabirds in the North Sea

2.4.1 Foraging methods of seabirds

The diets of seabirds are constrained by the foraging methods that they use to catch prey. Ashmole (1971) classified seabird feeding methods rather than birds, because individual species often exhibit multiple methods of feeding. He identified six categories: 1. wing-propelled underwater swimming; 2. foot-propelled underwater swimming; 3. plunging from the air using momentum to approach prey at high speed; 4. feeding while settled on the surface; 5. feeding when flying, capturing prey at or near the surface; and 6. piracy (kleptoparasitism). In the North Sea seabirds use each of these methods to differing degrees, and many species can make use of several methods (Table 2.5). The auks have particularly specialised feeding methods, though they differ in details of foraging and diets (Swennen and Duiven, 1977; Bradstreet and Brown, 1985; Piatt and Nettleship, 1985). Gulls show the greatest diversity of methods within and among species: differences among species are largely a function of body size and its implications for flight. Gannets and larger gulls are less agile in the air but more powerful and able to displace smaller gull species from food sources (Braune and Gaskin, 1982; Hudson and Furness, 1988; Garthe, 1993).

Many seabirds feed in flocks, and this is especially true of those that feed on fish shoals by plunge- or pursuit-diving. One reason for the development of flocks over shoals is the apparent reluctance of fish shoals to disintegrate when attacked by predators. Around Shetland, shoals of sand-eels at the sea surface used to attract large flocks of seabirds.

The behaviour of seabirds in such foraging flocks in the North Sea has not been studied, but flock foraging has been investigated elsewhere, in terms of interspecific

interactions and age-related feeding performance (Porter and Sealy, 1981, 1982).

2.4.2 Methods used to study seabird diets

Methods of sampling seabird diets and statistical considerations regarding necessary sample sizes and presentation of data have been reviewed by Duffy and Jackson (1986) and in the North Sea context by Dunnet *et al.*, (1990). Food samples may be obtained by killing birds and dissecting the alimentary tract, by removal of stomach contents from living birds using stomach pumps, emetics, or the natural tendency of some species to regurgitate when disturbed or handled, by examination of waste products (faeces or regurgitated pellets) containing identifiable hard parts of prey, or by direct observation or filming of food being consumed, carried, fed to chicks, or dropped at colonies. Recent work on N-isotope ratios in seabird tissues has shown that analysis of isotopes can provide information on the trophic status, but not species composition of diet (Hobson and Montevecchi, 1991; Thompson *et al.*, 1995).

All of these methods have their advantages and disadvantages. All can be used at breeding colonies during summer, but the study of diets in other seasons is restricted to analysing pellets at resting places, to the killing of seabirds or to observing directly the consumption of fish which is practicable behind fishery vessels and has been used in recent years (e.g. Hudson and Furness, 1988; Camphuysen *et al.* 1993; Garthe, 1993; Hüppop and Garthe, 1993). The problem of determining diets and foraging ecology is aggravated by the fact that some seabirds feed extensively or even predominantly at night. Seabirds found dead on coasts in winter can be examined to obtain some information on the foods recently consumed, but probably provide a biased picture. In general, knowledge of the diets of North Sea seabirds is poor for the non-breeding period (Blake 1983, 1984; Blake *et al.*, 1985), but moderate to very good for the breeding season, except for non-breeders.

2.4.3 Interspecific variation in diets

Many studies of the diets of seabirds have been made in recent years in the North Sea and adjacent areas. These show a strong selection for sandeels as food during the breeding season. North Sea seabirds eat many other kinds of animals (Table 2.6). In addition to natural diets, anthropogenic sources such as discards, offal and garbage are used by seabirds, particularly gulls.

Fish and crustaceans are of special importance for seabirds (Table 2.6). Fish is taken by most of the North Sea seabirds, and about 50% of the species take predominantly fish. In comparison, the percentage of fish in the diet often differs among closely-related species, e.g. lesser black-backed *Larus fuscus* and herring gull, Arctic and common tern *Sterna hirundo* or common and black guillemot *Cephus grylle*.

Table 2.5 Feeding methods employed by seabirds in the North Sea. From Dunnet *et al.* 1990.

Species	Wing propelled underwater swimming	Foot propelled underwater swimming	Plunge diving	Surface settled feeding	Flying near-surface feeding	Kleptoparasitism
Diver species	*	***				
Fulmar	*	*	**	***		
Sooty shearwater	*		**	***		
Manx shearwater	**		**	**		
Storm petrel					***	
Leach's petrel				*	***	
Gannet	*		***	*		
Cormorant		***				
Shag		***				
Seaduck species		***				
Pomarine skua	*			*	*	**
Arctic skua					*	***
Great skua			*	*	*	***
Little gull					***	
Black-headed gull			*	*	***	
Common gull			*	*	***	*
Lesser black-backed gull			*	**	***	**
Herring gull			*	**	*	*
Iceland gull			**	**	*	
Glaucous gull			*	***		
Greater black-backed gull			*	**	*	**
Kittiwake			*	*	***	*
Arctic tern			***			
Common tern			***		*	*
Roseate tern			***		*	*
Sandwich tern			***		*	*
Little tern			***		*	
Guillemot	***					
Razorbill	***					
Black guillemot	***					
Little auk	***					
Puffin	***					

*rarely used feeding method; **common feeding method; ***main and predominant feeding method.

Table 2.6 Regular food of seabirds in the North Sea (References: Bezzel, 1985; Bradstreet and Brown, 1985; Garthe, 1993; Harris and Wanless, 1986; Hudson and Furness, 1988; Smit and Wolff, 1980)

Species	Invertebrates			Vertebrates			Anthropogenic sources		
	cepha./moll.	crustaceans	others	fish	birds	mammals	discards	offal	garbage
Diver species	*	*		**					
Fulmar	*	*	*	*			*	*	*
Sooty shearwater	*	*		*				*	
Manx shearwater	*	*		*				*	
Storm petrel	*	*		*				*	
Leach's petrel		*		*				*	
Gannet				**			*		
Cormorant				**					
Shag	*	*	*	**					
Seaduck species	*	*	*						
Pomarine skua			*	*	*	*		*	
Arctic skua				*	*	*	*		
Great skua				*	*	*	*	*	*
Little gull		*	*	*					
Black-headed gull	*	*	*	*	*(eggs)	*	*	*	*
Common gull	*	*	*	*	*(eggs)	*	*	*	*
Lesser black-backed gull	*	*	*	**			*	*	
Herring gull	*	*	*	*	*		*	*	*
Iceland gull	*	*		*				*	*
Glacous gull		*		*	*		*	*	*
Greater black-backed gull				*	*	*	*	*	*
Kittiwake	*	*		**			*	*	
Arctic tern		*		*			*		
Common tern		*		**					
Roseate tern				**					
Sandwich tern				**					
Little tern		*	*	*					
Guillemot		*		**					
Razorbill		*	*	**					
Black guillemot	*	*	*	*					
Little auk		*		*					
Puffin		*	*	**					

**if fish is the predominant food.

Table 2.7 Most important fish families and species consumed by fish eating seabirds in the North Sea.

	Ammodytidae sandeels	Clupeidae clupeids (Herring, Sprat)	Gadidae gadoids (Cod, Haddock, Saithe, Whiting)	Gobiidae	Osmeridae (Smelt)	Scombridae (Mackerel)	Pleuron-ectiformes flatfish	Others	Source
Gannet	*	*	*			*			14
Cormorant	*		*				*	Cottidae	16,17
Shag	*	*	*	*			*	Cottidae	11,12,17
Lesser black-backed gull	*	*	*					Gasterosteidae	15,17
Herring gull		*	*		*		*	Triglidae, Carangidae	6,15
Kittiwake	*	*	*						17
Arctic tern	*	*	*					Gasterosteidae	3,4,17,18,20,21
Common tern	*	*	*		*			Gasterosteidae	2-5,17,18,20
Sandwich tern	*	*							4,19
Guillemot	*	*	*						10,13,17
Razorbill	*	*							9,12
Puffin	*	*	*						1,7,8,17

Sources: 1. Barrett *et al.* 1987; 2. Becker *et al.* 1987; 3. Boecker, 1987; 4. Dunn, 1972; 5. Frank, 1992; 6. Goethe, 1980; 7. Harris, 1984; 8. Harris and Hislop, 1978; 9. Harris and Wanless, 1991a; 10. Harris and Wanless, 1988; 11. Harris and Wanless, 1991b; 12. Harris and Riddiford, 1989; 13. Leopold *et al.* 1992; 14) Nelson, 1978; 15. Nordhuis and Spaans, 1992; 16. Okill *et al.* 1992; 17. Pearson, 1968; 18. Stienen and Tienen, 1991; 19. Veen, 1977; 20. Frick, 1993; 21. Uttley, 1991.

2.4.4 The preferred fish species

The preferred fish families taken by piscivorous seabirds whose diet composition is well known are presented in Table 2.7. The most important fish for the nutrition of seabirds in the North Sea are sandeels and clupeids, especially during the breeding season. Owing to a high fat content, sprat and herring are of high caloric value per unit mass, and sandeels also have relatively high energy content (Harris and Hislop, 1978; Massias and Becker, 1990; Hislop *et al.*, 1991). Clupeids and sandeels are small schooling fish. In other parts of the North Atlantic, the clupeids are replaced by the capelin. A few species of Gadidae are also important prey (Table 2.7), but together with other fish groups mentioned in Table 2.7, they are relatively rare in the diets of the smaller seabird species. They are supplementary prey to which the birds switch if sandeels and clupeids are not available in sufficient numbers to fulfil nutritional requirements.

The key prey of seabirds are also the object of the industrial fisheries. As a consequence, North Sea seabirds are in potential competition with fisheries and at risk if the stocks of prey fish are depleted (e.g., Furness, 1987b; Bailey *et al.*, 1991).

The quality of food can have major effects on the growth and survival of seabird chicks, although it appears to be less important for adults. In gulls and terns, chicks fed on fish grow better than those fed on marine invertebrates (Spaans, 1971; Murphy *et al.*, 1984; Massias and Becker, 1990), probably because fish have higher caloric and protein densities. Puffin chicks grow best on a diet of oily fish, their preferred prey, such as sprat or large sandeel (Harris and Hislop, 1978; Harris, 1984). Similarly, great skuas *Catharacta skua* feed their chicks on sandeels in preference to other food items and the proportion of the diet comprising sandeels is much higher in chicks than in breeding adults or non-breeders at the same time in the season (Furness, 1987a). Dietary studies on Arctic terns *Sterna paradisaea* at Sumburgh (Monaghan *et al.*, 1989) and puffins at Hermaness (Martin, 1989) indicated a marked decline in the size of 0-group sandeels brought back to the nest in the late 1980s. On the basis of a caloric value of sandeels, these changes in prey size represent a marked reduction in the energy content of fish fed to chicks (Hislop *et al.*, 1991).

Even within a prey species, quality can vary considerably. Capelin show large age class differences and seasonal changes in lipid water and protein content (Montevocchi and Piatt, 1984). Seabirds feeding on capelin in north Norway appear to select, or find more readily available, capelin that are ripe and energy rich rather than spent or immature fish (Furness and Barrett, 1985). Possibly the seasonal changes in chemical composition of prey fish in the North Sea are rather less pronounced than those in Arctic fish. However, variation in nutritional content is also found between individual lesser sandeels, herring and sprat at a given time and throughout the year (Hislop *et al.*, 1991). The calorific values and body mass of sandeels larger than 10 cm show marked seasonal trends. As a consequence, the total energy content of a sandeel of a given length in summer is approximately double the spring value. Thus selection by North Sea seabirds of nutritionally superior prey within fish species may occur.

2.4.5 The length and shape of fish chosen by seabirds

The length of fish taken by the seabirds species corresponds to body and gape size of the bird; large species take larger fish, and small species take small fish to feed their young and themselves (Table 2.8; Pearson, 1968). In discard experiments this phenomenon can also be observed (Table 2.9; Hudson and Furness, 1988; Hüppop and Garthe, 1993). Garthe and Hüppop (in press) found positive correlations between body lengths of birds and the lengths of four out of six fish species. Most sandeels eaten by seabirds are 4-16 cm, but sizes can vary among years.

Another factor to be considered is the shape of the fish. Discard experiments showed that, on average, only 30% (5-67%) of all flat fish (mainly dab *Limanda limanda*, flounder *Platichthys flesus* and plaice *Pleuronectes platessa*) but 80% (58-92%) of all round fish (mainly cod, whiting *Merlangius merlangus* and bib *Trisopterus luscus*) were eaten by herring gulls, great black-backed *Larus marinus* and lesser black-backed gulls (Garthe and Hüppop, 1993). This is partly due to the necessity for more complicated handling of flatfish (seabirds find them difficult to swallow) and partly to the higher survival rates of flatfish before being discarded (Kelle, 1976).

Table 2.8 Mean length (and range, mm) of fish collected at Welsh colonies over five seasons (Harris, 1984).

	Sandeel	Sprat
Puffin	61 (36-90)	46 (25-86)
Razorbill	73 (55-158)	54 (30-105)
Guillemot	122 (115-130)	102 (73-130)

Table 2.9 Average length (cm) of some fish species swallowed by seabirds during experimental discarding from fishery vessels in Shetland (area I, summer 1985) and in the North Sea (area II, spring and summer 1992). From Hudson and Furness (1988) and Garthe (1993).

	Area	Whiting	Haddock	Herring	Sandeel
Offered	I	29	28	-	-
	II	23	21	26	19
Fulmar	I	24	23	-	-
	II	22	20	24	20
Gannet	I	31	29	-	-
	II	24	24	27	20
G. black-backed gull	I	29	28	-	-
	II	22	-	27	-
Herring gull	I	26	26	-	-
	II	23	22	27	17
L. black backed gull	I	27	25	-	-
	II	24	23	22	19
Great skua	I	27	26	-	-
	II	21	-	26	-
Kittiwake	II	19	14	16	19

2.4.6 Geographic variation in diets

The diet composition of seabirds varies greatly between localities. Thus, obtaining an accurate picture of the diets of seabirds throughout the North Sea requires studies at a wide variety of localities. This is largely fulfilled for herring gull, common tern *Sterna hirundo*, common guillemot and puffin whose diets have been studied at several breeding sites on the North Sea coast.

The diets of these seabird species vary geographically depending on the site-specific food availability. In the herring gull, which forages predominantly intertidally, marine invertebrates are the main food source. In the Firth of Forth, discards were preferred (Table 2.10). The studied sites differed also in the percentage of marine fish and garbage in the food taken by herring gulls.

Common terns also show intersite differences in diets (Table 2.11). In contrast to common terns on the Farne Islands, common terns in the Wadden Sea rarely feed on sandeels. Crustaceans were taken in high numbers only on

Griend and Wangerooge (Boecker, 1967; Becker *et al.*, 1987). Common terns breeding on the coast of the Wadden Sea exploit smelt *Osmerus eperlanus* or fish caught inland, such as sticklebacks *Gasterosteus aculeatus*, as supplementary food (Becker *et al.*, 1987; Frank, 1992). Clupeids were an important prey in all colonies studied.

The proportion of clupeids in the diets of common guillemots varied from one colony to another (Table 2.12). Clupeids were of major importance only on Helgoland, and, to a lesser extent, on the Isle of May and the Farne Islands. At all colonies except Helgoland, sandeels were the most important food.

Sandeels are also the most common prey fed to young puffins in a number of colonies (Table 2.13). In contrast, on Runde and on the Isle of May (during the 1970s before the collapse of the sprat stock), clupeids or gadoids formed an important part of the diet during some of the breeding seasons studied. Along the coast of the southern North Sea clupeids are a preferred prey, and their share in chick diets often is greater than that of sandeels (Tables 2.11, 2.12).

Table 2.10 Geographic variation in the food of the herring gull in Shetland 1983–1985, Forth 1979–1981 (Furness, *et al.*, 1992) and in the Wadden Sea in summer 1987 (Noordhuis and Spaans, 1992) or in fall 1991 (Schleswig-Holstein, November: Dervedde, 1992). Shetland, Forth: Each pellet is assigned to the prey type of which it was predominantly or entirely composed; Wadden Sea: Occurrence of prey items in % of pellets.

Diet	Shetland	Forth	Texel	Vlieland	Terschelling	Schiermonn-koog	Schleswig-Holstein
Marine invertebrates	91	27	77	85	76	72	>80
Terrestrial invertebrates		7	1		12	12	
Marine fish		1	12	1	8	4	5
Freshwater fish			8	10	5	4	
Fish not specified			1		4		
Birds, Mammals	1			2	5	3	
Discards	6	52					
Garbage	1	12	3	2	7	4	7

Table 2.11 Geographic variation in the food of the common tern on the Farne Islands (Pearson 1968), Mousa (Uttley, *et al.*, 1989) and in the Wadden Sea (a) Stienen and van Tienen (1991); (b) Frank (1992).

Colony	Year	Percent food						
		n	Clupeoids	Sandeels	Gadids	Stickle-backs	Flatfish	Other or unidentified fish
Farne Islands	1961–1963	519	44	38	11	2		5
Mousa, Shetlands	1988	110		20				80 ^c
<u>Wadden Sea</u>								
Griend ^a	1989–1990	?	52				7	9
Oldeog ^b	1986	638	60	19		1		18
Augustgroden ^b	1986	1,457	31	3		55	2	4

^cmainly saithe

eat themselves (Taylor, 1979) or than they later feed to

2.4.7 Seasonal variation in diets

The diet composition of seabirds varies seasonally due to fluctuations in prey species availability (due to prey movements, weather, tides, predation) and to changing food demands during the different phases of the annual breeding cycle (e.g., puffin: Barrett *et al.*, 1987; kittiwake: Pearson, 1968, sandwich tern *Sterna sandvicensis*: Veen, 1977).

In terns, the food composition and length of fish fed varies between courtship feeding and the chick rearing period. Males feed females with fish longer than those they

chicks (Ewins, 1985; Monaghan *et al.*, 1989). Younger tern chicks get smaller fish or different prey species than older chicks (Lemmetyinen, 1973; Ewins, 1985; Uttley, 1991; Frick, 1993).

Herring gulls in the Wadden Sea off Schleswig-Holstein feed predominantly on shore crabs *Carcinus maenas* and mussels *Mytilus edulis*. From autumn to winter, the proportion of these prey species change in favour of the mussels and towards smaller sized crabs (Dervedde, 1992).

Table 2.12 Geographic and annual variation in the food of guillemot chicks on Fair Isle (Harris and Riddiford, 1989), the Isle of May (1981–1986, Harris and Wanless, 1988), the Farne Islands (Pearson, 1968) and on Helgoland (Leopold, *et al.*, 1992, Grunsky, unpubl. data). On the Isle of May fed clupeids consisted only of sprats.

	% of chick diet		
	Sandeels	Clupeids	Others
Fair Isle			
1986	96	4	0
1987	100	0	0
1988	99	0	1
Isle of May			
1981	58	41	1
1982	89	8	3
1983	75	24	1
1984	86	14	0
1985	80	20	0
1986	94	6	0
Farne Islands			
1961-1963	49	42	4
Helgoland			
1990	5	95	0
1991	69	31	0
1992	22	78	0
1993	49	51	0

Table 2.13 Geographic and annual variation in the food of puffin chicks (% by weight) on Runde (Barrett, *et al.*, 1987), Fair Isle and Isle of May (Harris and Hislop, 1978) and on the Farne Islands (Pearson, 1968).

	Sandeels	Clupeids			Gadids		Others
		Herring	Sprat	Saithe	Cod	Haddock	
Runde							
1980	17	29		22	4	6	18
1981	59	4				30	
1982	48			15		25	
Fair Isle							
1974	81						3
1975	94		4				
1976	96			4			
Isle of May							
1972	55		18	1			26
1973	90		7				3
1974	48		51	1			
1975	14		86				
1976	38		53	9			
Farne Islands							
1961-1963	80		13				7

2.4.8 Interannual variation in diets

Interyear variability in diets is a common phenomenon among seabirds. This may be caused by annual fluctuations in prey stocks, by the food availability changing due to environmental factors such as weather and ocean temperatures, by differences in prey migration behaviour or by interspecific food competition. Owing to the different energetic values of the prey species, this variation can significantly affect breeding biology, chick growth and condition, as well as breeding success.

In common guillemots and puffins (Tables 2.12, 2.13), the percentage of clupeids or other fish in the diet correlates negatively with the percentage of sandeels. For many seabird species of the Shetland Islands, Bailey *et al.*, (1991) show that the switching from sandeels to other prey species is in approximate proportion to the abundance of sandeels, and that there is no evidence of a non-linear functional response. If sandeels dominate the food, the breeding success of seabirds is comparably good (Shetland seabirds: Bailey *et al.* 1991; puffin: Barrett *et al.*, 1987; Arctic tern: Uttley, 1991; common tern: Frank, 1992).

Between 1972 and 1988, considerable changes in the species of fish fed to young puffins were found on the Isle of May (Table 2.13; Harris and Wanless, 1991): Sandeels were the most common prey except 1974-1978, when sprats formed 50-86% of the diet (by mass). During the 1980s, the proportion of sprats declined and the importance of herring increased gradually. As on the Isle of May, the proportion of herring fed to chicks on Røst, Norway, rose during the 1980s.

On the Wadden Sea island of Terschelling, the ratio between the number of breeding pairs of herring and lesser black-backed gulls has changed in favour of the latter species between 1966-1987 (Noordhuis and Spaans, 1992). This was concomitant with a change in the diet of the breeding herring gulls. The proportion of marine invertebrates has increased over the years, while that of fish has decreased. In contrast, lesser black-backed gulls still ate primarily marine fish. Noordhuis and Spaans suggested that lesser black-backed gulls, which out manoeuvre herring gulls when competing for discards behind

fishing boats, and are better long distance flyers, have forced herring gulls to concentrate on food sources other than discards.

2.4.9 Diets used in model

The estimation of fish consumed by seabirds in the North Sea, was obtained from published information on diets of seabirds in the North Sea and adjacent areas, including both seabird community studies and those of single-species (Table 2.14). From these data selected dietary information are presented in summary form in Table 2.15. This table includes, for each major energy-consuming seabird species, a best estimate of the fish species and sizes eaten. For some species it was necessary to separate sections IVa (west) and all other areas because diets clearly differed between areas. In general, sandeels were more strongly represented in the diet in IVa (west) than in other areas. The quality of the diet data varies considerably among species, being good for guillemot but poor for fulmar.

Diets are very poorly known outside the breeding season, and probably vary in detail from place to place and from year to year, especially in relation to changes in fish stocks (Crawford *et al.*, 1985; Hislop and Harris, 1985; Springer *et al.*, 1986; Montevercchi *et al.* 1988; Barrett and Furness, 1990; Hamer *et al.*, 1991; Bailey *et al.*, 1991; Wanless and Harris, 1992). For this model we have used the dietary summary data Table 2.15 as representing the best estimates of diets of North Sea seabirds at different times of year. We note here the uncertain nature of these data, especially with regard to seabird diet outside the breeding season. This is identified as one of the weakest aspects of the analysis. Another concern is the way in which many seabirds can switch diet according to food availability (Barrett and Furness, 1990; Hamer *et al.*, 1991). It is clear that in recent years many of the larger seabirds have obtained large amounts of food from fishing vessels, scavenging on offal and discards (Hudson and Furness, 1988, 1989; Furness *et al.*, 1992; Camphuysen *et al.*, 1993). The possible effects on scavenging seabirds of increases in net mesh size, decreases in fishing effort and increases in minimum landing size regulations in North Sea fisheries have been reviewed by Furness (1992).

Table 2.14 Papers giving details of diets of seabirds in the North Sea and adjacent areas, and used in the compilation of diet summaries for use in this study.

- a) Papers dealing with diets of several seabird species:
 Bailey, 1986; Bailey *et al.* 1991; Barrett and Furness, 1990; Camphuysen *et al.* 1993; Dunnet *et al.* 1990; Furness, 1983, 1989, 1990, 1992; Furness and Barrett, 1985, 1991; Furness *et al.* 1992; Garthe, 1993; Harris and Riddiford, 1989; Heubeck, 1989; Hislop *et al.* 1991; Hudson and Furness, 1988, 1989; Huppopp and Garthe, 1993; Madsen, 1957; Pearson, 1968; plus handbooks (e.g., Bezzel, 1985; Cramp and Simmons, 1977).
- b) Fulmar: Fisher, 1952; Fowler and Dye, 1987; Furness and Todd, 1984.
- c) Gannet: Martin, 1989; Montevecchi and Barrett, 1987; Nelson, 1978; Tasker *et al.* 1984; Wanless, 1984.
- d) Cormorant: Barrett *et al.* 1990; Dobben, 1952; Madsen and Spärck, 1950; Mills, 1969; Okill *et al.* 1992; Rae, 1969.
- e) Shag: Aebischer and Wanless, 1992; Barrett *et al.* 1990; Harris, 1992; Harris and Wanless, 1991, 1993; Johnstone *et al.* 1990; Rae, 1969; Wanless, 1992; Wanless *et al.* 1993.
- f) Great skua: Furness, 1987; Furness and Hislop, 1981; Hamer *et al.* 1991; Tasker *et al.* 1985.
- g) Black-headed gull: Gorke *et al.* 1988; Gorke, 1990.
- h) Lesser black-backed gull: Noordhuis and Spaans, 1992.
- i) Herring gull: Beaman, 1978; Coulson and Butterfield, 1986; Dervedde 1992; Goethe, 1980; Noordhuis and Spaans, 1992; Prüter, 1988; Sibly and McCleery, 1983; Spaans, 1971.
- j) Great black-backed gull: Taylor, 1985.
- k) Kittiwake: Coulson and Thomas, 1985; Galbraith, 1983; Wanless and Harris, 1989, 1992.
- l) Arctic tern: Boecker, 1967; Dunn, 1972; Ewins, 1985; Frick, 1993; Lemmetyinen, 1973; Monaghan *et al.* 1989; Stienen and Tienen, 1991; Uttley, 1991; Uttley *et al.* 1989.
- m) Common tern: Becker *et al.* 1987; Boecker, 1967; Dunn, 1972; Frank, 1992; Frick 1993; Lemmetyinen, 1973; Massias and Becker, 1990; Stienen and Tienen, 1991; Uttley *et al.* 1989.
- n) Sandwich tern: Dunn, 1972; Veen, 1977.
- o) Guillemot: Blake, 1983, 1984; Bradstreet and Brown, 1985; Camphuysen, 1990; Durinck *et al.* 1991; Harris and Wanless, 1985, 1986; Harris *et al.* 1990; Hislop and MacDonald, 1989; Leopold *et al.* 1992; Swennen and Duiven, 1977.
- p) Razorbill: Blake, 1983, 1984; Bradstreet and Brown, 1985; Harris and Wanless, 1986, 1989; Harris *et al.* 1990; Swennen and Duiven, 1977.
- q) Black guillemot: Ewins, 1986, 1990.
- r) Puffin: Anker-Nilssen, 1992; Anker-Nilssen and Lorentsen, 1990; Blake, 1983, 1984; Barrett *et al.* 1987; Bradstreet and Brown, 1985; Harris, 1984; Harris and Hislop, 1978; Harris and Wanless, 1986; Harris *et al.* 1990; Martin, 1989; Swennen and Duiven, 1977.

Table 2.15 Diets of seabirds in North Sea and adjacent areas and summary of diet used in the model.

Species	Area	Years	Months sampled	Diet	Reference
Fulmar	Shetland	1978-1982	6-8	72% sandeel, 14% offal	Furness and Todd, 1984
	Shetland	1984-1985	6-8	Sandeels 95% of fish (4-10 cm)	Fowler and Dye, 1987
		1991-1993	6-8	20% sandeel, 30% discard gadoids, 30% offal, 20% zooplankton	Furness, unpubl. data
	Fair Isle	1986-1988	7-8	3-29% sandeel, 65-96% offal and discard gadoids	Harris and Riddiford, 1989
	For model assume		May-Aug Sep-Apr	30% sandeel (4-10 cm), 30% offal, 30% discards, 10% zooplankton 0% sandeel, 50% offal, 25% discards, 25% zooplankton	
Herring gull	For model assume		All year	30% discard gadoids, 30% invertebrates, 30% terrestrial foods, 10% offal	
Guillemot	Shetland	1975-1983	5-7	100% sandeel (10-14 cm)	Bailey <i>et al.</i> , 1991
		1988	5-7	95% sandeel	Bailey <i>et al.</i> , 1991
	E. Scotland	1983	3-8	95% sandeel (10-16 cm)	Blake <i>et al.</i> , 1985
			9-2	30% sandeel, 30% sprat, 30% gadoids	Blake <i>et al.</i> , 1985
	Shetland	1985	1	50% sandeel	Tasker <i>et al.</i> , 1987
		1989	5-7	100% sandeel	Furness and Barrett, 1991
	Fair Isle	1986-1988	6-7	98% sandeel (10-14 cm)	Harris and Riddiford, 1989
	Skagerrak	1988	1-2	49% herring (5 cm), 21% sprat (11 cm), 3% sandeel (8 cm)	Durinck <i>et al.</i> , 1991
	East Anglia	1983	2	30% sprat (1-group), 15% sandeel (1-group), 9% gadoids	Blake, 1984
	Newcastle	1983	2	39% sandeel, 15% sprat, 7% gadoids	
Shag	Moray Firth	1983	2	22% sprat, 18% sandeel, 34% gadoids (12 cm)	
	Isle of May	1981-1984	5-7	82% sandeel (13-16 cm), 17% sprat, 1% herring	Harris and Wanless, 1985
			10-5	89% sandeel, 10% sprat	
	Helgoland	1990-1993	6-7	5-61% sandeel, 31-95% clupeids	Leopold <i>et al.</i> , 1992 Grunsky unpubl.
	Farnes	1961-1963	4-8	49% sandeel (10-13 cm), 42% sprat	Pearson, 1968
	Skagerrak	1981	1	70% gadoids, 15% clupeids, 15% gadoids	Blake, 1983
	For model assume areas IVa (West)		Mar-Aug Sep-Feb	100% sandeel (10-14 cm) 33% sandeel (10-14 cm), 33% sprat (10 cm), 33% gadoids (12 cm)	
	For model assume areas IVa (East), IVb, IVc		Mar-Aug Sep-Feb	80% sandeel (10-14 cm), 20% sprat (10 cm) 40% sandeel (10-14 cm), 30% sprat (10 cm); 30% gadoids (12 cm)	
	Shetland	1975-1983	4-8	100% sandeel (12 cm)	Furness, 1990
		1988	4-8	99% sandeel (12 cm)	Furness and Barrett, 1991
		1989	4-8	99% sandeel	Furness and Barrett, 1991

Table 2.15 Continued

Species	Area	Years	Months sampled	Diet	Reference
Shag		1990	1	90% sandeel	Furness, unpubl.
	Fair Isle	1986-1988	6-7	98% sandeel (12 cm)	Harris and Riddiford, 1989
	Isle of May	1991	7	99% sandeel (5-15 cm)	Harris and Wanless, 1993
	Isle of May	1985-1990	5-8	99% sandeel	Harris and Wanless, 1993
			10-2	93% sandeel, 6% rockling	Harris and Wanless, 1993
			3-4	90% sandeel, 8% rockling	Harris and Wanless, 1993
	Farnes	1961-1963	11-12	90% sandeel, 10% gadoids	Pearson, 1968
	For model assume		All year	100% sandeel (5-15 cm)	
Great Black-bached Gull	For model assume		Apr-Aug	60% gadoid discards, 20% sandeels (12 cm), 20% other prey	
			Sep-Mar	70% gadoid discards, 30% other prey	
Kittiwake	N shields	1968	2-4	75% clupeids, 13% sandeels	Coulson and Thomas, 1985
		1973		10% gadoids	Coulson and Thomas, 1985
			6-7	66% sandeels, 20% clupeids, 12% gadoids	
	Faroe Islands	1961	6-7	56% sandeels (7 cm), 22% clupeids	Pearson, 1968
		1973		21% gadoids	
	Isle of May	1982	6-7	94% sandeels (133 mm), 5% clupeidss	Galbraith, 1983
		1989	6-7	95% sandeels (15 cm)	Wanless and Harris, 1992
		1990	6-7	86% sandeels	
	Fair Isle	1986-1988	6-7	98% sandeels (8 cm)	Harris and Riddiford, 1989
	Foula	1975-1983	5-7	100% sandeels	Bailey <i>et al.</i> , 1991
		1988	6-7	65% sandeels (9 cm)	Furness, 1990
	Foula	1989	6-7	92% sandeels	Furness and Barrett, 1991
	For model assume IVa(west)		May-Aug Sep-Apr	100% sandeels (6-14 cm) 25% sprat (8 cm), 25% zooplankton, 25% offal, 25% discards	
	For model assume IVb, IVc, IVa(east)		May-Aug Sep-Apr	60% sandeels (6-14 cm), 20% sprat (8 cm), 20% zooplankton 25% sprat (8 cm), 25% zooplankton, 25% offal, 25% discards	
Gannet	Foula	1975-1989	5-8	50% sandeels	Furness, 1990

Table 2.15 Continued

Species	Area	Years	Months sampled	Diet	Reference
Garnet	Hermaness	1981-1988	6-7	1981: 90% sandeels, 5% mackerel, 0% herring, 5% gadoids 1983: 60% sandeels, 22% mackerel, 3% herring, 9% gadoids 1984: 39% sandeels, 31% mackerel, 8% herring, 21% gadoids 1986: 15% sandeels, 24% mackerel, 41% herring, 13% gadoids 1987: 16% sandeels, 25% mackerel, 47% herring, 13% gadoids 1988: 6% sandeels, 22% mackerel, 51% herring, 19% gadoids	Martin, 1989
	Bass Rock			Herring, mackerel, sandeel, gadoids	Nelson, 1978
	For model assume			30% sandeels, 30% herring, 30% mackerel, 10% discards (sandeels: 0-1 group)	
Puffin	Shetland	1973	6-7	90% sandeel (0-group)	Martin, 1989
		1974	6-7	79% sandeel, 14% haddock	
		1976	6-7	81% sandeel, 16% rockling	
		1978	6-7	87% sandeel	
		1979	6-7	90% sandeel	
		1981	6-7	99% sandeel	
		1983	6-7	98% sandeel	
		1984	6-7	90% sandeel	
		1986	6-7	100% sandeel	
		1987	6-7	19% sandeel, 31% rockling, 26% sprat	
		1988	6-7	36% sandeel, 42% rockling, 21% saithe	
	Fair Isle	1974-1987	6-7	75%-100% sandeel (4-8 cm)	Harris and Riddiford, 1989
		1988	6-7	42% sandeel, 51% whiting, 5% sprat	
	Farne Islands	1961-1963	6-7	80% sandeel, 13% sprat	Pearson, 1988
	E. Anglia	1983	2	60% sandeel, 38% clupeid	Blake, 1984
	Shetland	1975-1983	5-8	100% sandeel (8-12 cm)	Furness, 1990
		1988	6-7	39% sandeel	Furness and Barrett, 1991
		1989	6-7	91% sandeel	Furness and Barrett, 1991
	Isle of May	1972	6-7	45% sandeel, 4% sprat, 50% whiting	Harris and Hislop, 1978
		1973	6-7	93% sandeel, 3% sprat	
		1974	6-7	69% sandeel, 28% sprat	
		1975	6-7	21% sandeel, 74% sprat	
		1976	6-7	55% sandeel, 29% sprat, 14% saithe (Sandeels 7 cm, sprat 7 cm)	
	For model assume IVa (West)		May-Aug Sep-Apr	90% sandeel (0-group), 10% rockling 30% sandeel, 30% gadoids, 30% sprat, 10% zooplankton	
	For model assume IVa (East), IVb, IVc		All year	50% sandeel, 30% sprat, 20% gadoids (all 0-group)	

Table 2.15 Continued

Species	Area	Years	Months sampled	Diet	Reference
Razorbill	Fair Isle	1989	6-7	100% sandeel	Harvey <i>et al.</i> , 1989
	Canna	1989	6-7	100% sandeel	Swann, 1989
	East Anglia	1983	2	51% sandeel, 49% clupeid	Blake, 1984
	Moray Firth	1983	2	50% sandeel, 45% clupeid, 5% gadid	Blake, 1984
	Newcastle	1983	2	87% sandeel, 8% gobies, 5% clupeid	Blake, 1984
	Isle of May	1982-1987	6-7	70% sandeel (1015 cm), 20% sprat, 10% herring	Harris and Wanless, 1989
	Foula	1971-1982	6-7	100% sandeel (6-8 cm)	Furness and Barrett, 1991
	Fair Isle	1986 1987	6-7 6-7	100% sandeel 97% sandeel, 3% sprat	Harris and Riddiford, 1989
	For model assume IVa (west)		Mar-Aug Sep-Feb	100% sandeel (6-10 cm) 60% sandeel, 40% sprat	
	For model assume Iva (east), IVb, IVc		Mar-Aug Sep-Feb	70% sandeel, 30% sprat 60% sandeel, 40% sprat	

2.5 Energy content of foods

Calorific values of foods can be determined and have been listed in the literature, but values can differ between samples obtained in different ways. For example, seabirds appear to have selected ripe female capelin rather than catching fish at random near to Hornøy, north Norway, and so will be taking fish of higher calorific content than obtained by random sampling (Barrett and Furness, 1990). For this iteration of this model we have assumed the following calorific values of foods: sandeels, sprats and young herring 6.5 kJ/g; crustaceans 4 kJ/g; squid 3.5 kJ/g; gadid and flatfish discards 4 kJ/g, offal 10 kJ/g (Harris and Hislop, 1978; Hudson, 1986; Croxall *et al.*, 1991; Camphuysen *et al.*, 1993;). We are aware of the enormous variation in calorific value of 0-group sandeels (a major part of the seabird diet in summer) but it seems that, unless sandeels are particularly scarce, seabirds select the larger 0-group fish which have high lipid content. Further work is needed on the assignment of energy values to fish prey.

2.6 Food utilisation efficiency

Assimilation efficiency varies among food types, and for fish it varies according to the lipid content of the fish, being higher when lipid content is higher. However, in general, assimilation efficiency is around 75-85% for fish diets and around 70% for other marine prey (Nagy *et al.*, 1984; Jackson, 1986; Gabrielsen *et al.*, 1987; Brown, 1989; Crawford *et al.*, 1991). In view of the relatively small variation in assimilation efficiency, in relation to other errors in this calculation, use of a constant value of 75% seems satisfactory for our model.

2.7 Energetics model

Although there are more labelled water studies of seabirds than there are for other avian groups, most species have been studied at only one location in one or a short series of years. Thus we lack information on the extent of variation in energy expenditures as a consequence of variations in food availability and other environmental factors. It would be unwise to assume that measured FMRs (Field Metabolic Rates) for one site in one season represent figures that can be applied to that seabird species at all sites (Montevicchi *et al.*, 1992). Indeed, Koteja (1991) was able to explain only 25% of variance in FMRs of birds (or of seabirds) as a consequence of species-specific physiology (reflected by deviations of BMR (Basal metabolic Rate) from the allometric prediction). Much of the remaining variance may be due to environmental conditions affecting the birds sampled for FMR determinations rather than to species-specific characteristics.

For

example, Furness and Bryant (1996) found that the at-sea metabolism of fulmars decreased with increasing wind speed (this accounting for nearly 50% of the variance in individual FMRs), while Gabrielsen *et al.* (1991) found that higher wind speed caused higher at-sea metabolism of little auks. Thus, it makes as much sense to use the mean of all labelled water studies with seabirds as a BMR multiplier, as to use each individual species FMR estimates in a model based on individual species determinations summed for the community. This is particularly so when the seabird community in question (that of the North Sea) shares few species in common with the set of seabird species for which doubly labelled water estimates of FMR have been made.

A total of 34 species-measurements of seabird energetics using labelled water or using allometric equations and activity budgets gave daily energy expenditures mostly in the region of 3 to 4 x BMR during the breeding season, with medians of 2.9 BMR during incubation and 3.5 BMR during chick-rearing (Furness, 1990). Tabulation of labelled water studies of seabird FMR and measured BMR of the same populations (Table 2.16) shows that the FMR/BMR ratio varied among studies from 1.8 to 6.6, with a mean of 3.6 for a sample of 27 studies. Three of these studies were of albatrosses, which have especially efficient flight and thus lower than average at-sea energy expenditures (Birt-Friesen *et al.*, 1989), so that the appropriate multiples of BMR for North Sea seabirds are probably higher than these. For seabirds other than albatrosses the mean FMR/BMR ratio during the breeding period was 3.8, while for the small sample of six studies on seabirds that are numerous in the North Sea, the mean FMR/BMR ratio was 4.2. FMR outside the breeding season must be greater than 1 x BMR, but less than that during breeding (as shown by Bennett and Harvey, 1987). Thus we have decided to use an FMR of 3.9 BMR during the breeding season and 2.5 BMR during other periods in the model.

BMR for each species was estimated from the allometric equation derived by Bryant and Furness (1995) for North Sea seabirds. In that study, the BMRs of individual species were found to deviate from the common regression by relatively small amounts, and some species considered to have 'above average' BMRs fell below the regression and vice versa. Thus the view that the BMR of individual species should be taken into account in modelling was not strongly supported; for ease of computation the predicted BMRs have been used; this will have very little effect on the overall total energy demands of the community since some species fall above and others below the regression. Estimated and measured BMR data are listed in Table 2.17.

Table 2.16 Field Metabolic Rates (FMRs) of seabirds (determined using labelled water) as multiples (using mass-specific values) of Basal Metabolic Rate (BMR).

Species	Mass	BMR	Mass	FMR	FMR/BMR	References
Reproducing birds	(g)	(kj/d)	(g)	(kj/d)		
<i>Aptenodytes patagonicus</i>	13,000	2948	16,200	9,307	3.1	5
<i>Pygoscelis papua</i>	6,290	1,605	6,100	3,900	2.5	1
<i>Pygoscelis adeliae</i>	3,868	1,039	3,868	4,002	3.9	2
<i>Eudyptes chrysolophus</i>	3,870	747	4,250	3,084	3.8	1
<i>Diomedea exulans</i>	8,130	1,756	8,305	3,288	1.8	1
<i>Diomedea immutabilis</i>	3,103	637	3,064	2,072	3.3	1
<i>Diomedea chrysostoma</i>	3,665	718	3,665	1,729	2.4	2
<i>Macronectes giganteus</i>	4,044	976	4,044	4,443	4.6	2
<i>Fulmarus glacialis</i>	728	313	730	1,005	3.2	3
<i>Oceanites oceanicus</i>	36	37	42	157	3.6	1
<i>Oceanodroma leucorhoa</i>	47	43	43	123	3.1	1
<i>Oceanodroma leucorhoa</i>	45	42	45	89	2.1	2
<i>Puffinus pacificus</i>	384	146	384	614	4.2	2
<i>Pelecanoides georgicus</i>	119	122	109	464	4.2	1
<i>Pelecanoides urinatrix</i>	132	126	136	557	4.3	1
<i>Sula bassana</i>	3,030	701	3,210	4,865	6.6	1
<i>Sula bassana</i>	2,574	1,115	3,244	5,867	4.2	3
<i>Sula capensis</i>	2,660	731	2,580	3,380	4.7	7
<i>Stercorarius parasiticus</i>	351	198	351	752	3.8	3
<i>Rissa tridactyla</i>	386	322	386	794	2.6	2
<i>Sterna hirundo</i>	125	93	128	356	3.8	8
<i>Sterna fuscata</i>	148	69	184	340	4.0	1
<i>Anous stolidus</i>	195	95	195	352	3.7	2
<i>Aethia pusilla</i>	83	115	84	358	3.1	1
<i>Uria aalge</i>	940	348	940	1,789	5.1	2
<i>Uria lomvia</i>	834	525	834	1,420	2.7	2
<i>Alle alle</i>	152	178	164	696	3.9	6
Mean FMR/BMR (all seabirds) n=27 studies					3.64	
Mean FMR/BMR (excluding albatrosses) n=24 studies					3.78	
Mean FMR/BMR (regular N. Sea species only) n=6 studies					4.25	
Non-reproducing seabirds						
<i>Eudyptula minor</i>	900	384	1,076	986	2.2	1

References: 1=Koteja, 1991 (review, Appendix), 2=Birt-Friesen *et al.*, 1989 (Table 1 review) 3=Bryant and Furness 1995 and unpubl., 4=Bennett and Harvey, 1987, 5=Kooyman *et al.*, 1992 6=Gabrielsen *et al.*, 1991, 7=Adams *et al.*, 1993, Klaassen *et al.*, 1992.

Table 2.17

Estimated and measured Basal Metabolic Rates (BMRs) of seabirds. Mean body mass for North Sea populations taken from Cramp & Simmons (1990), Furness (1983), Furness (1990). BMR in column 3 is the estimated value from the general allometric equation derived by Bryant & Furness (1995) for North Sea seabirds: $BMR (kJ/d) = 2.30 W^{0.774}$

Species	Mean body mass (g) for this species in the North Sea	Predicted BMR (kJ/d) from Bryant & Furness (1995)	Measured BMR for this species (kJ/d)	Mean body mass (g) of birds of measured BMR	Reference for meas- ured BMR data
Fulmar	810	410	330	728	1
			314	651	2
Gannet	3,000	1,130	1,079	2,574	1
			742	3,210	3
Cormorant	2,200	889			
Shag	1,810	764	739	1,619	1
Great skua	1,400	626	543	1,159	1
Black-headed gull	250	165	188	252	7
			177	285	8
Common gull	380	228	201	428	8
Lesser black-backed gull	800	406			
Herring gull	900	445	428	924	1
			415	1,000	4
			349	1,115	9
Great black-backed gull	1,600	695			
Kittiwake	390	233	237	305	1
			289	365	2
			322	386	3
Arctic tern	100	81	79	85	5
Common tern	125	97			
Sandwich tern	235	157			
Guillemot	980	475	390	771	1
			588	956	6
			348	940	3
Razorbill	620	333	311	589	1
Black guillemot	410	242	262	342	2
Puffin	390	233	222	329	1

References: 1 = Bryant & Furness (1995), 2 = Gabrielsen *et al.* (1988), 3 = Birt-Friesen *et al.* (1989), 4 = Bennett & Harvey (1988), 5 = Klaassen *et al.* (1989), 6 = Johnson & West (1975), 7 = Davydov (1972), 8 = Gavrilov (1985), 9 = Lustick *et al.* (1978). Note that comparisons between measured and predicted BMR values for particular species should only be made after correcting for differences in body mass between columns 2 and 5.

2.7.1 Model output

Monthly figures for food consumption in terms of energy requirement in each area of the North Sea by eighteen seabird species were computed from the above data. These figures are summarized as annual energy requirements in Table 2.18. Two species, northern fulmar and common guillemot are responsible for more than half of the energy requirements of the seabird species. Only one other species, herring gull, requires more than 10% of the total seabird energy requirement. The largest energy requirement is in ICES Division IVa (west).

These energy requirements were converted to food consumption needs using the data outlined in Sections 2.4, 2.5, and 2.6. The results of this are presented in Table 2.19 for the eight greatest consumers of energy in the North Sea (responsible for 94% of the energy demand), and the shag. This latter species, although only requiring 1.2% of the total seabird energy demand, is included as it consumes mostly sandeel. The mackerel *Scomber scombrus* and large herring sections of this table are truncated as they are consumed only by gannets.

Table 2.18 Annual energy requirements (KJ x 10⁹) of 18 species of seabirds in the North Sea.

Species	Annual energy requirements	Percentages
Fulmar	1,094.90	28.1
Gannet	273.22	7.0
Cormorant	6.15	0.2
Shag	46.94	1.2
Great skua	21.08	0.5
Black-headed gull	39.37	1.0
Common gull	44.18	1.1
Lesser black-backed gull	69.52	1.8
Herring gull	451.40	11.6
Great black-backed gull	301.29	7.7
Kittiwake	307.01	7.9
Arctic tern	2.75	0.1
Common tern	2.70	0.1
Sandwich tern	2.38	0.1
Guillemot	1,024.86	26.3
Razorbill	99.54	2.6
Black guillemot	7.86	0.2
Puffin	108.02	2.8
	3,903.17	

Table 2.19 Seven types of food consumed by nine species of seabird by quarter in six areas of the North Sea. (tonnes).

SANDEEL CONSUMPTION					
ICES IVa (west) sandeel	First	Second	Third	Fourth	Totals
Fulmar	0	11,723	4,790	0	16,513
Gannet	867	1,448	1,652	554	4,522
Shag	1,062	1,447	1,291	1,086	4,917
Herring gull	0	0	0	0	0
Great black-backed gull	0	771	143	0	914
Kittiwake	0	5,260	3,681	0	8,941
Guillemot	6,994	36,759	16,358	1,923	62,034
Razorbill	862	3,009	3,077	511	7,459
Puffin	395	3,256	2,582	41	6,275
Total	10,180	63,704	33,574	4116	111,574
ICES IVa (east) sandeel	First	Second	Third	Fourth	Totals
Fulmar	0	1,218	2,974	0	4,191
Gannet	367	381	214	222	1,184
Shag	138	192	168	141	640
Herring gull	0	0	0	0	0
Great black-backed gull	0	204	181	0	385
Kittiwake	0	165	50	0	215
Guillemot	2,010	2,752	2,069	2,268	9,098
Razorbill	1	4	8	0	13
Puffin	209	198	130	3	540
Total	2,726	5,114	5,792	2,635	16,267
ICES IVb (west) sandeel	First	Second	Third	Fourth	Totals
Fulmar	0	256	1,267	0	1,522
Gannet	499	1,793	1,404	352	4,047
Shag	359	500	437	367	1,664
Herring gull	0	0	0	0	0
Great black-backed gull	0	56	591	0	647
Kittiwake	0	2,381	2,843	0	5,225
Guillemot	2,448	10,972	10,971	3,037	27,469
Razorbill	203	608	1,287	882	2,981
Puffin	344	1,349	768	142	2,603
Total	3,894	17,915	19,567	4,781	46,157

Table 2.19 Continued

SANDEEL CONSUMPTION					
ICES IVb (centre) sandeel	First	Second	Third	Fourth	Totals
Fulmar	0	508	1,507	0	2,015
Gannet	488	161	561	900	2,110
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	28	19	0	47
Kittiwake	0	523	288	0	810
Guillemot	1,703	1,196	2,695	2,968	8,562
Razorbill	148	118	72	401	740
Puffin	294	137	20	118	570
Total	2,633	2,671	5,163	4,388	14,854
ICES IVb (east) sandeel	First	Second	Third	Fourth	Totals
Fulmar	0	333	717	0	1,050
Gannet	12	40	87	80	218
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	94	73	0	168
Kittiwake	0	81	61	0	141
Guillemot	913	680	479	898	2,969
Razorbill	212	1	6	153	372
Puffin	240	1	0	5	246
Total	1,376	1,230	1,424	1,135	5,165
ICES IVc sandeel	First	Second	Third	Fourth	Totals
Fulmar	0	97	118	0	215
Gannet	68	43	159	255	525
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	30	9	0	40
Kittiwake	0	113	68	0	181
Guillemot	558	206	440	473	1,677
Razorbill	105	17	55	96	273
Puffin	102	2	19	9	132
Total	834	509	868	833	3,044

Table 2.19 Continued

SPRAT AND SMALL HERRING CONSUMPTION					
ICES IVa (west) sprat	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	1,997	502	239	732	3,471
Guillemot	1,600	0	2,149	1,923	5,673
Razorbill	209	0	486	341	1,036
Puffin	395	187	33	41	657
Total	4,202	689	2,907	3,038	10,836
ICES IVa (east) sprat	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	141	59	95	96	391
Guillemot	1,323	688	719	1,701	4,431
Razorbill	0	2	3	0	6
Puffin	126	119	78	2	324
Total	1,590	867	895	1,800	5,152
ICES IVb (west) sprat	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	388	1,097	1,154	303	2,942
Guillemot	1,214	2,743	3,693	2,278	9,928
Razorbill	106	261	631	588	1,586
Puffin	207	809	461	85	1,562
Total	1,915	4,910	5,398	3,254	16,017

Table 2.19 Continued

SPRAT AND SMALL HERRING CONSUMPTION					
ICES IVb (centre) sprat	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	468	255	133	554	1,410
Guillemot	935	299	907	2,226	4,367
Razorbill	83	51	43	268	444
Puffin	176	82	12	71	342
Total	1,663	687	1,096	3,118	6,564
ICES IVb (east) sprat	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	222	40	29	117	407
Guillemot	498	170	154	673	1,495
Razorbill	130	1	3	102	236
Puffin	144	1	0	3	148
Total	994	211	186	895	2,286
ICES IVc sprat	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	158	61	29	152	401
Guillemot	282	52	275	355	963
Razorbill	55	7	37	64	163
Puffin	61	1	11	6	79
Total	556	121	352	577	1,606

Table 2.19 Continued

LIVE GADID CONSUMPTION					
ICES IVa (west) live gadids	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	0	0	0	0	0
Guillemot	1,600	0	2,149	1,923	5,673
Razorbill	0	0	0	0	0
Puffin	395	403	317	41	1,156
Total	1,995	403	2,465	1,965	6,829
ICES IVa (east) live gadids	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	0	0	0	0	0
Guillemot	1,231	0	303	1,701	3,235
Razorbill	0	0	0	0	0
Puffin	84	79	52	1	216
Total	1,314	79	355	1,702	3,451
ICES IVb (west) live gadids	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	0	0	0	0	0
Guillemot	888	0	1,426	2,278	4,592
Razorbill	0	0	0	0	0
Puffin	138	539	307	57	1,041
Total	1,026	539	1,733	2,335	5,633

Table 2.19 Continued

LIVE GADID CONSUMPTION					
ICES IVb (centre) live gadids	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	0	0	0	0	0
Guillemot	764	0	350	2,226	3,340
Razorbill	0	0	0	0	0
Puffin	118	55	8	47	228
Total	881	55	359	2,273	3,568
ICES IVb (east) live gadids	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	0	0	0	0	0
Guillemot	405	0	51	673	1,129
Razorbill	0	0	0	0	0
Puffin	96	0	0	2	98
Total	501	0	51	675	1,228
ICES IVc live gadids	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	0	0	0	0	0
Guillemot	213	0	248	355	816
Razorbill	0	0	0	0	0
Puffin	41	1	8	4	53
Total	254	1	255	359	868

Table 2.19 Continued

MACKEREL CONSUMPTION					
	First	Second	Third	Fourth	Totals
Gannet (IVa west)	867	1,448	1,652	554	4,522
Gannet (IVa east)	367	381	214	208	1,170
Gannet (IVb west)	499	1,793	1,404	352	4,047
Gannet (IVb centre)	488	161	561	900	2,110
Gannet (IVb east)	12	40	87	80	218
Gannet (IVc)	68	43	159	255	525
Total	2,300	3,866	4,077	2,363	12,592

LARGE HERRING CONSUMPTION					
	First	Second	Third	Fourth	Totals
Gannet (IVa west)	867	1,448	1,652	554	4,522
Gannet (IVa east)	367	381	214	208	1,170
Gannet (IVb west)	499	1,793	1,404	352	4,047
Gannet (IVb centre)	488	161	561	900	2,110
Gannet (IVb east)	12	40	87	80	218
Gannet (IVc)	68	43	159	255	525
Total	2,300	3,866	4,077	2,349	12,592

OFFAL CONSUMPTION					
	First	Second	Third	Fourth	Totals
ICES IVa (west) offal					
Fulmar	8,659	13,157	8,230	8,302	38,347
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	293	333	177	1,000	1,803
Great black-backed gull	0	0	0	0	0
Kittiwake	1,997	502	239	732	3,471
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	10,949	13,992	8,646	10,034	43,621

Table 2.19 Continued

OFFAL CONSUMPTION					
ICES IVa (east) offal	First	Second	Third	Fourth	Totals
Fulmar	1,763	1,456	9,422	1,813	14,455
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	106	157	104	78	444
Great black-backed gull	0	0	0	0	0
Kittiwake	141	3	78	96	319
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	2,010	1,616	9,604	1,988	15,218
ICES IVb (west) offal	First	Second	Third	Fourth	Totals
Fulmar	934	415	2,395	1,101	4,845
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	855	226	189	90	1,360
Great black-backed gull	0	0	0	0	0
Kittiwake	388	303	206	303	1,200
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	2,178	944	2,790	1,494	7,405
ICES IVb (centre) offal	First	Second	Third	Fourth	Totals
Fulmar	1,654	753	2,873	2,291	7,571
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	161	38	9	150	359
Great black-backed gull	0	0	0	0	0
Kittiwake	468	81	37	554	1,140
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	2,284	873	2,920	2,995	9,070

Table 2.19 Continued

OFFAL CONSUMPTION					
ICES IVb (east) offal	First	Second	Third	Fourth	Totals
Fulmar	274	408	1,284	794	2,761
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	179	434	285	176	1,074
Great black-backed gull	0	0	0	0	0
Kittiwake	222	13	9	117	360
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	674	855	1,578	1,088	4,195
ICES IVc offal	First	Second	Third	Fourth	Totals
Fulmar	176	151	228	93	648
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	447	863	157	435	1,902
Great black-backed gull	0	0	0	0	0
Kittiwake	158	24	6	152	340
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	781	1,038	391	681	2,891
DISCARD FISH CONSUMPTION					
ICES IVa (west) discards	First	Second	Third	Fourth	Totals
Fulmar	4,329	11,364	6,510	4,151	26,354
Gannet	289	483	551	185	1,507
Shag	0	0	0	0	0
Herring gull	879	1,000	530	3,001	5,410
Great black-backed gull	2,631	2,312	1,024	2,406	8,373
Kittiwake	1,997	502	239	732	3,471
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	10,126	15,661	8,854	10,475	45,115

Table 2.19 Continued

DISCARD FISH CONSUMPTION					
ICES IVa (east) discards	First	Second	Third	Fourth	Totals
Fulmar	882	1,337	6,198	907	9,323
Gannet	122	127	71	74	395
Shag	0	0	0	0	0
Herring gull	317	470	311	233	1,331
Great black-backed gull	229	611	1,745	98	2,682
Kittiwake	141	3	78	96	319
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	1,691	2,549	8,403	1,408	14,051
ICES IVb (west) discards	First	Second	Third	Fourth	Totals
Fulmar	467	335	1,831	551	3,184
Gannet	166	598	468	117	1,349
Shag	0	0	0	0	0
Herring gull	2,566	678	567	270	4,081
Great black-backed gull	2,253	167	2,475	2,144	7,040
Kittiwake	388	303	206	303	1,200
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	5,841	2,081	5,547	3,385	16,854
ICES IVb (centre) discards	First	Second	Third	Fourth	Totals
Fulmar	827	630	2,190	1,145	4,793
Gannet	163	54	187	300	703
Shag	0	0	0	0	0
Herring gull	483	115	28	451	1,077
Great black-backed gull	1,539	84	404	6,231	8,257
Kittiwake	468	81	37	554	1,140
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	3,480	964	2,846	8,681	15,970

Table 2.19 Continued

DISCARD FISH CONSUMPTION					
ICES IVb (east) discards	First	Second	Third	Fourth	Totals
Fulmar	137	371	1,001	397	1,905
Gannet	4	13	29	27	73
Shag	0	0	0	0	0
Herring gull	536	1,303	856	528	3,223
Great black-backed gull	824	282	458	387	1,952
Kittiwake	222	13	9	117	360
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	1,722	1,982	2,353	1,456	7,513
ICES IVc discards	First	Second	Third	Fourth	Totals
Fulmar	88	124	173	47	432
Gannet	23	14	53	85	175
Shag	0	0	0	0	0
Herring gull	1,341	2,589	471	1,305	5,706
Great black-backed gull	1,289	91	275	1,378	3,033
Kittiwake	158	24	6	152	340
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	2,899	2,842	978	2,967	9,686

Table 2.20 Estimated quantities of food consumed by seabirds (tonnes) in each quarter of the year in each ICES statistical rectangle of the North Sea.

Area	Prey	Quarters				Total
		1	2	3	4	
IVa west	Sandeel	10,180	63,704	33,574	4,116	111,574
	Sprat/Herring	4,202	689	2,907	3,038	10,836
	live Gadid	1,995	403	2,465	1,965	6,829
	Mackerel	867	1,448	1,652	554	4,522
	adult Herring	867	1,448	1,652	554	4,522
	offal	10,949	13,992	8,646	10,034	43,621
	Discards	10,126	15,661	8,854	10,475	45,115
	Total	39,186	97,345	59,750	30,736	227,017
IVa east	Sandeel	2,726	5,114	5,792	2,635	16,267
	Sprat/Herring	1,590	867	895	1,800	5,152
	live Gadid	1,314	79	355	1,702	3,451
	Mackerel	367	381	214	208	1,170
	adult Herring	367	381	214	208	1,170
	offal	2,010	1,616	9,604	1,988	15,218
	Discards	1,691	2,549	8,403	1,408	14,051
	Total	10,065	10,987	25,477	9,949	56,479
IVb west	Sandeel	3,894	17,915	19,567	4,781	46,157
	Sprat/Herring	1,915	4,910	5,398	3,254	16,017
	live Gadid	1,026	539	1,733	2,335	5,633
	Mackerel	499	1,793	1,404	352	4,047
	adult Herring	499	1,793	1,404	352	4,047
	offal	2,178	944	2,790	1,494	7,406
	Discards	5,841	2,081	5,547	3,385	16,854
	Total	15,852	29,975	37,843	15,953	99,623
IVb centre	Sandeel	2,633	2,671	5,163	4,388	14,854
	Sprat/Herring	1,663	687	1,096	3,118	6,564
	live Gadid	881	55	359	2,273	3,568
	Mackerel	488	161	561	900	2,110
	adult Herring	488	161	561	900	2,110
	offal	2,284	873	2,920	2,995	9,070
	Discards	3,480	964	2,846	8,681	15,970
	Total	11,917	5,572	13,506	23,255	54,250
IVb east	Sandeel	1,376	1,230	1,424	1,135	5,165
	Sprat/Herring	994	211	186	895	2,286
	live Gadid	501	0	51	675	1,228
	Mackerel	12	40	87	80	218
	adult Herring	12	40	87	80	218
	offal	674	855	1,578	1,088	4,195
	Discards	1,722	1,982	2,353	1,456	7,513
	Total	5,291	4,358	5,766	5,409	20,824
IVc	Sandeel	834	509	868	833	3,044
	Sprat/Herring	556	121	352	577	1,606
	live Gadid	254	1	255	359	868
	Mackerel	68	43	159	255	525
	adult Herring	68	43	159	255	525
	offal	781	1,038	391	681	2,891
	Discards	2,899	2,842	978	2,967	9,686
	Total	5,460	4,597	3,162	5,927	19,146

Consumption by seabirds is further summarized by food species and by quarter and area in Table 2.20. These show a very large proportionate demand of Division IVa (west) and the large demand for sandeel (33% of total food usage of seabirds), and waste products from fisheries (30% comprising 12% from offal, and 18% discards).

2.8 Discussion

The results of the modelling can be compared with those by other studies of the North Sea, and from further afield. The results of all but one of these other studies have been based on populations of breeding seabirds in an area, with suitable extrapolation to allow for non-breeding birds. In an area such as the North Sea, where there is substantial immigration, emigration and passage of seabirds through the area the assumption that only local populations of birds use an area does not hold. This study and that of Tasker *et al.* (1988) are the only studies to use at sea information from the North Sea to derive the bird population input.

Bailey (1986) used breeding population data from around the North Sea, and estimated about 1.9×10^{12} kJ of energy was required by seabirds. This is about half that estimated by the current model (3.9×10^{12}), but Bailey's seabird population data were from 1969/70, and there has been a substantial increase in breeding numbers since then (Lloyd *et al.*, 1991). Tasker *et al.* (1988) used at sea data and estimated 2.7×10^{12} kJ was consumed by seabirds; this earlier data set did not adequately allow for numbers of birds in some unsurveyed areas of the North Sea.

All of the above studies, and those of Furness (1978, 1984) indicate that food consumption is not uniform across the North Sea, but is distinctly heterogeneous, with particular "hot-spots" in the western north-western North Sea and around seabird colonies. These areas of high food consumption are not confined to colonies and their environs, but can occur elsewhere in the North Sea, particularly outside the summer breeding season. The present analysis was not sufficiently spatially disaggregated to identify these hot-spots.

Sandeels and waste products from fisheries clearly dominate as foods consumed. There are, though, from the seabird point of view, some important temporal and spatial variations in foods consumed. Temporally, sandeels fulfill just under a half of the total food supply of seabirds in the early part of the breeding seasons (April to June); this ratio declines to about 35% in July to September, and about 20% for the remainder of the year. During the period that sandeels are not taken, presumably through being unavailable while buried in the sediments, sprats, young herring and gadids become much more important as food (from a total of 4% of total food in April/June to about 20% in October/December. Other studies have also shown substantial emigration of birds from the study area in winter. Guillemots, for instance, are found in substantial numbers in the Skagerrak/Kattegat area in winter (H. Skov, unpubl. data) and the English Channel (Webb *et al.*, unpubl. data). These areas are not used by guillemots to any great extent during the summer. Use of offal and discards is also considerably more important during the winter than in spring or summer. In this case, most of the diet switching is by fulmars. However, the evidence for fulmar diet composition (and any changes) is, as outlined above, not great.

Estimated consumption by seabirds can be compared to the figure previously used in the MSVPA. Consumption by seabirds is quite small relative to fish stock biomass and annual production, and relative to the mass of prey taken by the main MSVPA predatory fish. Our estimate of total live prey consumed (270,000 tonnes per year) is similar to that previously estimated in the MSVPA (230,000 tonnes per year). However, the species composition of seabird prey is very different from that of the MSVPA predatory fish, and hence from the prey spectrum for seabirds assumed in the MSVPA (Table 2.21). The seabirds feed highly selectively, especially on sandeels and small clupeids, and consume virtually no benthic invertebrates ("an important other food of predatory fish") in Table 2.21. Thus, the mortality of sandeels due to seabirds is much greater than in the MSVPA model. Moreover, seabird predation on sandeels is highly concentrated in a small portion of the North Sea.

Table 2.21 Diet of the 5 MSVPA predator species in 1981 according to the MSVPA keyrun (Anon., 1987) and diet of North Sea seabirds as estimated in this study.

Prey	Tonnes x 10^3 taken by MSVPA fish predators	% of total mass of prey taken by MSVPA fish	Tonnes x 10^3 taken by seabirds	% of total mass of prey taken by seabirds
Mackerel	-	-	13	2.2
Cod	29	0.4	22	3.7
Whiting	117	1.8		
Haddock	233	3.5		
Norway Pout	812	12.3		
Herring	173	2.6	13	2.2
Sprat	190	2.9	30	5.0
Sandeel	624	9.4	197	32.8
Discards	-	-	109	18.2
Offal	-	-	71	11.8
Other food	4,443	67.1	146	24.3
Total	6,621	100.0	600*	100.1

*Note: This total is derived from estimated energy needs (3.9×10^{12} kJ per year) assuming an average calorific value of foods of 6.5 kJ/g.

2.8.1 Further research priorities

To refine this model, several areas need to be addressed. The most important of these is the relative lack of knowledge of seabird diet outside the breeding season, and in areas away from land. The major energy demands during this period are those of fulmar and guillemot, and better information on their winter diets must be a high priority, especially for fulmar where few data currently exist. The serious logistic problems of obtaining representative samples in offshore areas in winter are obstacles that will be difficult to overcome.

Further work should be undertaken to refine the population estimates, both of at-sea and breeding birds for input to the model. These refinements would undoubtedly improve the model, but it is thought that they would not substantially alter its findings. Further model refinements could include estimation of food demand by nestlings.

3 Analysis of fish consumption by seabirds by age class of prey fish

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3.1 Introduction

Knowledge of the age classes of fish taken by seabirds is important in understanding the impact of seabird predation on prey populations and is required for multispecies virtual population analysis. There has never been a systematic survey of seabird diet for any given year as has been undertaken for fish diet, e.g. the ICES Year of the Stomach. Consequently, there are many inadequacies in the coverage of diet data, both for areas of the North Sea, and for seasons. Many of the reported data on lengths of prey only provide a mean or range in length rather than length frequency composition. Sample sizes are also generally small (often less than 100). Nevertheless, available data can be used to give an indication of seabird prey size for at least the most important North Sea region for seabird fish consumption, ICES areas IVa west (Anon., 1994a).

3.2 Diet analysis

Studies of seabird diet in the North Sea were summarised in section 2.4. The methods used in these studies varied from direct measurements of loads brought by adults to chicks, to measuring hard parts of prey that remained in

regurgitates or stomach samples. These latter measurements are combined with predetermined relationships between the growth of hard parts and body length to infer fish body length. The problems involved with such indirect estimates of length have been discussed by Johnstone et al. (1991). In the case of fish brought to chicks, or intact fish recovered from the stomachs of sampled birds, it is possible to determine the age of the fish. This has been done on a few occasions.

Age-length keys (ALKs) have been constructed for the three main prey species, sandeels, sprats and herring, for use in the ICES fish stomach sampling programme. Separate ALKs have been constructed for standard North Sea Roundfish areas and for each quarter of the year. However, age/length data for sandeels are incomplete. Further, Wright & Bailey (1993) have demonstrated that there can be marked changes in sandeel ALK due to interannual differences in growth rates. Using information on mean or range in length of prey together with these keys, the mean or range in age of prey consumed for a given study has been estimated.

There have been very few studies on the selection of prey in relation to prey abundance in the sea. Wright & Bailey (1993) showed that diving birds tended to bring in a higher proportion of older age-classes of sandeel than would be expected if they were selecting fish randomly. This would be expected given the high energetic cost of carrying fish to the colony.

3.3 Predation on sandeels

All species of seabird considered in the analysis preyed on 0-group sandeels. However, older age-classes of sandeels often appeared in the diets of guillemot, razorbill and shag during the summer breeding season (quarters 2 & 3). At least in the case of guillemots, the large prey taken in the summer may not reflect adult diet since most prey assessments were based on loads brought to colonies for chicks. The predominance of 0-group in the diet during quarter 4 and the same year class in quarter 1 of the following year (now aged 1) suggests a seasonal shift in the size of prey taken. As 0-group sandeels are generally the most abundant age-class, this diet shift may simply reflect the availability of different age-classes.

Information is not adequate to assess consumption by age class for the whole North Sea. Most information exists on Area IVa (west) and, by making several assumptions, it is possible to attempt to model the consumption of sandeels in this area (Table 3.1). The figures presented are based on those in Table 2.19. There is no evidence to apportion the sandeels consumed by gannet and great black-backed gulls to age classes. From this information it can be seen that over a third of the predation in this region is on potential spawners (i.e. sandeels > 2 years old).

Table 3.1 Consumption by age-class of sandeels in IVa west, as estimated from the calculation of fish consumption by seabirds (Section 2) and data on sizes of sandeels selected by different seabirds: A) data used on the proportions of each age class in seabird diets.

	First	Second	Third	Fourth
Fulmar	n/a	20% 0-group 80% 1-group	All 0-group	n/a
Shag	All 2-group	All 2-group	All 2-group	All 2-group
Kittiwake	n/a	20% 0-group 80% 1-group	All 0-group	n/a
Guillemot and razor-bill	75% 1-group, 25% 2-group	10% 0-group 40% 1-group 25% 2-group 25% 3-group	25% 0-group 25% 1-group 25% 2-group 25% 3-group	All 0-group
Puffin	All 1-group	20% 0-group 80% 1-group	All 0-group	All 0-group

Consumption by age-class of sandeels in IVa west, as estimated from the calculation of fish consumption by seabirds (Section 2) and data on sizes of sandeels selected by different seabirds: B) Consumption of 0-group sandeels (tonnes).

	First	Second	Third	Fourth	Total
Fulmar	0	2,345	4,790	0	7,135
Kittiwake	0	1,052	3,681	0	4,733
Guillemot	0	3,676	4,090	1,923	9,689
Razorbill	0	301	769	511	1,581
Puffin	0	814	2,582	41	3,437
Total	0	8,188	15,912	2,475	26,575

Consumption by age-class of sandeels in IVa west, as estimated from the calculation of fish consumption by seabirds (Section 2) and data on sizes of sandeels selected by different seabirds: C) Consumption of 1-group sandeels (tonnes).

	First	Second	Third	Fourth	Total
Fulmar	0	9,378	0	0	9,378
Kittiwake	0	4,208	0	0	4,208
Guillemot	745	14,704	4,089	0	19,538
Razorbill	646	1,204	769	0	2,619
Puffin	395	2,605	0	0	3,000
Total	1,786	32,099	4,858	0	38,743

Consumption by age-class of sandeels in IVa west, as estimated from the calculation of fish consumption by seabirds (Section 2) and data on sizes of sandeels selected by different seabirds: D) Consumption of 2-group sandeels (tonnes).

	First	Second	Third	Fourth	Total
Shag	1,062	1,447	1,291	1,086	4,886
Guillemot	1,748	9,189	4,089	0	15,026
Razorbill	215	725	769	0	1,709
Total	3,025	11,361	5,459	1,086	21,621

Table 3.1 Continued

Consumption by age-class of sandeels in IVa west, as estimated from the calculation of fish consumption by seabirds (Section 2) and data on sizes of sandeels selected by different seabirds: E) Consumption of 3-group sandeels (tonnes).

	First	Second	Third	Fourth	Total
Guillemot	0	9,189	4,089	0	13,278
Razorbill	0	725	769	0	1,494
Total	0	9,914	4,858	0	14,772

References: Blake *et al.* (1985); Furness (1990); Wanless and Harris (1985)

3.4 Predation on sprats

Data on the sizes and ages of sprat consumed by seabirds are scarce. Available information suggests that seabirds mainly take sprat of between 40–90 mm TL in winter and around 120 mm TL in summer (Blake *et al.*, 1985; Harris & Wanless, 1985). The majority of the fish in this size range will belong to the same year class (0-group in winter, 1-group in summer).

3.5 Overview

There is plainly a need to elaborate the model of fish consumption by seabirds presented by Anon. (1994) to allow multispecies models to incorporate seabirds adequately. This is not possible at present, but future sampling of seabird diet should, where possible, include an assessment of the age of fish in the diet. This will require seabird researchers to record the lengths of prey fish and, ideally, to collect scales and/or otoliths. Furthermore, it appears that most of the studies of seabird diet in the North Sea were made in summer, and are based on an analysis of the food brought to the chicks. There is therefore a need to investigate the food of adults, nonbreeders and chicks, throughout the year. A co-ordinated study of the diets of both adult seabirds and their chicks throughout a single year is desirable.

4 Effect of fisheries for small fish on seabirds in the eastern Atlantic

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4.1 Introduction

Many of the species of small fish preyed upon by seabirds are also exploited by fisheries. This common utilisation of a fish resource has led to concern over potential competition between fisheries and seabirds. This section evaluates evidence for the potential effects of fisheries on the local abundance of prey species in the context of the spatial and temporal scales relevant to seabirds. Discussion of this subject is limited by the lack of integrated studies of fisheries, fish stocks and seabirds. Nevertheless, it is possible to consider the relevant scales at which interactions between seabirds, fish and fisheries may occur. Evidence for competition between seabirds and fisheries for a prey resource is then discussed.

4.2 Spatial and temporal interactions

Before considering whether competition between fisheries and seabirds occurs, it is useful to first consider the temporal and spatial scales at which seabirds and fishermen seek their prey in the North Sea. These scales are not the same, either in time or space, and consequently the likelihood of finding direct effects of fisheries on prey-fish populations, and consequently on seabird populations, is considerably reduced. In this section, we briefly describe the scales at which the main groups of avian predators, three of their most important prey-fish, and the fisheries on these prey-fish operate.

4.2.1 Distribution of seabirds in the North Sea

When breeding, seabirds are more restricted in their foraging area than at other time of the year. This restriction influences the geographical location of large breeding colonies, which are usually situated close to a local food source. Nevertheless, seabirds can forage at greater distances from their colonies when forced to by lack of locally available prey. Although changes in foraging range may be reflected in some of the more sensitive breeding parameters, such as length of time spent at the nest, they do not necessarily affect overall breeding output (Monaghan *et al.*, 1992).

Prey fish availability is not predictable from year to year, even in the absence of a fishery, and seabirds have evolved in response to this fluctuating food supply. Their

adaptations include the ability to switch from one prey to another, a relatively long life span (so that lifetime reproductive output is not affected greatly by a few poor years), delayed maturity (providing a long learning period prior to foraging for food for chicks), not breeding in years of poor food supply (removing the constraint of having to forage near the colony), and abandoning breeding attempts if food supply becomes critically low. These buffering mechanisms mean that it is difficult to demonstrate the effects of short-term variations in prey abundance on the long-term dynamics of seabird populations.

Three species of auk, guillemot *Uria aalge*, razorbill *Alca torda* and puffin *Fratercula arctica*, range across much of the North Sea, and are present there throughout the year. These species can dive to considerable depth (180m in the case of guillemot, Piatt and Nettleship, 1985) to take their prey. Although for at least the last one-third of the year adult auks are free of the need to return to land, from early January until the fledging of chicks in August, adult birds are constrained in their foraging distribution by the need to visit their colonies for a considerable portion of each day. Thus for much of the year, they have a relatively restricted area over which they can interact with their prey. Nearly all colonies of auks in the North Sea are located in the north and west, away from the centre of sprat *Sprattus sprattus* and herring distributions and close to areas with sandeels. Guillemot and razorbill, in particular, appear to prefer to feed their chicks on older age-classes of sandeel (see Section 3, above); this would therefore constrain these seabirds to specific areas where sandeels are present. Many guillemots and razorbills move to the southern and eastern parts of the North Sea in winter, but with a substantial proportion remaining near their breeding sites. Puffins tend to move towards the centre of the North Sea.

Many seabird species cannot dive to any great depth and are constrained to take food near the surface. Those species that rely mostly on fish caught at the surface include some of the *Larus* gulls, kittiwake *Rissa tridactyla* and the terns. The breeding distribution of gulls and terns is more widely spread than that of the cliff-nesting diving species in the North Sea, with more colonies in the southern and eastern North Sea. Terns, in particular, appear to be particularly constrained to feed within 10-20 km of colonies. As with diving seabirds, surface-feeding seabirds disperse following the breeding season. Many move away from the North Sea in winter; terns migrate southwards (one species as far as the Antarctic), and others such as kittiwakes and gulls may also switch from more natural foods to discarded fish and offal produced from fishing boats (Camphuysen *et al.*, 1993).

4.2.2 Distribution of prey fish in the North Sea

The three most important prey species of diving seabirds are small herring (generally less than 16 cm long), sprat and sandeel (predominantly *Ammodytes marinus*). These are pelagic species which can form dense schools, although the size and density of schools shows marked seasonal and even diel changes.

Small herring are mostly distributed across the central and eastern North Sea, most are found south of 58°30'N, north of 53°N and east of 3°E; but with some in the Moray Firth and in the Skagerrak (see Anon., 1993a,b). Smaller fish tend to be distributed closer to the shore than larger fish. In the one year (1991) for which quarterly estimates of abundance are available, there was an indication that herring were further south in the eastern North Sea in summer compared to winter (Jensen *et al.*, 1994). Small herring appear to have a restricted distribution in the North Sea, although the extent of distribution may vary between years and may be regulated by factors occurring outside its main distributional range.

Currently, sprat tend to be found further south in the North Sea than the bulk of the herring population. The distribution of the North Sea sprat population extends into the eastern part of the English Channel. However, sprat distribution is patchy, and concentrations in the northern and western North Sea have varied considerably in their extent and location in the 1970s and 1980s (Bailey and Edwards, 1981; Anon., 1992c). During the 1980s, the highest densities of sprat were in the south-eastern North Sea. Sprat spawn in spring and summer in areas about 100 km off the eastern coast of Britain, along the southern edge of the Dogger Bank and in the inner German Bight. Sprat distribution thus appears to be more patchy, localised and variable than that of herring.

The distribution of the lesser sandeel (*A. marinus*) varies with age. Juvenile 0-group fish are widely distributed across the North Sea. Larger 0-group sandeels settle in areas of sandy substrates, usually in depths of < 100 m. These areas include many coastal regions (<12 km from shore) around the northern UK and Denmark, and large sand banks in the north, east, and central North Sea. Once settled, sandeels appear to be relatively sedentary. Sandeels are thus available over a wide area when young, but are considerably more localised when older (see Anon., 1994b for distribution). Sandeel availability to seabirds and fisheries is also strongly seasonal. Between October and March, sandeels generally remain buried in the sediments, with the exception of a period in December or January when they emerge to spawn. During the summer months when they are active, sandeels also exhibit a daily pattern of emergence and move up into the water column during day light. This vertical migration makes them accessible to surface feeding seabirds.

4.3 Spatial distribution and temporal trends of North Sea fisheries on small herring, sprat and sandeel

Sprat, sandeel and small herring are taken predominantly for industrial purposes (fish meal and fish oil) in the North Sea. Fish caught for industrial purposes have a low unit value and large catches and catch rates must be achieved if the fishery is to be economically viable. Most fish reduction plants are located in Denmark or Norway; this may have considerable influence on the location of the fisheries. The expansion of the industrial fishery in the North Sea before 1975 is described by Popp Madsen (1975). From 1975, information about the industrial fisheries in the North Sea can be found in the reports of the Industrial Fisheries Working Group (now named Working Group on the Assessment of Norway Pout and Sandeel), and the Herring Assessment Working Group for the area south of 62°N.

Most small herring are fished in the southern and eastern North Sea in the third and fourth quarters of the year. Areas exploited tend to be relatively close to the Danish coast in July, expanding further offshore in August and September, with this offshore area emphasized in the final three months of the year. The overall biomass of herring and the amount taken by fisheries in the North Sea has varied considerably during recent years, but the spatial patterns of abundance and the fishery have not. North Sea annual landings of small herring varied between 4,000 tonnes and 177,000 tonnes in the 1980s.

Currently, sprat are fished predominantly in the south and central North Sea from July to December. Catches have varied between 32,000 tonnes and 299,000 tonnes since 1980. In the mid-1970s, the North Sea sprat stock was at a high level, estimated at more than 1 million t. At that time, sprats were more widely distributed. The fishing effort increased in the same period, and the catch peaked at more than 600,000 tonnes in 1975 and 1976 (Burd and Johnson 1983). After 1978, the biomass of sprat decreased significantly, and there was a decreasing trend in catches after 1979. The fishery is unlikely to have been the only factor behind this decrease, as environmental influences on larval survival may also have been important (Anon., 1990). Surveys indicated that the decrease in abundance was accompanied by shoals becoming more patchily distributed in coastal waters. The International Bottom Trawl Survey data indicate that the stock biomass decreased early in the 1980s, but has recovered slightly in more recent years. Strong year classes in 1986 and 1988 led to a significant increase in the sprat stock in the early 1990s (Anon., 1992c).

Sandeels (predominantly *A. marinus*) have been caught in the North Sea in significant quantities since the 1950s. Sandeels are taken on or close to the seabed using light demersal trawling gear. The fishery is thus limited to times of year and day when sandeels emerge from the sand.

The total landings from the North Sea have fluctuated between 536,000 and a peak of 1,039,000 tonnes over the period 1980–1992. In the northern North Sea, catches are predominantly composed of 1 year old fish, whereas there is a greater proportion of older age-classes in southern North Sea catches (Warburton 1982, Anon., 1994a). During the last 20 years, there have been significant changes in the distribution of exploitation, such as the development of fisheries around the Fisher Banks in the 1980s and Wee and Marr Bankie, off the Scottish east coast, in the 1990s (see Anon., 1993). The fishery on sandeel in the North Sea occurs between April and July, the period when post-settled sandeels are foraging above the sediment.

The sandeel fishery around Shetland has been relatively small compared to those elsewhere in the North Sea. The fishery started in 1974 on several grounds close (<5 km) to the islands. Annual landings increased steadily from less than 9,000 tonnes in 1974 to 52,600 tonnes in 1981. The fishing season lasted from March to October. Sandeels around Shetland recruit to the fishery usually in June or July, when approximately 7–9 cm long, and the major part of the catch after July consisted of 0-group recruits. The spawning stock biomass of sandeels at Shetland decreased in the early 1980s and fell from about 35,500 tonnes in 1984 to about 6,000 tonnes in 1992 following a series of poor year classes. This trend was halted by the strong 1991 year class which matured in 1993, leading to a large increase in spawning stock biomass. In 1991, the sandeel fishery around Shetland was closed, but it reopened in 1995.

Currently the north-eastern Atlantic is divided into four regions for sandeel assessment purposes. These divisions are based on regional differences in growth rate (Anon., 1991), and evidence for a limited movement of adults within divisions. However, whilst adult sandeels appear largely sedentary (Kunzlik *et al.*, 1986; Popp-Madsen, pers comm.), the larvae are planktonic. Consequently, passive dispersal of larvae by currents may lead to gene flow between geographically discrete spawning areas.

4.4 Large scale comparison of the distribution of seabirds, fish and fisheries

As shown above, seabirds, their prey and fisheries on those prey operate at different spatial and temporal scales in the North Sea. Jensen *et al.* (1994) studied the overlaps in spatial and temporal distributions between the groups described above. Significant correlations between sprat and guillemot and sprat and razorbill abundance were found in February (correlation coefficients between 0.299 and 0.468 for $n > 10$). These correlations coincided with changes in the distribution of the birds. After 1987, correlations between the distributions of the three bird species became weaker, especially for the guillemot-puffin and puffin-razorbill combinations. Sprat biomass also increased after 1987. Abundances of herring and guillemot were negatively correlated. The interaction between razorbill, guillemot and sprat, as described above, took

place mainly off the UK coast, and in the southern part of the North Sea.

Comparisons between puffin, razorbill and guillemot abundances and sandeel abundance showed significant positive correlation in seven cases out of twelve in the third quarter of the year, but not for any other quarter (Jensen *et al.*, 1994). Correlation coefficients ranged between 0.296 and 0.578. This association between birds and sandeel occurred mainly off the northeast Scottish coast and around Shetland. The Moray Firth area and the coast off eastern Scotland to the south of Aberdeen appear to be the areas where guillemot, puffin, and razorbill are most likely to forage on sandeel in the third quarter.

Correlations between fisheries and birds at the scale of ICES rectangles showed no general trend in spatial overlap between fisheries and bird distribution (Jensen *et al.*, 1994). However when making comparisons by year (using averages of months), some of the same trends were seen for sprat-razorbill and sprat-guillemot, as were seen for the same comparisons for abundance of the birds and fish. Some significant positive correlations were found between sandeel catches and guillemot density. This suggests that some fisheries and some birds are exploiting the same fish species in the same places, but at different times of the year. Fisheries for sprat have taken place mainly in autumn, and spatial overlap between sprat and seabirds was found mainly in winter.

The work of Jensen *et al.* (1994) highlighted some inherent deficiencies in the bird data. Because ornithologists were unable to sample the whole North Sea, there were significant variations between months in the areas of the North Sea sampled, which limited the ability to compare seabird and fishery use of fish stocks. If this problem could be solved, considerably more powerful analyses would be possible. Surveys such as those carried out in the past during the IBTS programme could provide suitable strategic coverage.

4.5 Small-scale comparison of the distribution of seabirds, fish and fisheries

Seabird-fish interactions have been studied at a small-scale (2–6 km) in Shetland waters (Wright & Bailey, 1993). During the period of this study the overall abundance of sandeels in Shetland waters changed markedly, with the lowest abundance occurring in 1990 and the highest in 1991. Significant correlations were found between the densities of sandeel and Arctic tern *Sterna paradisaea*, guillemot, and shag only in 1990. Sandeel density was also a highly significant predictor of Arctic tern and shag abundance in 1990 and guillemot and shag abundance in 1991, once the effect of distance from colony had been removed. It was concluded that seabirds only needed to feed in areas of relatively elevated prey density in 1990 but not in 1991 and 1992. Consequently, seabirds only appeared to track prey densities when sandeels were relatively scarce in the vicinity of their colony. Wright & Bailey (1993) demonstrated that these

changes in the local abundance of sandeels were influenced by density-related changes in overall stock distribution.

4.6 Competition between fisheries and seabirds

Many studies have indicated a link between changes in seabird and prey fish populations (see Anon., 1994, Table 1.2). However, only a few such studies have demonstrated that declines in prey availability were related to fishery exploitation. Examples of fishery induced changes in prey availability include the slow recovery of "guano birds" following recruitment overfishing of the Peruvian anchovy, *Engraulis ringens* (Nelson, 1978) and the repeated breeding failures of Puffins at Røst (Lid, 1981; Anker-Nilssen, 1987) that coincided with the reduction in Norwegian herring stocks (Hamre, 1988; see Anon., 1994). In most other cases/studies in which a fishery-induced change in prey availability has been inferred, there is little or no direct evidence for such an effect from fishery assessments. This is because changes in prey availability can often be ascribed to natural variations in fish recruitment for a given spawning stock size. Continued fishing pressure following periods of reduced recruitment may delay the recovery of a stock (Murphy, 1977), but this can be difficult to distinguish from other factors influencing the recovery of a stock. It is also possible that the scale at which fish stocks are monitored may be too large to account for reductions in fish prey in the vicinity of seabird colonies (Monaghan, 1992).

4.7 Competition for sandeels

The lesser sandeel *Ammodytes marinus* predominates both in the diet of seabirds and in the landings of industrial fisheries in the North Sea (Anon., 1992). In comparison to consumption by fish predators and fisheries landings (Table 2.21), overall sandeel consumption by seabirds in the North Sea is relatively low (< 8 % of total annual consumption of sandeels by predators and fisheries). However, regional comparisons of sandeel consumption indicate that most seabird predation is concentrated in the western North Sea, in ICES Division IVa (west) and to a lesser extent in Division IVb (west) (Table 4.1). In contrast, fishery catch data indicate that most sandeels are caught in other areas of the North Sea. For example, the largest sandeel catches were from Division IVb (central) in the early 1980s and Division IVa (east) in the late 1980s. These data suggest that there is relatively little overlap in the main areas of sandeel exploitation by fisheries and seabirds. This latter finding is not unexpected given that, while the largest seabird colonies are concentrated around the northern UK coast, the most productive areas for sandeel fishing occur at offshore banks beyond the normal foraging range of most breeding seabirds (see Gislason and Helgason, 1985). Major fishing grounds for sandeels include the western part of Dogger bank, the Jutland Reef, the Inner Shoal, the western edge of the Norwegian Deep to Viking Bank.

Table 4.1 Area comparison between sandeel and sprat fishery landings and seabird consumption. Landings of sandeels for 1984 and 1989 and sprat for 1985 are derived from Anon. (1992). Seabird consumption on estimates are from Section 2.

Area	Sandeel Landings (x 1,000 tonnes)		Sandeel Consumption by Seabirds (x 1,000 tonnes)	Sprat Landings (tonnes) 1985	Sprat Consumption by Seabirds (tonnes)
	1984	1989			
IVa (west)	40.1	21.9	111.6	7,594	0
IVa (east)	32.4	234.9	16.3	24	5,200
IVb (west)	195.6	136.8	46.2	1,829	16,000
IVb (central)	245.0	409.6	14.9	0	6,600
IVb (east)	99.1	189.1	17.6	36,640	2,300
IVc	44.7	26.1	3.0	2,922	900

The impact of seabird predation on sandeels in Division IVa (west) is difficult to assess owing to differences in the regional classifications of stocks and the lack of data on sandeel concentrations in this region. Industrial fisheries assessments divide the North Sea into three assessment divisions; Northern, Southern and Shetland, although the Shetland sandeel fishery was closed in 1990. ICES Division IVa (west) includes both the Shetland assessment area and part of the northern assessment area. Furness (1990) estimated that annual consumption of sandeels by seabirds at Shetland accounted for 27% (49,000 tonnes yr⁻¹) of Shetland sandeel stock production between 1981 and 1983, which was similar to the percentage taken by the local fishery. In addition to the sandeel grounds which form the Shetland assessment division, research surveys of adult and larval distribution have identified the presence of many sandeel concentrations around Orkney and the Scottish mainland coast. Little is known about long-term changes in sandeel abundance in these areas, since they are rarely fished. The degree to which these inshore sandeel concentrations inter-mix with the major offshore concentrations is also unknown, although investigations of larval and juvenile distributions suggest that inter-mixing between inshore and offshore sandeel concentrations in Division IVb (east) is unlikely (Langham, 1971; Wright and Bailey, 1993).

Based on these comparisons of seabird and fishery exploitation patterns and the possible differences in stocks exploited by seabirds and major industrial fishing fleets, it would seem unlikely that changes in sandeel stocks reported for the two large industrial fish assessment divisions are particularly relevant to most seabird populations in the North Sea. However, it is feasible that increases in fishing pressure within Division IVa (west) and other inshore grounds could result in competition between seabirds and fisheries.

Seabirds prey on all age-classes of sandeels. However, the species of seabirds that have been found to be most vulnerable to declines in sandeels are those that feed pre-

dominantly on young of the year (0-group), close (<0.5m) to the sea surface. These include terns, kittiwakes and skuas. In addition, the diet and breeding success of puffins, a small shallow-diving species which mainly feeds on 0-group sandeels, appears sensitive to changes in sandeel availability.

It is unlikely that there is much direct competition between seabirds and fisheries for 0-group sandeels during the chick rearing period because most fishing mortality on 0-group occurs after 1 July. 0-group sandeels only become accessible to the fishery once they have metamorphosed to the juvenile stage and settled. 0-group settlement extends from late May-July. Due to the limited scope for direct competition between seabirds and fisheries for 0-group sandeels, it may be assumed that the main impact on prey availability is through reductions in spawning stock biomass, and hence egg production. The main question, so far as the target stocks themselves are concerned, is therefore whether fishing is capable of reducing the stocks to a level at which recruitment is affected as a result of insufficient egg production (recruitment overfishing). This is an area of great uncertainty because it is not clear how low the spawning stock has to be before recruitment is affected.

In the case of Shetland, the sudden recovery of the stock may partly be explained by changes occurring outside the traditional assessment area. Studies by Wright & Bailey (1993) indicated that these changes were related to immigration of juvenile 0-group sandeels. This view is supported by the presence of a much larger spawning concentration to the north and west of Orkney, and by the coincidence between years of high recruitment at Shetland and a continuous distribution of juvenile 0-group sandeels between Orkney and Shetland. The possible involvement of an additional and unsampled spawning stock may therefore explain the lack of any apparent relationship between recruitment and spawning stock biomass in the Shetland sandeel stock assessments, even at low stock levels.

tionship between recruitment and spawning stock biomass in the Shetland sandeel stock assessments, even at low stock levels.

The need for a better understanding of sandeel population structure has been highlighted by recent changes in the breeding success of seabirds near the Firth of Forth and at Shetland. The rapid expansion of a sandeel fishery close to the Scottish east coast since 1990 has coincided with declines in seabird breeding success at nearby colonies (M. Harris pers comm.). The Scottish east coast grounds are regarded as part of the southern North Sea division, for the purposes of assessment. However, sandeel concentrations from the Scottish east coast grounds are geographically isolated from other areas of fishing operations, and so their inclusion in the large southern division may be questionable. Clearly, if sandeel grounds on the Scottish coast are distinct from those in other parts of the North Sea, the current scale at which North Sea sandeel stocks are monitored will be too large to consider the impact of local fishing pressure.

4.8 Competition for sprat

Sprat are an important prey species for many seabirds, particularly in the winter (Anon., 1994). Harris & Bailey (1992) demonstrated that overwintering survival of guillemots from the Isle of May was correlated with changes in North Sea sprat stocks. This would indicate that the decline in the North Sea sprat stock did have an influence on seabird survival. The sprat fishery is believed to have been involved in the stock decline, and hence it may be argued that the fishery could have indirectly affected seabird survival. A lack of dedicated studies on the interaction between seabirds, sprats and the sprat fishery makes it difficult to consider question more fully.

Sprat occur throughout the shallow southern North Sea and in the Moray Firth, Firth of Forth and over the Fladen Grounds east of Orkney. Sprat distribution varies seasonally as a result of migrations (Feldman, 1986). Traditional sprat fisheries are largely dependent on sprats moving close inshore to overwinter. Seabirds also take advantage of these overwintering concentrations, and so, in addition to overall stock levels, the factors influencing these sprat migrations may affect sprat availability to seabirds.

As with sandeels, estimates of consumption suggest that seabird predation on sprats is relatively small in relation to consumption by piscivorous fish (see Tables 2.21; 4.1). However, it should be noted that seabird consumption estimates were based on dietary data collected in the 1980s. Sprat fishery landings declined as a result of a reduction in the size of the spawning stock and the ratio of spawning and 1-year-old sprats between 1974 and 1984. By 1985, annual catches were approximately only double that taken by seabirds (Table 4.1). If seabird consumption data are representative of 1985, there would appear to be a spatial difference in seabird and fishery exploitation, with most seabird consumption of sprat be-

ing in Division IVb (west), while most sprat landings were from IVb (east) and the Skagerrak.

The 1970s decline in sprat stocks has been indicated as a possible cause of seabird mortality (Harris and Bailey, 1992). Although its relative importance has been questioned, overfishing, at least during the period of the stock decline, has been implicated in the decline of sprat stocks (Anon., 1986; Burd and Johnson, 1983). Burd and Johnson (1983) concluded that recruitment overfishing was a major contributor to the decline of the sprat stock. In contrast, fishery scientists from the 1986 ICES Sprat Working Group believed that stock fluctuations were largely related to long-term environmental changes, since the decrease in sprat abundance occurred almost instantaneously over a very wide area (Anon., 1986). The nature of such environmental influences are unknown, but Corten (1986) and others have discussed the possibility that changes in Atlantic water inflow into the North Sea may have been important.

4.9 Case Studies

The stability of seabird populations is far more sensitive to changes in adult mortality rates than to changes in reproductive output. Fluctuations in fish stocks are likely to affect both parameters but the former is less likely to be affected by the usual range of interannual changes in fish availability because of the ability of most seabird populations to seek alternative prey. However, even though most seabirds are generalists in their choice of diet, some populations are dependent on a few or even one prey species at certain times of the year. This narrow dependence makes them particularly vulnerable to fluctuations in that particular stock. This vulnerability of seabirds is demonstrated by several case studies within the ICES area where collapses in stocks of sandeels, capelin, and herring have had dramatic consequences for local populations of seabirds on Shetland, the Faroes and in Norway, as summarized below.

4.9.1 Shetland

Shetland is an internationally important area for breeding seabirds, with colonies of 13 species forming between 25 and 100% of their total breeding populations within the North Sea (Tasker *et al.*, 1987). Many seabirds breeding in Shetland are largely dependent on a single prey species, the lesser sandeel *Ammodytes marinus*, particularly during the breeding season (e.g. Martin, 1989b; Monaghan *et al.*, 1989). For most seabird species, no other suitably sized, energy-rich prey occurs near Shetland (Kunzlik, 1989; Hislop *et al.*, 1991). Seabird species with relatively large chicks tend to provision them with larger (and generally older) sandeels than species with small chicks. For example, Arctic terns, kittiwakes and puffins tend to feed their chicks on O-group sandeels (young of the year), whilst large pursuit diving birds, such as shags and guillemots tend to feed on large (1 year old and older) sandeels (Martin, 1989b).

During the 1980s, the breeding success of several seabirds at Shetland declined markedly. This was coincident with a marked decline in landings of sandeels (mainly *Ammodytes marinus*) from an industrial fishery that operated close to the Shetland and Fair Isle coasts. Due to the proximity of the fishery grounds to areas where seabirds foraged, many ornithologists have argued that the fishery competed for the same resource as the seabirds, and that the fishery was responsible for the decline in sandeel availability to seabirds. However, fishery studies carried out by the Scottish Office Agriculture and Fisheries Department indicated that the decline in both landings and sandeel abundance was the result of a decline in recruitment to the Shetland stock (recruitment here defined as the number of young surviving to 1 July from each year's spawning), which preceded any change in the spawning stock (Kunzlik, 1989). The Scottish Office maintained that natural fluctuations in sandeel survivorship prior to exploitation by the fishery were the main cause of the decline in fishery landings and prey for seabird chicks. Despite these arguments, there was still considerable controversy over the impact of the fishery, and in particular the possibility that local depletions near seabird colonies were not detected by fishery assessments (see Monaghan, 1992). Further, regardless of any direct impact on sandeel stocks that the fishery may have had, it was also not clear whether the decline in sandeel abundance alone was sufficient to explain the extent of seabird breeding failures since the breeding success of large pursuit diving species, which preyed on sandeels, did not decline to the extent seen in surface feeding seabirds (Heubeck, 1989; Okill, 1989).

The Shetland sandeel fishery

The Shetland sandeel fishery was established in 1974 and reached a peak in landings of 52,000 tonnes in 1982. The fishery was relatively small compared to other North Sea sandeel fisheries, and in contrast to most other industrial fisheries, operated at a number of small (0.5–10 km²; Gauld unpubl. data) inshore grounds (< 10 km from the coast) throughout the Shetland Isles. For assessment purposes, sandeels from these grounds were considered as belonging to a single stock. This distinction was based on the relatively slow growth rates of Shetland sandeels and the geographical discreteness of Shetland grounds in relation to other fished grounds. Landings declined following 1982 as a result of low recruitment, and the fishery was closed in June 1990. The decision to close the fishery was based on the small size of the spawning stock and the continued low recruitment.

Changes in seabird populations and breeding performance

Seabirds appear to be a major predator of sandeels in the vicinity of Shetland. Furness (1990) estimated that seabirds consumed 49,000 tonnes yr⁻¹ of sandeels between 1981 and 1983, an amount similar to that taken by the fishery. Historical data on seabird numbers at Shetland are limited, and it is, therefore, not possible to assess with confidence changes in numbers of most species in this

area before 1969. During the 1970s, numbers of most species increased (Okill, 1989; Heubeck, 1989; Furness, 1990; Heubeck *et al.*, 1991), possibly in part due to immigration (Bourne and Saunders, 1992), although changes were largely in line with national trends.

The species of seabirds whose breeding success was most affected by the decline in sandeels were those that fed predominantly on young of the year (O-group), close (<0.5m) to the sea surface. These species included Arctic terns (Monaghan *et al.*, 1989), kittiwakes (Heubeck and Ellis, 1986), and great skua *Catharacta skua* (Hamer *et al.*, 1991). Arctic skuas *Stercorarius parasiticus*, which are kleptoparasites of the surface feeding seabirds, were also affected (Heubeck, 1989). Of these, the Arctic terns suffered the lowest breeding success, with almost complete breeding failure throughout Shetland between 1984 and 1990 (Heubeck and Ellis, 1986). The puffins also suffered breeding failures in some areas of Shetland (Martin, 1989a). On the basis of census data collected in the early and mid-1980s (Joint Nature Conservancy Committee/Seabird Group, 'seabird colony register', Lloyd *et al.*, 1991), there were approximately 160,000 pairs of guillemots, 100,000 pairs of puffins, 50,000 pairs of kittiwakes and 30,000 pairs of Arctic terns in Shetland. By 1990, there appear to have been some notable declines in numbers of several species. For example, whereas numbers of Arctic terns in Shetland appear to have remained fairly constant between 1969 and 1980 (representing around 40% of the British and Irish population) (Bullock and Gomersall, 1981), a survey in 1989 indicated that numbers subsequently declined by 50% or more (Avery *et al.*, 1991). Additionally, significant declines also occurred in kittiwake (Heubeck, 1989) and guillemot colonies (Heubeck *et al.*, 1991). Numbers of Arctic terns dramatically increased again in 1991, just prior to the appearance of the large 1991 sandeel year class.

Studies of seabirds at Foula, begun in the 1970s, showed a decrease in feeding on sandeels by great skuas (68%–95% of food regurgitates from chicks in 1974–83, but only 5% and 14% of regurgitates in 1988 and 1989), and a concomitant drop in chick survival and growth. Furthermore, adults worked harder to try to rear chicks, and adult mortality increased (Hamer *et al.*, 1991). This increased adult mortality led to a slight fall in breeding numbers which was partially buffered by an increased rate of recruitment of immature great skuas (Klomp and Furness, 1992). Thus, although great skuas showed only a small initial decline in breeding numbers in response to the sandeel shortage, when sandeel populations recovered in 1991–1993, great skua numbers not only failed to increase, but continued to decrease because the pool of prebreeders was depleted. In contrast, the numbers of Arctic terns, which chose not to breed when food availability was low, recovered almost immediately once the sandeel numbers recovered. It is evident from these data that seabird responses differ between species, and in this case Arctic terns, by refraining from breeding when costs of foraging were elevated, showed a more successful response than did the skuas.

Seabird studies carried out at Sumburgh and Fair Isle showed that there were very marked changes in the breeding and foraging success of both surface feeding and diving seabirds between 1990 and 1992. In 1990, Arctic terns and kittiwakes suffered a total breeding failure. Guillemots and shags also experienced difficulties in provisioning chicks in 1990 (Monaghan *et al.*, 1992).

Changes in sandeel availability

Wright and Bailey (1993) investigated the availability of sandeels to Shetland seabirds between 1990 and 1992. They found that changes in seabird breeding performance and foraging success were associated with marked changes in sandeel abundance and distribution. In 1990, sandeels were scarce and restricted to within 5 km of colonies, in 1991, they were widely distributed with the largest concentrations occurring offshore, and in 1992, numbers were intermediate between those in 1990 and 1991, with the highest concentrations occurring inshore. Age composition analysis indicated that these changes in abundance were due to changes in O-group abundance; a large year class in 1991 gave rise to a large number of 1+ sandeels in 1992. O-group abundance was very low in both 1990 and 1992 in south Shetland. These changes in O-group abundance were not associated with any marked changes in the size of the potential spawning stock. The restricted sandeel range in 1990 appeared to mark the end of a period of stock contraction. The expansion of sandeel distribution in 1991 and 1992 was associated with the appearance of sandeels in many areas of unsuitable habitat.

Variability in year class strength was not the only factor that affected prey availability to seabirds. In 1990, densities of O-group sandeels were markedly lower during the kittiwake chick period than in late July, owing to the late appearance of appreciable numbers of O-group sandeels into south Shetland waters. This observation demonstrates the importance of O-group sandeel movements to seabird foraging success. Interannual differences in the size and energetic value of O-group sandeels during the 1990-1992 study were also evident from both direct sampling of fish and from seabird diets. For example, it was estimated that O-group sandeels found in kittiwake regurgitates in 1990 would have had approximately 5–10% of the energetic value of O-group sandeels taken in 1991.

The problem of low sandeel availability to seabirds in 1990 may have also been exacerbated by the patchiness of shoal distribution and its effect on encounter rate, since sandeel patchiness was found to covary with abundance. Kittiwakes spent a longer time foraging and searched over a greater range (>40 km from colony) in 1990 than in later years. Radio tracking studies on guillemots and shags from Sumburgh colonies indicated that the

these birds foraged from the colony decreased from 1990–1992, although tagged birds foraged within 10 km of their colony in all years (Monaghan *et al.*, 1992). Comparisons between the areas and frequency at which shags and guillemots returned to a feeding site, and sandeel distribution and sediment data indicated that these diving species were able to select areas of suitable sandeel habitat.

Causes of varying sandeel year class strength

Investigations into the early life-history of sandeels around Shetland seabird colonies found evidence for changes in factors likely to affect O-group abundance (Wright and Bailey, 1993). The poor year classes in 1990 and 1992 were associated with relatively early larval hatch dates and consequent low growth rates. From a review of historic survey data and dedicated surveys of larval abundance, evidence was also found for immigration of O-group sandeels from outside the Shetland assessment area. Temporal trends in recruitment, spawning stock and offshore densities of O-group sandeels indicated that high offshore densities of O-group sandeels coincided with years of relatively high recruitment per spawning stock biomass. Larval surveys indicated that by far the most important region of larval production in the Shetland-Orkney region was to the north and west of Orkney. Densities of late larvae were also found to be significantly higher in this region than in the inshore waters around Shetland. Thus it was postulated that spawning in Orkney gave rise to the high offshore densities of O-group sandeels seen in 1991 and other years of high recruitment and that these schools eventually immigrated into the Shetland grounds.

While the results of the Shetland sandeel research programme (Wright and Bailey, 1993) did not prove that the fishery had no deleterious effect on sandeel 'stocks' around Shetland, it was evident from the fluctuations in sandeel abundance observed following the closure of the fishery, that such an effect need not be invoked. The study highlights the variability in year class strength and the importance of understanding prey population structure, given the possibility that there may be immigration of sandeels from other areas.

4.9.2 Faroe Islands

Nearly 2 million pairs of seabirds breed on the Faroe Islands (Table 4.2). During the breeding period these birds and a great portion of the immatures feed close to the islands. Outside this period, the situation is more complicated. Some of the local populations, e.g., that of the common guillemots, migrate to other areas, while a portion of the Scottish guillemot population spends the winter around the Faroe Islands.

Table 4.2 Approximate numbers of seabirds breeding on the Faroe Islands in the 1980s.

Species	Number of pairs
Fulmar	600,000
Puffin	550,000
Storm petrel	250,000
Kittiwake	230,000
Common guillemot	175,000
Manx shearwater	25,000
Others (13 species each <10,000 pairs)	31,000
Total	1,861,000

Due to the relative isolation of the Faroes and their fish stocks, seabird/fish interactions there may be less complicated than in other ICES areas. Furthermore the most important seabird food during the chick rearing period, the sandeel, is not locally exploited. The seabirds therefore have only to compete with larger fish and grey seals for the sandeels. Because the sandeels are not exploited, we know very little about their populations. Recent O-group cod surveys, however, give an index of sandeel recruitment.

Harvests over many years of seabirds and their eggs give an impression of great natural year-to-year variations in the production of seabirds, as well as long-term fluctuation in the seabird populations (Reinert, 1976; Nørrevang, 1977; Olsen, 1991). Reinert (1976) showed a close correlation between these fluctuations and the occurrence of spawning herring in the Faroes and in Norway. Records of the amounts of feathers exported between 1710–1910 suggest variation in seabird numbers with a periodicity of 100 years, with the guillemot population reaching a third maximum in the 1950s.

In the late 1980s, the production of young guillemots and puffins almost completely failed. The situation is now improving. This improvement may be as much a positive response to an improvement in the environment of the prey species, as a result of the reduced competition by the groundfish stocks, which also collapsed.

Common guillemots

Censuses indicate that the breeding population of common guillemots is now only 5–10% of the numbers breeding in the 1950s. Since 1973, a guillemot study plot has been censused. Following a decline until 1990, including a 25% crash between 1989–1990, guillemot numbers in the study plot have increased over three consecutive years.

Puffins

The puffin population has been rather stable, but in 1989 and 1990, many dead young were found in the colonies. The same happened in 1991, when an experiment with supplementary feeding of the young showed that they were starving.

The survival of young during the last three years has improved from less than 50% in 1991 to about 70% and 98% in 1992 and 1993, respectively. The food brought to the young has also changed. The normal food is sandeels, but in 1991 and 1992, there were periods in which Norway pout *Trisopterus esmarkii* and capelin dominated in the diets of chicks. In 1993, sandeels were again the most common food, supplemented with Norway pout. The size of individual sandeels brought to chicks increased during these years.

Arctic terns

In 1984–1992, no Arctic tern chicks fledged, but in 1993, young were fledged in almost all of the colonies.

Using these three species of seabirds as indicators of the availability of sandeels and of other forage fish during the last decades, they indicate a period with relatively low production of forage fish reaching a minimum around 1990. Since then, there has been an improvement, and 1993 was the most productive for seabirds in the last 10 years.

The increase in sandeel availability for seabirds may also have been the result of reduced competition by groundfish stocks, which are at their lowest level in several decades. The groundfish stocks, however, have been low for many years, and it has been suggested that the recruitment of food for both birds and fishes was low in the late 1980s (Olsen, 1991). The recruitment of cod and haddock has been low for many years and the mean weight of individual fishes in each year class has been decreasing; in 1993 the recruitment of cod, sandeels and Norway pout was fairly good (J. Reinert, pers. comm.).

4.9.3 Norway

Seabirds in Norway depend, in large part, on two stocks of fish, the Norwegian spring-spawning herring and the Barents Sea capelin. Norwegian spring-spawning herring and Barents Sea capelin represent two of the largest fish stocks in the North Atlantic. Both are pelagic and migratory, and their migrations are key factors in their availability to avian predators. The main difference in the use of these fish by birds is that only the smallest/youngest stages of the herring are suitable as prey to most seabirds. Capelin, on the other hand, are rarely too large for seabirds to handle and some even seem to select for the large, gravid and hence energy-rich females (Furness and Barrett, 1985; Erikstad and Vader, 1989).

There have been recent and severe changes in these stocks of herring and capelin. Attributed to these changes

are massive declines in the Røst population of the puffin and the Barents Sea population of the common guillemot respectively. However, the linkages between the declines in the respective seabird species and the changes in prey availability were very different.

Puffins and herring

The Norwegian spring-spawning stock of the Atlanto-Scandian herring spawn off south-western Norway in February-April. After hatching ca. 2–3 weeks later, the larvae rise into the upper water layers (0–50 m) and are transported northwards, mainly by the Norwegian coastal current. The autumn distribution of the 0-group fish is widespread from the fjords of North Norway to offshore water in the Norwegian and Barents Seas (Dragesund *et al.*, 1980; Loeng, 1989). By then the juvenile herring have reached a length of 10–13 cm (Toresen, 1990).

Between 1957 and 1971, the herring stock collapsed from >11 million tonnes to 20,000 tonnes. After the collapse in the herring spawning stock, there was virtually no production of 0-group herring in the coastal waters. However, in the warm period of 1983–1985, three relatively strong year classes were produced, and after a slight increase in the spawning stock in 1988, a number of good year classes have been recorded in the Barents Sea annually.

Anker-Nilssen (1992) recently estimated that the puffin population at Røst, Lofoten Islands was >1 million pairs at the end of the 1970s and was thus one of the most important concentrations of seabirds in the North Atlantic. On their way northwards, juvenile herring pass these puffin colonies, where the 50–60 mm long fish constitute a major part of the puffin chick diet (Myrberget, 1962; Anker-Nilssen, 1992). Based on 16 seasons since 1975, Anker-Nilssen (1992) demonstrated a strong positive correlation between estimates of puffin fledging success and corresponding indices of the abundance of 0-group herring, with herring abundance accounting for 67% of the observed variance in fledging success. During the period when the production of 0-group herring in coastal waters ceased, puffins failed to raise young. More recently with the increase in Herring year class strength, the puffins have successfully produced young at Røst.

Between 1979–1989, the number of occupied puffin burrows on Røst decreased by 64%, an average decline of 14% per annum between 1983–1987 (Anker-Nilssen and Røstad, 1993). The years of repeated breeding failure combined with a relatively high rate of adult nest-site fidelity (Harris, 1976) are considered to be the direct cause of these declines (Anker-Nilssen and Røstad, 1993). Although the decline now seems to have ceased through the recruitment of chicks produced in 1983–1985 (Anker-Nilssen and Barrett, 1991), the long-term recovery of the population will depend on repeated recruitment in the herring stocks.

The lack of food in the Røst area also affected the common guillemots. Although less well documented, the

common guillemot population on Røst decreased by nearly 95% between 1960 and 1988. This decrease was attributed to the production of few and underweight young, and subsequent recruitment failure (Bakken, 1989). However, some of the decline may also have been due to drowning of adults in fishing nets, and/or adverse feeding conditions outside the breeding season in the Barents Sea, where many of the adults spend the winter (Strann *et al.*, 1990; Vader *et al.*, 1990a).

Guillemots/capelin

Since the collapse in the Atlanto-Scandian herring stocks, capelin have become the dominant pelagic schooling fish in the Barents Sea and, together with sandeels, the main food source of most of seabirds in the region (Furness and Barrett, 1985; Erikstad and Vader, 1989; Barrett and Furness, 1990). The distribution of this capelin stock is restricted to the Barents Sea. Spawning occurs along the coast of Troms, Finnmark and Murmansk, with a more westerly spawning during cold years (Loeng, 1989). Spawning occurs mainly in March and April, but also as late as June and July. The capelin larvae drift north-eastwards and maturing capelin feed in the northern Barents Sea.

Between 1972 and 1975, the stocks of two-year-old and older capelin increased to ca. 7 million tonnes. However, after 1975, there was a steady decline in the stock until 1986/1987, by which time it had decreased to 20,000 tonnes. However, capelin have a much shorter generation time (at present 2–3 years) than herring (5–7 years) and, following a brief moratorium on the capelin fishery, the stock rapidly recovered. By 1991, it had reached approximately 4 million tonnes (Anon., 1993).

Seabirds nesting along the Barents Sea coast were strongly affected by the changes in the capelin stock. On Hornø, capelin was a major part of the diet of many seabird species (Tables 4.3–4.5). During the period 1980 to 1983, which was early in the decline of the capelin, the breeding success of kittiwakes, puffins, common guillemots and shags nesting there was high. Chick growth was rapid and guillemot chicks were heavier than average when leaving the cliffs (Furness and Barrett, 1985). In all respects, the Hornø seabirds seemed to have had an exceptionally rich food supply in the early 1980s (Furness and Barrett, 1985). However, in 1986 and 1987, the situation was very different. In both of these breeding seasons, seabird reproductive output was greatly reduced all along the south coast of the Barents Sea, and several species of seabirds produced no young at all (Vader *et al.*, 1987). For example, in 1986, the kittiwakes all but gave up breeding on Syltefjord, the largest colony in Norway (ca. 140,000 pairs), and the common guillemots on Hjelmsøy in West Finnmark had a very poor season (Vader *et al.*, 1987). Kittiwakes there also laid smaller than normal clutches and hence produced fewer than normal young.

Table 4.3 Composition (% by number) of fish brought to puffin chicks, Hornøy, North Norway. N = no. of loads observed.

Year	N	Capelin	Sandeel	Herring	Other
1980	72	76	21	0	0
1981	52	37	63	0	0
1982	49	74	26	0	0
1983	193	76	24	0	0
1989	15	72	1	0	26
1992		20	23	30	27

Table 4.4 Composition (% by number) of fish brought to common guillemot chicks, Hornøy and Syltefjord (1985), North Norway. N = no. of fish observed.

Year	N	Herring	Capelin	Sandeel	Other
1980	46	2	72	20	6
1981	22	0	54	46	0
1982	28	0	61	39	0
1983	1,580	0	59	41	0
1985	21	5	33	43	19
1989	190	0	91	6	3
1990	481	8	45	44	0
1991	707	7	47	46	0
1992	149	51	24	26	0

Table 4.5 Composition (% by wet mass) of Kittiwake adult and chick regurgitates, Hornøy and Syltefjord, N. Norway. N = no. of regurgitates.

Year	N	Herring	Capelin	Sandeel	Crustacea	Other
1980	31	0	92	0	8	0
1981	32	0	54	4	41	0
1983	72	0	93	3	0	4
1985 ^a	24	25	66	7	0	2
1988	17	0	82	0	7	11
1988 ^a	63	0	84	0	3	13
1989 ^b	74	0	80	0	12	8
1990	67	34	62	2	2	1
1992	89	26	70	2	0	3

^a Syltefjord

^b Syltefjord + Hornøy

By 1989, when capelin stocks were still very low (200,000 tonnes), all seabird species were again breeding successfully along the coast and there was no evidence of food shortage (Barrett and Furness, 1990). Furthermore, the birds' diet contained more capelin in 1989 than in 1983, and Barrett and Furness (1990) suggested that they may have included an unidentified local fjordic stock of capelin that is distinct from the Barents Sea stock. The existence of such a stock has still to be validated.

The most dramatic effect of the collapse in the capelin stock was seen in the breeding populations of guillemots. Until 1985/1986, the numbers of common guillemots breeding in East Finnmark and along the Murmansk coast were relatively stable (Syltefjord) or increasing (Hornøy, Bolshoi Kharlov). In 1987, a massive decline in the numbers of guillemots breeding on Hjelmsøy, Hornøy, Bolshoi Kharlov and Bear Island was registered. Counts made in 1987 revealed that since 1985/86, the breeding populations of common guillemots and Brünnich's guillemots *Uria lomvia* had declined by ca. 80% and 33–63%, respectively (Table 4.6; Vader *et al.*, 1990a,b; Barrett and Krasnov, unpubl. data). At the same time, numbers of both species diminished at their traditional wintering area in the Barents Sea (Vader *et al.*, 1990b), and during the winter 1986/87 thousands of emaciated common guillemots were washed ashore along the coast of Finnmark (Vader *et al.*, 1987).

Table 4.6 Monitoring counts of common guillemots, kittiwakes and puffins on selected sites on Hornøy, N. Norway, 1980–1993. N=no. of sites counted.

	C.guillemot N=16	Kittiwake N=6	Puffin N=6
1980	967	(1,848) ^a	-
1981	990	(1,767) ^a	530
1982	990	1,712	542
1983	1,017	2,123	540
1985	1,006	1,583	569
1987	154	1,729	564
1988	145	1,686	635
1989	146	1,822	-
1990	158	1,600	734
1991	168	1,630	732
1992	195	1,557	632
1993	194	1,537	689

^aInterpolations based on counts on 4 of the 6 sites

The decline in numbers and the breeding failures in 1986/1987 coincided with the collapse in the capelin stock and have been attributed to both winter starvation by adults and problems in finding enough food for chicks during the summer. Since 1989, the capelin stocks have risen further, and parallel to this increase, numbers of common guillemots on Hornøy and Bolshoi Kharlov have started to recover.

While the effect of the near demise of the herring stocks on the puffin population is a clear demonstration of the effects on seabirds of repeated recruitment failures in a prey stock, the effect of the collapse of the capelin stocks on guillemots also demonstrates the consequences of changes in adult mortality of prey on long-lived birds with low reproductive potentials. In both cases, large changes in the abundance of a key prey species had serious implications for seabird populations.

A further response by seabirds to changing prey availability is the recent appearance of herring in the diet of several species breeding on Hornøy and Bolshoi Kharlov. As the herring stocks increase, more and more of the youngest year classes are entering the Barents Sea and are being preyed on by the seabirds. Since 1990, herring has made up a substantial amount of the diet of seabirds breeding on Hornøy (Tables 4.3–4.5). It is possible that the situation is reverting to that of the 1930–1940s when Belopol'skii (1957) recorded herring as an important constituent of the summer diet of many seabird species breeding in the region.

4.10 Overview

Several studies have clearly shown that variations in prey availability can have profound effects on the population parameters of seabirds, including breeding success and overwintering survival. However, it seems unlikely that questions about the potential for competition between seabirds and fisheries can be resolved adequately with the present differences in scale at which seabirds and fish populations are monitored, and with the lack of integrated studies between ornithologists and fishery scientists. From this review it is apparent that if one is to determine the potential impact of fisheries on seabird populations, it will be essential to focus on local changes in prey concentration in areas important to seabirds rather than overall stock changes at a North Sea scale. With respect to this, there is a need to monitor changes in the size and spatial distribution of both traditional and developing fisheries, particularly when these fisheries occur in areas which are known to be important for seabirds.

5 Consumption of shellfish by seaducks and oystercatchers

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5.1 Introduction

Close to 10 million seaducks forage for shellfish in northwest Europe in winter, as do over 1 million waders and several hundreds of thousands of gulls (Rose and Scott, 1994, Durinck *et al.*, 1994). In the North Sea, the most important consumption of shellfish by seabirds occurs on the southeastern and southern coasts, in and offshore of the Wadden Sea. In these areas, shellfish are used primarily by eiders and common scoters. Both species occur in substantial numbers and have high food demands. The distribution of eiders in the Wadden Sea and common scoter in the zone offshore of the Wadden sea generally corresponds with the areas in which fisheries harvesting shellfish. These seaducks mainly take the same molluscs as the shellfish fisheries, and fishermen are concerned about competition from these seaducks. Because of this potential conflict, there has been support for research on duck feeding ecology, and information about the consumption of shellfish by these seaducks is relatively good.

The most detailed information available on the food habits and numbers of birds foraging for shellfish comes from the southeastern North Sea, including the Wadden Sea, Dutch delta, and adjacent coastal strip of the North Sea.

Key species involved are: the eider *Somateria mollissima*, common scoter *Melanitta nigra*, oystercatcher *Haematopus ostralegus*, and herring gull *Larus argentatus*. The most important shellfish species, to birds and fisheries alike, are: mussels *Mytilus edulis*, cockles *Cerastoderma edule* and trough shells *Spisula subtruncata* and *S. solida*.

At present it is not possible to provide information on all ICES areas and all species of either shellfish or birds. Interactions such as those observed in the present area of focus also occur in other areas of interest to ICES. Information on the consumption of prey by waders in other areas could be made available, if sufficient time and resources were devoted to the task. Areas for which a great deal of information has been gathered include many estuaries around the British Isles.

5.2 The numbers of seaducks and oystercatchers, by area

Four abundant bird species that occur in the Wadden Sea and adjacent waters have a substantial proportion of bivalves in their diet. The sizes of these populations vary seasonally, and are shown in Table 5.1 (Meltotte *et al.*, 1994; Swennen *et al.*, 1989; Skov *et al.*, in press).

Table 5.1 Number of individuals (in thousands) in different seasons in the Wadden Sea for the most important bivalve feeders. Numbers according to Meltotte *et al.* (1984) and total numbers are average estimates for a 10 year period (1981–1991). Numbers in the different countries are maximum numbers during the same period.

Species		Summer	Autumn	Winter	Spring
Oystercatcher	Total	103	739	593	481
	Netherlands	57	302	324	166
	Germany	103	386	280	323
	Denmark	10	60	25	45
Herring gull	Total	79	328	157	141
	Netherlands	39	123	82	43
	Germany	35	231	64	112
	Denmark	20	32	40	16
Eider duck	Total	250	250	331	140
	Netherlands	40	40	147	50
	Germany	220	200	174	50
	Denmark	25	23	67	18
Common scoter	Total	96	242	300	196
	Netherlands	12	35	100	100
	Germany	15	40	40	48
	Denmark	69	167	160	48

5.2.1 Eider – Total numbers in northwest Europe: 3,000,000

A small, but increasing population of 7,000 pairs of eider breed in the Wadden Sea (Swennen *et al.*, 1989; Becker, 1992). Much larger numbers of non-breeding eiders use this area in summer, autumn and winter. These birds originate from the Baltic Sea population (Swennen, 1976), which has increased during the last 20 years from 250,000 pairs in the 1970s (Almkvist *et al.*, 1974) to 600,000 pairs in 1980 (Stjernberg, 1982). Numbers of eider wintering in the Wadden Sea may be between 243,000 and 331,000; numbers moulting there are between 228,000 and 282,000 (Swennen *et al.*, 1989). Up to 100,000 eider occur in the waters off the Wadden Sea.

Although total numbers of eider in autumn and winter are similar, their distribution within the Wadden Sea changes seasonally. In winter, the highest numbers of eider occur in the Danish and Dutch sectors of the Wadden Sea; in late summer, moulting eiders concentrate in the German sector (Swennen *et al.*, 1989). In the past, the density of eiders did not differ much between the different parts of the Wadden Sea (Swennen *et al.*, 1989). During the 1980s, however, the spatial distribution of wintering eiders within the Wadden Sea changed dramatically. As a result of poorer feeding conditions in the Danish and Dutch parts, eider densities are now higher in Germany.

Swennen *et al.* (1989) examined the distribution of eiders with respect to beds of cultured mussels and found that the distribution of eider was apparently unrelated to the distribution of the plots of cultured mussels. In Schleswig-Holstein, the large concentrations of moulting eiders avoid the mussel cultures (Nehls *et al.*, 1988). Similarly, in the Dutch sector of the Wadden Sea, during both the breeding and moulting periods, eiders concentrate far from the plots of cultured mussels.

5.2.2 Common scoter – Total numbers in northwest Europe: 1,300,000

The common scoter is an arctic bird that breeds mainly in the northern part of European Russia, and in the north-western part of Siberia. Common scoters arrive in the North Sea from the breeding grounds in October and November and leave in April and May. Non-breeding common scoters use the extensive shallow area in front off the Wadden Sea, approximately delimited by the 5 and 20 m depth contours (Laursen *et al.*, unpubl. data). Staging and wintering populations of common scoters off the Wadden Sea total about 200,000 birds (Laursen and Frikke, 1987a; Offringa, 1991; Laursen *et al.*, unpubl. data; Leopold, unpubl. data). Substantial numbers are also found in summer during moult. As the entire habitat of the species offshore of the Wadden Sea has only recently been surveyed, little is known about trends in the numbers of wintering birds. Limited data suggest that in recent years, numbers have declined to about 100,000

birds, and that in the 1960s, far higher numbers were present off the Danish part of the study area. Large concentrations of common scoters (> 100,000 individuals) have so far been found only on Terschelling bank (Leopold *et al.*, unpubl. data) and offshore of the Danish Wadden Sea islands.

During winter, there are at least 5 million seaducks in the Baltic Sea. In cold winters, ice cover may force parts of these populations of common and velvet scoters *Melanitta fusca* to move from the western Baltic Sea and Kattegat into the coastal areas of the eastern North Sea (Pihl *et al.*, 1992; Durinck *et al.*, 1993). In contrast, the substantial population of long-tailed duck *Clangula hyemalis* remains within the Baltic Sea throughout the winter.

5.2.3 Oystercatcher – Total numbers in northwest Europe: 874,000

The oystercatcher is a local breeding bird (appr. 40,000 pairs) in the Wadden Sea, but birds from Scandinavia and north-western Russia also winter in the Wadden Sea. Oystercatcher numbers peak in autumn and exceed one half million from autumn to spring. Most birds winter in the Dutch and German sections of the Wadden Sea.

5.2.4 Herring gull – Total numbers in north-western Europe: 2,700,000

Herring gulls breed in the Wadden Sea, with an estimated population of 90,000 pairs. The Wadden Sea population of Herring Gulls is mostly resident, but in autumn and winter, birds from Scandinavia, the Baltic area and north-western Russia join this population. Maximum numbers recorded in the Wadden Sea reach 330,000 individuals.

5.3 Prey stocks

Owing to the eutrophication of the North Sea, the biomass of benthic invertebrates has increased during the last decades in the western part of the Wadden Sea (Beukema, 1989). The populations of molluscs and other benthic organisms in the Wadden Sea fluctuate markedly in response to weather conditions. Losses are especially severe in cold winters (*e.g.*, Michaelis, 1992) and during storms (Nehls and Thiel, in press). Spatial variation in environmental conditions may cause regional differences in the size of mussel stocks; Michaelis (1992) recorded small, reduced populations in some parts of the Wadden Sea of Niedersachsen between 1985 and 1990.

5.3.1 Mussels

The blue mussel is a key species of the benthic fauna of the Wadden Sea, and it is important in terms of biomass, filtration rate, and because it generates habitats for other animals (Asmus, 1987; Dankers, 1993). Total mussel stocks in the Wadden Sea are thought to have increased over the last decades, possibly due to eutrophication and

the mussel fisheries (van der Veer, 1989; Dankers, 1993). In the Wadden Sea, assessments of mussel stocks are available only for the Dutch sector and the Schleswig-Holstein region of Germany. In these areas, mussel beds have an average biomass of 26g AFDM (ash free dry mass) m⁻² (Beukema, 1981), and peak values of up to 1.8 kg AFDM m⁻² (Asmus, 1987, Nehls & Ketzenberg, in press).

Standing stocks in the intertidal part of the Dutch Wadden Sea range from 6 500 to 187,000 tonnes wet weight. Sublittoral stocks were estimated at 165,000 to 204,000 tonnes wet weight and stocks found on the culture beds ranged up to 350,000 tonnes wet weight (Dekker, 1989). Total stocks may thus reach about 600,000 tonnes wet weight, with half of the mussel stocks found on the cultures and, on average, less than a quarter on intertidal beds. The total area of intertidal beds was estimated to be 3,360 ha (Dijkema *et al.*, 1989), which represents about 3% of the intertidal area.

Mussel stocks in Schleswig-Holstein are lower, and are mostly restricted to the northern half of the area, where islands offer shelter against storms from the west (Nehls and Thiel, 1993). Intertidal stocks may reach 60,000 tonnes wet weight, but the biomass is lower in most years. Sublittoral stocks are generally low (around 10,000 tonnes wet weight), but may reach 40,000 tonnes wet weight in some years. Total stocks, including the cultured mussels, may reach 100,000 tonnes wet weight. The area covered by intertidal mussel beds is about 2,000 ha when the population is high, which represents about 1% of the intertidal area.

In the Danish sector of the Wadden Sea, mussel beds are estimated to cover up to 1,000 ha, and represent about 1.5 % of the intertidal area (Kristensen, 1994). However, as mentioned for the Wadden Sea as a whole, the area covered by mussel beds is subject to large annual variations.

5.3.2 Cockles

The cockle is the other dominant species of the benthic fauna in the Wadden Sea. Dense beds may reach biomass values of 350 g AFDM m⁻² (Ruth, unpubl.). On the intertidal sector of the Dutch Wadden Sea, cockles comprise, on average, one quarter of the total biomass of the benthic communities (4.2 g AFDM m⁻² of 26.6 g AFDM m⁻², Beukema, 1981). Stock assessment data are available for the Dutch Wadden Sea and Delta area. Total stocks varied from 10,000 to 220,000 tonnes wet flesh weight. Cockle stocks in the Wadden Sea exhibit marked annual fluctuations, mainly as a result of high mortality in cold winters. Total stocks have been increasing over the last decades, probably as a result of eutrophication (Beukema and Cadée, 1986).

5.3.3 Trough shells

Spisula spp. have probably been the most abundant bivalves in the coastal southeastern North Sea in recent

years. In the Dutch Delta area, stock sizes were estimated to vary from 1,600 to >50,000 tonnes of flesh (equivalent to 430–13,300 tonnes AFDM). In a study plot chosen on the basis of seaduck presence off the Wadden Isle of Terschelling, $(8.153 \pm 2.063) \cdot 10^9$ individuals (median length 28 mm) *Spisula* spp. were present in February 1993 and $(3.647 \pm 1.566) \cdot 10^9$ individuals in May 1993 (den Hollander, 1993). In terms of biomass, this was equivalent to 5,775,000 and 2,625,000 tonnes of flesh, respectively (1 gram of AFDM is equivalent to 3.75 grams of fresh flesh weight; van Stralen and Kesterloo-Hendrikse, 1993).

In Denmark, two areas have been rich in juvenile *Spisula solida*, Horns Reef and the shallow 'Rode Klitsand' (Kristensen, 1994; Skov *et al.*, in press). In June/July 1993, 15,000 tonnes and 54,000 tonnes, total weight, were present on these two locations, respectively (Kristensen, 1994). Using a flesh content of 12%, which is slightly less than the 15% used for the less robust *Spisula subtruncata* (van Stralen and Kesterloo-Hendrikse, 1993), this is equivalent to 1,800 and 6,500 tonnes of flesh, respectively.

No stock assessments exist for the German sector, but fisheries for *S. solida* take place in the waters west of Amrum.

5.4 Fisheries

5.4.1 Mussels

The commercial culture of mussels started in the Netherlands in the 1950s and increased rapidly to cover an area of 70 km² (Drinkwaard, 1987; Veer, 1989). Since 1960, mussel culture has also increased markedly in the German part of the Wadden Sea. At present in the Dutch Wadden Sea, about 60 % of mussel biomass is found on cultivated mussel beds (Dekker, 1989). With the increasing practice of cultivating mussels, the annual harvest of mussels has also grown. In the German Wadden Sea, the yield increased five fold between the 1940s and the 1980s. In the Danish Wadden Sea, commercial culture of mussels is not allowed, but since 1983, an intensive fishery on natural mussel beds has developed (Dahl, 1992).

Mussel fisheries in the Wadden Sea today mainly rely on bottom cultures which are stocked with seed mussels (<25 mm), or with half grown mussels (25–40 mm) from natural mussel beds. Harvested mussels are generally larger than 50 mm. Mussel cultures are situated in sheltered shallow subtidal areas where growth conditions are higher and mortality lower than on natural beds (CWSS, 1991). About 10,760 ha are presently declared as culture plots, but only part of them are permanently used (Table 5.2). Fishing for seed mussels takes place on intertidal and subtidal beds, depending on the availability of mussel spat. In Schleswig-Holstein, spatfall in sublittoral areas seems to more predictable and has supplied the main share of seed mussels in the last years (Nehls and Ruth, 1994; Ruth, in prep.).

5.4.2 Cockles

Total landings of mussels in the Wadden Sea fluctuate between 78,000 tonnes and 166,000 tonnes and have shown no clear trend over the last decades (Table 5.3). Annual landings often include a substantial part of the overall mussel stocks of the Wadden Sea. The available data imply that half of the stocks found on the cultures in a year are harvested in the course of a winter. On average this will reduce the mussel population by a quarter, but the proportion may be higher in some years.

Cockle fishing is permitted in the Dutch Wadden Sea and Delta area and to a very limited extent in Denmark. Annual landings in the Netherlands range from near zero to about 7 000 tonnes of flesh or 50 000 tonnes total wet weight (Smit, 1994). The proportion of total stocks harvested by the fisheries is below 10% in most years, but may reach 40% when cockle stocks are low.

Table 5.2 The areas designated for culture lots and the areas covered with mussels for the majority of the time in the different parts of the Wadden Sea.

	Designated culture lots	Culture lots covered with mussels for the majority of the time
The Netherlands	About 7,000 ha	About 3,750 ha
Niedersachsen	About 960 ha	About 250 ha*
Schleswig-Holstein	About 2,800 ha	About 1,000 ha

*Presently this number is very low. In general it can be said that of all culture lots available only between 30 to 70% are covered with mussels, which shows a high fluctuation rate in the coverage.

Table 5.3 Landings of blue mussels in tonnes in the Netherlands (Wadden Sea and Delta), Denmark and Germany (Niedersachsen and Schleswig-Holstein) since 1965.

Year	Netherlands		Denmark	Germany		Total
	WS	Delta		SH	Nds	
1965	40,000	51,300	0	3,500	3,977	98,777
1966	33,100	48,400	0	6,900	4,367	92,767
1967	49,200	34,200	0	6,900	4,090	94,390
1968	71,400	36,200	0	6,900	4,213	118,713
1969	48,800	39,700	0	1,900	4,549	94,949
1970	32,600	43,000	0	5,300	4,245	85,145
1971	80,600	38,200	0	1,500	4,826	125,126
1972	122,100	35,700	0	2,750	5,169	165,719
1973	66,000	35,300	0	6,100	4,239	111,639
1974	69,000	34,500	0	10,600	4,642	118,742
1975	58,300	31,000	0	11,250	5,736	106,286
1976	56,200	33,200	0	15,300	7,979	112,679
1977	95,300	32,300	0	5,000	6,085	138,685
1978	63,400	39,900	0	7,200	5,341	115,841
1979	41,900	40,200	305	2,000	894	84,299
1980	34,100	33,300	293	8,300	2,017	78,010
1981	89,300	36,300	131	5,800	4,579	136,110
1982	111,400	46,800	1,144	11,800	5,033	176,177
1983	74,300	34,800	2,147	20,600	11,009	142,856
1984	27,500	39,200	14,533	34,600	24,731	140,564
1985	72,900	33,400	27,099	15,500	5,423	154,322
1986	38,600	25,800	17,564	23,800	5,076	110,840
1987	57,100	29,600	17,384	20,000	5,467	129,551
1988	36,700	27,300	1,161	19,800	9,842	94,803
1989	80,500	28,600	1,403	9,525	9,024	129,052
1990	69,659	22,511	1,190	15,625	3,775	111,710

Source: Miljøministeriet Skov- og Naturstyrelsen; Fischereiamt Kiel; Staatliches Fischereiamt Bremerhaven; Ministerie van Landbouw, Natuurbeheer en Visserij-Directie Visserijen

Note: Dutch data are seasonal, e.g. 1965 = 1 July 1965 – 1 April 1966

5.4.3 Trough shells

Within the shallow (5 to 20 m) waters along the continental coast of the North Sea, *Spisula subtruncata* is a widespread and abundant species, reaching densities of 8,000 individuals per m⁻² (Thorson, 1979). Fisheries for *Spisula* spp. commenced around 1990 in Denmark, Germany and the Dutch Delta area, and have been increasing since then. In Denmark, three vessels are licensed to fish 5,000 tonnes of *S. solida* per year. No landings statistics are available for Germany and the Netherlands. In 1993, up to 7 vessels were seen fishing simultaneously off the Dutch Wadden Sea (M. F. Leopold, pers. obs.).

5.4.4 Restrictions on the fisheries

Restrictions of the shellfish fishery in the German Wadden Sea were caused by the founding of the Nationalpark Niedersächsisches Wattenmeer in Lower Saxony in 1986, and the cockle fishery was banned there in 1992. The fishery argues that the cockle catch was halved during the 1980s due to the restrictions by the national park (Meixner, 1992). In the Nationalpark Schleswig-Holsteinisches Wattenmeer of Schleswig-Holstein, which was founded in 1985, the harvest of cockles is not allowed. The fishermen have been required to transfer their mussel culture plots to other areas (Franz, 1992).

The shellfish fishery in Denmark has been under strict regulation since the severe decline in the mussel stock in the Danish Wadden Sea in 1988 (Dahl, 1992). In contrast, the Dutch fishery has been unregulated.

5.5 Food choice and intake by mollusc-eating birds

5.5.1 Eiders

Eiders use various feeding techniques on tidal and sub-tidal areas (Nehls, 1991; Ketzenberg, 1991). They prefer feeding by head-dipping at low water levels, during the rising or falling tide, depending on the position of the feeding grounds. In winter, when the food requirements of eiders are highest, eiders tend to feed at mussel beds close to the low water line, where feeding is not restricted during low tide. Eiders may dive to depths of more than 30 m and are thus able to reach bottom in any area of the Wadden Sea.

Molluscs form the main share of the diet of eiders in the Wadden Sea. In the Dutch sector, mussels and cockles each make up about 40% of eider diets (Swennen, 1976). In Schleswig-Holstein, cockles comprise 75% of eider diets, with most of the remainder of the diet being mussels (Nehls, 1991). At Königshafen, Sylt, eiders preferred mussels from May to December, except during October, when cockles predominated in their diets (Ketzenberg, 1991). Based on the percentage of eiders near cultivated mussels, Swennen *et al.*, (1989) estimated that over the year, eiders in the Dutch Wadden Sea took about 50% of

their mussel food from culture plots (30,000 tonnes). The percentage taken from culture plots is probably much lower in other areas of the Wadden Sea. The diets and the distribution of eider feeding grounds are subject to marked annual fluctuations. For example, about 100,000 eiders recently moved to the North Sea, where they joined common scoters on *Spisula subtruncata* banks (Leopold, 1993).

The size of mussels taken by eiders range from 5 to 65 mm, with the median between 32 and 52 mm, which is generally smaller than those taken by the fishery (Ketzenberg, 1991; Nehls and Ketzenberg, in press). Ketzenberg (1991) found that the foraging intensity of eiders increased from summer to autumn, as did the length of the mussels consumed (32 mm median length in May; 47 mm median length in November). Eiders show no clear size preferences among cockles; the sizes of cockles taken by eiders are usually similar to the size distribution of the stocks (Nehls, 1991, and unpubl.).

Swennen *et al.* (1989) estimated that the food consumption of eiders in the Wadden Sea was about 160,000 tonnes per year, based on their estimated daily food demand (Swennen, 1976). This estimation is rather rough, however, as neither the seasonal variation in the number of birds using the Wadden Sea (Swennen *et al.*, 1989), nor variation in their energy and food demands (Laursen and Frikke, 1987b) were considered. Eiders annually consume about 60,000 tonnes of mussels, and 100,000 tonnes of cockles (Table 5.4).

5.5.2 Common scoter

The diets of common scoters have been inferred mainly from where major concentrations of scoters forage. In the 1960s, about 40,000 scoters wintered in the western Wadden Sea, and are presumed to have taken primarily mussels and cockles. In the 1970s and 1980s, concentrations of scoters in the coastal North Sea were observed over banks of cockles, several species of smaller tellins, and recently, exclusively over banks of *Spisula subtruncata* (The Netherlands and Belgium) and *Spisula solida* (Denmark) (van Steen, 1978; Leopold *et al.*, in press). Stomach analyses of oiled scoters in The Netherlands showed a rather catholic diet in the Delta in 1988, but with a majority of *Spisula subtruncata* (Offringa, 1991), and in 1993, a mixture of *S. subtruncata* (majority) and *Donax vittatus* off Terschelling (den Hollander, 1993). Further north, off Jutland in 1987, scoters preyed mainly on *S. subtruncata* (Durinck *et al.*, 1993). In all areas, scoters showed no obvious size preferences. For example, for 4 consecutive years, scoters returned to a bank of *S. subtruncata* off The Netherlands where no recruitment occurred. The scoters took year classes 1-4 (median length 9 to 30 mm) in different years.

Using values of daily energy demands (60 g AFDM/day) for common scoters given by Offringa (1991), the annual food consumption of common scoters occurring off the Wadden Sea can be roughly estimated at between 25,000

and 35 000 tonnes wet weight, of which the major portion is *S. subtruncata* (Table 5.4).

5.5.3 Oystercatcher

Individual oystercatchers tend to specialize on certain prey types making it difficult to estimate the composition of oystercatcher diets over large areas. The highest densities of oystercatchers are reached on mussel beds, where mussels are their primary food (Zwarts and Drent, 1981; Meire, 1993) and on dense beds of cockles (Meire, 1993). Alternative food species include several bivalves, polychaetes and snails. However, in most areas, bivalves are the most important prey species. It is estimated that about 75% of the winter food consists of cockles with the rest mainly being mussels (Lambeck *et al.*, in press). This finding is consistent with the low proportion of intertidal areas covered with mussel beds. Oystercatchers select mainly mussels of 30 to 45 mm length, but they take other lengths if the preferred size-classes are not available. When feeding on cockles, oystercatcher prefer the larger size classes of 15 to 40 mm (overview in Bos, 1994).

Total food consumption of oystercatchers in the Wadden Sea amounts to 160,000 tonnes of molluscs (wet weight), which is of a similar magnitude as the consumption of eiders (Table 5.4).

5.5.4 Herring Gull

The food of herring gulls includes a wide variety of the smaller animal species that occur in the Wadden Sea (Spaans, 1971; Vauck and Pruter, 1987; Dernelde, 1993). Molluscs form a high proportion of herring gull diets during all times of the year. In pellets collected on the island of Sylt, mussels were present on average in about 40% of the samples and cockles in about 10% (Dernelde,

1993). Due to the lack of quantitative data on food intake in terms of energy equivalents, we assume that molluscs (mussels and cockles) constitute about 25% of herring gull diets in the Wadden Sea. Under the above assumption, herring gull consumption of molluscs amounts to 12,000 tonnes wet weight (Table 5.4).

5.6 Impact on food stocks

Studies of the impact of food consumption on the biomass of the macrozoobenthos in the Wadden Sea region are available only for eiders. In the Schleswig-Holstein area, eiders eat 34% of the total food taken by carnivorous birds (Nehls, 1989), and are therefore important consumers. Eiders consume 3–5% of the total macrozoobenthos on the tidal flats of the Wadden Sea, and about 12.5% of the stocks of mussels and cockles there (Nehls, 1989; Swennen *et al.*, 1989). These estimates are lower than have been reported for eider from other areas. For instance, in the Ythan estuary in eastern Scotland, eiders are estimated to consume 39% of the annual mussel production, which is 20% of all zoobenthos production (Milne and Dunnet, 1972). Similarly, in the St. Lawrence estuary, Canada, in summer, eiders take 10–30% of their preferred prey, a *Littorina* species (Cantin *et al.*, 1974).

The data presented in this report suggest that the overall consumption of mussels and cockles by all species of birds is about 20% of the average stocks of these bivalves. However, mussel and cockle stocks exhibit marked annual stock fluctuations, and the proportion of mollusc stocks taken by birds varies accordingly. The bird species select preferred feeding areas and size classes of prey, and thus bird predation is not evenly distributed over all parts of the mollusc stocks. Although eiders could not be shown to affect the biomass of mussels present, even on heavily predated mussel beds (Nehls and Ruth, 1994), a reduction of preferred size classes was evident (Nehls and Ketzenberg, in press).

Table 5.4 Estimated average annual consumption (in tonnes wet weight) of the main bivalve eating birds in the Wadden Sea. Eider consumption after Swennen (1976), common scoter after Offringa (1990), oystercatcher after Bos (1994), herring gull, after Anonymous (1994).

	Mussel	Cockle	Spisula species
Eider	60,000	100,000	750
Common scoter	-	-	35,000
Oystercatcher	40,000	120,000	-
Herring gull	10,000	10,000	-

5.7 Synthesis: interactions between shellfish, fisheries and birds

Over the last few years two interpretations of the interactions of birds and fisheries in the Wadden Sea have emerged. On the one hand, it has been suggested that fisheries in the Wadden Sea reduce the food stocks available to birds and thus have affected bird numbers (Swennen, 1991; Laursen *et al.*, 1990; Leopold, 1993). On the other hand, fishermen have claimed that birds feeding at cultures or on natural mollusc stocks reduce their income and measures have been taken to expel the birds (Brull, 1963; Esser, 1988; Nehls, pers. obs.).

Mytilus numbers are probably regulated by the availability of suitable substrate, and their biomass is regulated by the food brought in by the tide (Dankers 1993). High mortality occurs during severe winters. In years with rich mussel stocks, fisheries reduce the biomass by about 25%, but locally and, in some years, fisheries reduce mussel stocks by a far higher percentage. As food resources needed by birds are on the order of 20% of the average standing stock of mussels, birds can, in some cases, be short of food. They then are forced to switch to alternative foods or leave the area, and may be subject to increased mortality or reproductive failure.

Consumption of mussels by seaducks is a long-term process, directed to the more abundant, smaller sizes of a mussel population, and likely to be compensated by production in most cases. Exploitation by fisheries may completely remove a mussel bed within a few days. Removals may be compensated by new recruitment.

In Schleswig-Holstein, Nehls and Thiel (1993) identified storms as being an important factor limiting the distribution of mussel beds to the sheltered parts of the Wadden Sea, where beds may persist over long periods. Mussel beds in exposed parts of the Wadden Sea are highly dynamic, and are removed frequently. The impact of the fishery will vary accordingly (Nehls and Thiel, 1993). In years of low mollusc stocks, fisheries may reduce the stocks below the level of natural variation. Recruitment of mussels and cockles in the Wadden Sea does not happen annually and predictably (Beukema *et al.*, 1993). In mussels, a successful recruitment is partly dependent on the existence of stable beds with adult mussels (McGrorty *et al.*, 1990; Dankers, 1993). Effects of fisheries on mollusc stocks may thus last over several years, particularly when natural, older beds are fished. Fishing on persistent beds in sheltered areas may remove crucial food reserves needed by mussel-feeding birds in times of low mussel populations.

For cockles, stocks vary greatly from year to year. Severe winters may reduce the stocks extremely. In years with low stocks, fisheries can remove a fairly high proportion of the cockles. Predation by birds will on average amount to about 20% of the standing stock, but in years with a low biomass birds utilize a higher proportion of the cockles, which are in the same size range as those taken by

the fishery. Reduced food availability at that point could force the birds to feed in less suitable areas (Bos, 1994) or to leave the area, with the risk of increased mortality.

Competition between birds and fisheries is most likely to occur in situations where a combination of natural variation in stock size and fishery impacts have resulted in low stocks. In those instances, an impact of fisheries on eiders and common scoters appears to be more likely than *vice versa*. In general, birds, such as oystercatchers that are restricted to the intertidal zone, will be most strongly affected by fisheries, as they are immediately affected by the removal of mussel spats, whereas eiders may also utilize the culture plots and other subtidal areas.

Pehrsson (1984) has shown that the availability of food is the key factor regulating the number of eiders. A combination of failing recruitment and continuous intensive fishing in the Dutch Wadden Sea led to a reduction of both mussel and cockle stocks in 1990, and, in the following years, resulted in extremely low mollusc stocks in this part of the Wadden Sea. This change was paralleled by increased mortality of alternative prey species (Beukema, 1993). As a consequence, numbers of eiders and oystercatchers declined (Swennen, 1991; Smit, 1994). A similar incident occurred in the Danish Wadden Sea after 1986 (Laursen and Frikke, 1987). Due to fishing pressure and ice damage in winter 1986/1987, only 3,000 tonnes of mussels were caught during the following 2.5 years, and the eider population was much affected. Since 1987, the numbers of eiders in the Danish Wadden Sea have not increased.

Concurrently with the decrease in Denmark, the numbers of eiders decreased in The Netherlands and increased in the German Wadden Sea. Swennen (1991) attributed the large decreases in the Dutch Wadden Sea to overfishing of the populations of cockles and mussels. The shift of eiders towards Germany possibly may be the result of the presence of large mussel populations in the East-Frisian Wadden Sea (Nehls, pers. comm.).

The fishery for the two *Spisula* species has the potential for interacting with wintering seaducks, particularly common scoters, for which the coastal zone of the south-eastern North Sea is an important habitat (Skov *et al.*, in press). Interaction of fisheries and seaducks only occurs when both use the same area, which is usually an area of high *Spisula* density. Fishermen apparently use the presence of large flocks of seaducks as an indication of the presence of good fishing grounds, and in several of the areas where fisheries and seaduck have co-occurred, numbers of ducks have decreased significantly. This happened in the Dutch Delta area in 1990, off the Dutch Wadden islands in 1993, and off the Dutch mainland coast in 1994 (Leopold *et al.*, in press). Seaduck counts in the two areas off the Danish and German coasts where *Spisula* fisheries started in 1992 have not been sufficiently frequent to monitor bird numbers. However, ducks were only numerous at the Rode Klitsand location, whereas fisheries at the other two locations, Horns Reef and Amrum Bank, probably took place in areas without

significant numbers of seaducks present (Skov *et al.*, in press). When the fishery is directed to areas that have no ducks present, then the impact is probably minimal, since the fishery targets relatively mature *Spisula* that may not remain available to seaducks for long.

The proportion of mussels and cockles taken by birds is of the same order of magnitude as the fisheries yield, but bird predation is spread over the year. As production of benthic bivalves in the Wadden Sea is food limited, and density dependent growth regularly occurs (Dankers 1993), predation is likely to be compensated by growth and recruitment. High numbers of eider may utilize the mussel cultures, but even in heavily used cultures, no effects on mussel production have been found (Nehls and Ruth, in press). Most birds also focus their predation on juvenile molluscs where other causes of natural mortality are high. For *Spisula* species, the stock sizes, and especially production and fishery takes are generally unknown, which makes a comparison of (relative) impacts of fisheries and seaducks impossible at present.

5.8 Research needs

The interactions of shellfish fisheries and seaducks are not yet clearly understood, and further studies on the mussel beds in the Wadden Sea and on the offshore banks of the German Bight are required. More information on the feeding ecology of eider and common scoter and their possible effects on the mussel beds is needed. The relationship between the mussel harvest of these birds and the shellfish fishery need to be studied, as do influences of the shellfish fisheries on the seaduck populations and their temporal and spatial distribution (Nehls, 1989).

6 Spatial and temporal variability in the breeding success of seabirds around the British Isles: evidence for distinct sandeel stocks?

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6.1 Introduction

Geographical patterns in the breeding success of kittiwakes around the British Isles have been examined, with a view to identifying separate domains within which reproductive success of seabird colonies fluctuates among years in a concordant fashion, but in a pattern distinct

(statistically uncorrelated) with that found in other domains. There are several lines of evidence that suggest that such an approach is a potentially useful one. First, considerable data are now available on the potential foraging range that may be covered by breeding seabirds that are obliged to return periodically to their nests to relieve mates or to feed young (Furness and Monaghan, 1987; Anker-Neilsen and Lorentsen, 1990). When at sea, seabirds show preferences for particular water masses, reflecting not only differences in the productivity of the water (*e.g.*, as primary production), but also qualitative differences in their ecological structure (such as grazing of primary production by zooplankton and the transfer of energy to pelagic fish and seabirds *versus* recycling by bacterioplankton, benthos, and demersal fish) (Joiris, 1978, 1983; Joiris *et al.*, 1982; Schneider *et al.*, 1986, 1987).

Some local very high concentrations of seabirds are also encountered, often at biologically active fronts. These concentrations of feeding seabirds are often concordant with groups of marine mammals, and they reflect local concentrations of food. Interannual shifts of prey abundance within water masses, or fluctuations in the position of currents, water masses, or fronts where seabirds forage, can result in fluctuations in aspects of seabird reproductive ecology (Anderson and Gress, 1984; Blake, 1984; Hislop and Harris, 1985; Anker-Neilsen, 1987, 1990; Barrett and Furness, 1990; Vader *et al.*, 1990; Furness and Barrett, 1991; Bailey, 1991; Hamer *et al.*, 1991; Frank, 1992; Monaghan *et al.*, 1992a, 1992b).

6.2 Concordance in the breeding success of kittiwakes

Seabird ecologists tend to collect seabird breeding data (*e.g.*, numbers of breeding pairs, breeding success, chick growth, etc.) from a single site and from one or a few study species at that site, but often over a period of years. No integrated research programme has been set up to study the variations among sites in breeding ecology and performance of seabirds over spatial scales appropriate to interpretation in relation to oceanography or fish stocks. However, many studies have been carried out at seabird sites around the British Isles, and since 1986, data have been collected using standardised methods from many seabird colonies by the Joint Nature Conservation Committee (JNCC) seabird monitoring programme, which is administered by JNCC and the Royal Society for the Protection of Birds (RSPB). This database includes information from various independent studies and from monitoring work supported by JNCC and The Seabird Group. Those data sets have been used to prepare annual summaries of the breeding performance of seabirds around the British Isles from 1986–93 (Walsh *et al.*, 1990, 1991, 1992, 1993). Longer data sets, spanning periods from the early 1970s, exist for a rather small number of sites (such as Foula in Shetland, Isle of May in Firth of Forth, Skomer in South Wales). However, in this analysis we have concentrated our attention on the JNCC data set for breeding success (chicks per nest) of samples of kitti-

wakes from 33 colonies around the British Isles that were obtained between 1986 and 1993 (Figure 6.1). This analysis extends the work of Harris and Wanless (1990). Smaller data sets (for the same years, but fewer and not necessarily the same colonies) for common guillemots and shags were also examined.

Kittiwakes are surface feeding seabirds and forage over moderately large ranges from the colony (typically up to 50 km). Reductions in breeding success (from the average of about 2 eggs laid per nest) are to a considerable extent due to losses of growing chicks caused by lack of food. Additionally, breeding success can be affected by predators (especially gulls and skuas) at some colonies. Diets of breeding kittiwakes have been examined at a number of colonies around the British Isles, and at many sites during chick-rearing, diets consist largely of 0-group sandeels (Pearson, 1968; Galbraith, 1983; Harris and Riddiford, 1989; Furness, 1990; Bailey *et al.*, 1991; Furness and Barrett, 1991; Wanless and Harris, 1992) though, particularly in the southern areas, sprats and zooplankton may be used (Coulson and Thomas, 1985; Anon., 1994).

Overall variation in breeding success was low in the common guillemots ($n = 41$ means of annual breeding success at individual colonies, overall average mean = 0.729 chicks per pair, CV = 11.49%). For shags, breeding success was more variable ($n = 42$ means, overall mean =

1.259 chicks per nest, CV = 34.47%). However, kittiwakes showed by far the greatest variation in breeding success ($n = 248$ means, overall mean = 0.721 chicks per nest, CV = 60.61%). A number of biological interpretations are available for this result. Guillemots and shags, as diving species, may be less sensitive to variations in food supply than the surface-feeding kittiwake (Decker *et al.*, 1995). Also, guillemots feed their chicks on large sandeels (12–14 cm typically), whereas kittiwakes and shags feed more on smaller sandeels and so will be more sensitive to year to year variations in sandeel recruitment.

The greater variance in kittiwake breeding success suggested that this species would be particularly suitable for an analysis of geographical concordance in year to year breeding success. In addition, data were available for a large number of colonies (we used only those for which breeding success had been monitored in at least six of the eight study years).

Examining the variances in breeding success among years at colonies in particular regions, it is evident that breeding success was much more variable at Shetland than at Orkney, with variation at other sites tending to be intermediate (Table 6.1). This pattern of low variance at Orkney but high variance at Shetland coincides with low variance in 0-group sandeel abundance among years at Orkney, but high variance at Shetland in the June/July sandeel surveys from 1969-88 (Wright & Bailey 1993).

Table 6.1 The mean breeding success of kittiwakes around the British Isles grouped according to Figure 5.2 (except Orkney).

Group	Mean	SD	CV	N	p	Remarks
Southwest	0.58	0.35	61	69	ns	excl Marwick and Kettla
Northeast	1.01*	0.37	37	52	ns	
Northwest	0.65	0.47	72	23	<0.01	
Shetland	0.51	0.47	92	46	ns	excl Ailsa Craig
South	0.94*	0.39	41	16	<0.01	excl Mull Head
Orkney	1.04*	0.16	15	14	ns	

SD - standard deviation

CV - coefficient of variation (%)

N - number

p - significance of differences in breeding success within groups

ns - not significant

* - groups have significantly higher mean breeding success than the three other regions

Pearson product moment correlation coefficients between kittiwake breeding success at pairs of colonies over the eight years showed high correlations (>0.8 is significant at $p<0.05$ for these samples of 8 years of data) for many pairs of colonies that are geographically close. For example, within Shetland, breeding success of kittiwakes at Foula correlated with that at Fair Isle ($r=0.89$), Troswick ($r=0.84$), Sumburgh ($r=0.90$), and Noss ($r=0.83$). However, breeding success of kittiwakes at Foula did not correlate with breeding success at colonies in southern Britain.

Using cluster analysis (Distance = Pearson, Linkage = Complete), a cluster tree was produced (Figure 6.2) that showed fairly consistent grouping of kittiwake colonies into geographically (and presumably oceanographically) coherent units (Figure 6.3). In the case of Shetland, we know that the poor breeding success that occurred in all those kittiwake colonies between 1988 and 1990 was a consequence of the birds having difficulty in finding sandeels (Hamer *et al.*, 1994) during a period of low sandeel recruitment (Wright and Bailey, 1993).

The cluster analysis is based only on year-to-year variation in breeding success (correlations in pattern between colonies), and ignores differences in absolute breeding success between colonies. The latter also shows variation between regions. Kittiwake colonies in two of the domains, for example, show higher average breeding success than in the other three (Table 6.1). In principle, it would be possible to use the mean breeding success as a second axis to separate colonies orthogonal to the correlation tree.

The high dependence of Shetland kittiwakes and guillemots on sandeels to feed chicks despite the high coefficient of variation of sandeel 0-group abundance at Shetland, and so the high variance in kittiwake breeding success at Shetland (and lower mean value than at Orkney), suggests that Shetland might be a marginal breeding area for these seabirds and/or their prey. That this is not the case is evident from the population sizes. They were estimated in the mid-1980s to be 163,000 guillemot adults and 50,000 kittiwake nests at Shetland compared with 183,000 guillemot adults and 64,000 kittiwake nests at Orkney. Thus, Shetland and Orkney are very similar in terms of the numbers of these two species that they support (Lloyd *et al.*, 1991).

Assuming that interannual variation in kittiwake breeding success in other regions is also predominantly driven by local food supplies, we suggest that the reproductive success of kittiwakes around the British Isles may be divided into distinct domains. In our analysis, five such domains were evident: 'Shetland', 'northeast', 'south', 'southwest' and 'northwest'. An alternative model, that breeding success varies among years according to local variations in weather, is considered less likely, but cannot at this stage be ruled out. However, the ornithological literature suggests that kittiwake breeding success is much less susceptible to effects of weather than it is to effects of food supply. We feel that the patterns suggested by this analysis

invite further study, and in particular may suggest regional structuring of kittiwake food (perhaps particularly in stocks of sandeels) into a number of distinct units with differing dynamics. Perhaps the domains of kittiwake breeding success correspond to major water masses; oceanic Atlantic water, continental shelf Atlantic water, entering the North Sea, both north of Scotland and through the Channel, and coastal/North Sea water. In particular it would be useful to investigate whether similar regional groupings can be identified by analysis of other seabird data sets, such as guillemot chick growth rates or tern numbers or breeding success, or from analysis of fish stock structure or communities. Interpretation of such patterns also invites input from physical oceanographers.

7 Relationships between fish populations and reproductive biology of common terns in the Wadden Sea

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7.1 Introduction

Because the reproduction of seabirds depends on marine food sources, several parameters of their reproductive biology can be used as indicators of the availability and distributions of the prey species on which they feed (review: Montevecchi, 1993). Also, the analysis of food taken by seabirds and fed to mates or chicks can provide valuable information about the state of the food supplies. In this respect terns are especially useful as indicators of the marine resources they use, because:

- owing to small body size, their energy reserves are low, and food availability immediately affects body condition and reproduction in adults (Monaghan *et al.*, 1989; Frank and Becker, 1992) and growth of young (Mlody and Becker, 1991);
- the transport of single food items in the bill makes it easy for ornithologists to identify prey;
- the distribution of common and arctic terns *Sterna hirundo* and *S. paradisaea* on the coasts around the North Sea, as well as the accessibility of many colony sites, make them suitable as monitors of temporal and spatial variations in the populations of prey organisms necessary for successful reproduction.

The responses of arctic terns to changes in the supply of sandeels have been well documented on the Shetlands and Orkneys during the period of low sandeel availability in the 1980s (Furness, 1987; Monaghan *et al.*, 1989, 1992; Uttley, 1992). In the southern North Sea, however, sandeels are not so important as prey for terns as are herring and sprat, two commercially important species (Table 2.11).

Table 7.1 Correlations of breeding success of four common tern colonies on the Wadden Sea coast, southern North Sea, from 1981-1993. Pearson correlation coefficients are presented.

	Oldeoog	Wilhelmshaven	Augustgroden
Wilhelmshaven	0.11 (13)		
Augustgroden	0.52 (13)*	0.27 (13)	
Griend	0.29 (12)	0.15 (12)	0.20 (12)

n.s.; *p<0.1

7.2 Spatial and temporal trends in breeding success of four common tern colonies

Since 1981, long-term studies of common tern reproductive and foraging ecology have been carried out on the Wadden Sea coast. At the island of Griend, The Netherlands, the mean breeding output was low (0.38 ± 0.20 fledged chicks per pair per year, $n=12$, Stienen and Beninkmeijer, 1992; Breninkmeijer and Stienen, 1993), compared with three colonies at Jade Bay, Germany: At the island of Minsener Oldeoog 0.76 ± 0.58 , and at two coastal sites, at Wilhelmshaven 1.11 ± 0.55 and at Augustgroden 0.83 ± 0.63 chicks fledged ($n=13$ each; Becker, 1991, and unpubl. data). Correlations between the annual reproductive output of the colonies were weak but positive, with the exception of Oldeoog/Augustgroden (Table 7.1). The reason for the weak correlation is that tern reproductive success is not only influenced by food availability, but also by factors like predation and flooding which vary strongly among sites. In consequence, to focus on interactions between reproduction and food supply, parameters should be studied which are more directly affected by food availability, which has been preliminarily done for the common terns on Minsener Oldeoog.

7.3 Reproductive performance and fish stocks at Minsener Oldeoog

7.3.1 Temporal trends

Reproductive biology: Except for 1981, when many common terns resettled to the new, man-made sandy island of Minsener Oldeoog, the number of breeding pairs fluctuated between 1,500 and 2,500 pairs. In both 1985 and 1988, the low numbers of breeding pairs may be the result of low breeding output during the previous year. It

may be that after the previous year's failure some adults did not breed owing to poor condition, or resettled to another colony site. Variation in clutch size was low, with the exception of 1991, when the weather was cold and water temperature low in spring. In that year, the migration of herring was delayed, and thus were not available during the courtship period of the terns.

Tern reproductive output fluctuated between 0.0 and 1.6 chicks fledged (survival to >18 d) per pair per year. This interannual variation in reproductive output resulted from changes in the availability of food, as well as from the influence of various predators (in 1987, rats were a problem; in 1993, gulls). In 1984, a stormy period at the end of June resulted in the death of a majority of chicks through starvation. In 1986 and 1988, breeding success peaked, and these years were characterized by chick growth rates that were above the average. The lowest chick growth rates occurred in 1984, when a food shortage led to high chick mortality. In that year, chicks that did survive fledged at an older age than usual (Data from Becker, 1991; Becker and Finck, 1985, 1986; Becker and Specht, 1991; Mlody and Becker, 1991, and unpubl.).

Fish stocks: The size of the herring stock (Herring Index, < 20 cm, no./h; ICES young fish survey, Dornheim and Wegner, 1993) was lowest in 1981, and increased to a peak in 1987, after which the stock decreased through 1992. In 1986 and 1987, the catches of clupeoids and other animals by a stationary stow net peaked at the Wadden Sea island of Minsener Oldeoog, with $70 \pm 20\%$ of the animals caught being clupeoids. Herring was the dominant species of clupeoid in all years (e.g., 1991: herring 99%, sprat 1%, $n=5145$). The sprat index (< 10 cm, no./h, see above), which showed greater interannual fluctuations than the herring index, peaked in 1989 (Dornheim and Wegner, 1993). Both 1982 and 1983 were characterized by high indices of the sandeel population in the Wadden Sea (Tiews, 1989).

Chick diets: The percentages of clupeoids in chick diets (studied in 1984–1986 and 1991–1992) was highest in 1984 and lowest in 1991 (Frank, 1992, unpubl. data).

Table 7.2 Spearman correlation coefficients of reproductive parameters in common terns and data on food supply (Wadden Sea, Germany). Only correlations with $n \geq 5$ and coefficients $r_s \geq 0.5$ are presented.

Variable a	with	Variable b	r_s	p	n
Growth rate		Age at fledging	-0.76	≤ 0.05	8
Growth rate		Herring index	0.53		9
Age at fledging		No of animals (stow net)	-0.70		5
Age at fledging		No of clupeoids (stow net)	-0.70		5
Age at fledging		Chicks fledged/pair	-0.67	≤ 0.05	9
Chick loss*		Clutch size	0.57	≤ 0.05	13
Chick loss*		Growth rate	-0.85	≤ 0.01	0
Chick loss*		Age at fledging	0.77	≤ 0.05	10
Chick loss*		No of animals (stow net)	-0.66		6
Chick loss*		No of clupeoids (stow net)	-0.66		6
Chick loss*		Herring index	-0.52		12

*weather and food situation

7.3.2 Correlations of fish stocks and tern reproduction

For all of the variables mentioned, Spearman correlation coefficients were calculated and are presented in cases in which $r_s > 0.5$ and $n > 5$. Within the fish stock data, no clear correlations were found (clupeoids in stow net with herring index: $r_s = 0.37$, n.s., $n = 6$). Within the tern reproduction data, growth rates and chicks fledged/pair were negatively correlated with age at fledging (Table 7.2); chick losses from bad weather and from food shortages correlated positively with clutch size and age at fledging, and negatively with chick growth rates.

With respect to the correlations of fish stocks and tern reproductive biology, the data in Table 7.2 showed interesting tendencies, even though there were no significant correlations:

- the frequency of clupeoids in the stow net, as well as the total stow net catch, were negatively correlated with chick losses by starvation and weather, and with chick age at fledging;
- the herring index was positively correlated with chick growth rates and negatively with chick losses by starvation and weather.

The sample sizes were often low, and we can expect that a better data base (more years) would result in stronger correlations.

7.4 Conclusions

The data show that the reproduction of terns on the southern North Sea coast is linked with the herring stock. The fishery on this economically important fish species (industrial fishery on small herring in the North Sea, Jensen *et al.*, 1994; bycatch of the shrimp fishery in the Wadden Sea, Walter and Becker, 1994) has the potential to interact negatively with the most important food supply

of the terns and other seabirds affecting their reproductive output and population size. Unfortunately the data presented are limited and incomplete, constraining the analysis. This underlines the importance of long term data series as the basis of understanding of interactions between seabirds and fish. To investigate interactions between tern reproduction and fish stocks, parameters which are directly related to food availability, like chick growth or chick starvation, should be studied in addition to breeding success.

The results from Minsener Oldeog also indicate the value of obtaining fish population data from the vicinity of seabird colonies to secure information on local fluctuations in fish stocks. To manage stow nets is relatively easy and cheap. In comparison with catches by fishery vessels, the stationary stow net has the advantages that it can be installed yearly at the same site, and that it catches the small fish which are required for many seabirds during reproduction.

8 General conclusions

Although there is considerable spatial variation in the amount of dietary data available for all seabird species, the Study Group was able to provide a substantial analysis of the amounts, types, and spatial distribution of the consumption of important prey species. Most prey data originate from studies made in Shetland or east Scotland, where consumption by seabirds is concentrated, and thus for the most important area, our estimates of seabird consumption by prey type are most robust. The following conclusions highlight the results of the two Study Group Reports (CM 1994/L:3 and L:34).

1 Seabirds in the North Sea are estimated to consume 600,000 tonnes of food per annum. This estimate is based on data obtained over the last decade, when seabird numbers have been at an historically high level, and excludes consumption by seaducks and waders. Seabird

consumption can be partitioned approximately as 200,000 tonnes of sandeel, 30,000 tonnes of sprats and small herring (predominately sprats), 22,000 tonnes of live, small gadids and 13,000 tonnes each of large herring and mackerel. Seabirds consumed an additional 109,000 tonnes of discards and 71,000 tonnes of offal. The remainder of their prey was partitioned between zooplankton, intertidal and terrestrial foods.

This apportionment of prey species is different from that assumed for seabirds in the MSVPA, particularly in the case of sandeels. This difference results because seabirds are selective foragers and concentrate their foraging on a relatively small number of fish species.

2 Seabird consumption of prey is unevenly distributed across the North Sea. The highest proportion of total consumption is in Area IVa (west), where breeding colonies of seabirds are concentrated. In the breeding season (April-July), the foraging of breeding seabirds is restricted to within tens of km of their breeding sites. Therefore, much of their prey during this season is from coastal waters.

Consumption of sandeels varies from 111 574 tonnes in ICES IVa west to 3 044 tonnes in ICES IVc. In general, sandeel consumption is concentrated in the nearshore waters off the Orkneys and Shetland, and to a lesser extent off the northeast coast of the main island of Great Britain.

3 There is temporal variation in the consumption of sandeels by seabirds in the North Sea. Sandeels comprise nearly 50% of food consumption in the second quarter of the year, and remain the most important prey item in the third quarter. In winter, when sandeels become less available, they represent about 20% of the total seabird diet. In winter, a large proportion of the population of the primary seabird consumer of sandeels, common guillemot, emigrates from the North Sea. In winter, the importance and total consumption of other fish species increases considerably.

4 There is relatively little spatial overlap in sandeel harvest by seabirds and sandeel fisheries.

5 Northern fulmars and common guillemots account for 54% of total seabird energy demand. The diet of guillemots is quite well known, even for the winter period. In contrast, little is known about the diet of fulmars, especially in winter.

6 Discards and offal represent 30% of total food consumed by seabirds in the North Sea, and over half of the food taken in winter. Northern fulmars take the largest portion of these foods.

7 The consumption of shellfish by seaducks in the North Sea is concentrated in the German Bight and the Wadden Sea. There, annual consumption is estimated to be 100,000 tonnes of bivalves. Data on the consumption of shellfish by waders on the coasts of the North Sea and

for seaducks in areas other than the German Bight remain to be assessed.

8 Although there is considerable information available on the length distributions of fish and shellfish taken by seabirds, studies to date have rarely assigned fish or shellfish to age classes. Considerable work is required to provide information on the age classes of fish consumed by seabirds.

9 For useful linkage of seabird prey consumption to fisheries management models, it is essential that temporal and spatial scales used in the two types of analyses correspond. Populations of many species of seabirds are concentrated at sea in relatively few areas.

10 Preliminary analyses suggest that there are significant spatial correlations in the interannual variability of the reproductive success of seabirds breeding around the British Isles. This result suggests that the birds breeding within regions with similar interannual patterns are responding to changes in the availability of the same fish stocks. This approach provides an novel mechanism for assessing the appropriate spatial scales for matching fisheries and seabird management.

11 Seabirds are characterised by having high rates of adult survival and low annual reproductive potential (1–3 young). Because adults can shift between prey species or foraging grounds, moderate variations in prey populations are unlikely to have severe effects on the survival of adult seabirds. However, because breeding birds are tied to insular and coastal colonies, and because many species depend on one or a few prey species to feed chicks, local fluctuations in fish recruitment can have major effects on seabird reproduction. Surface- and near-shore-foraging seabirds generally experience greater inter-annual variability in reproductive performance than do pursuit-diving and offshore-foraging seabirds.

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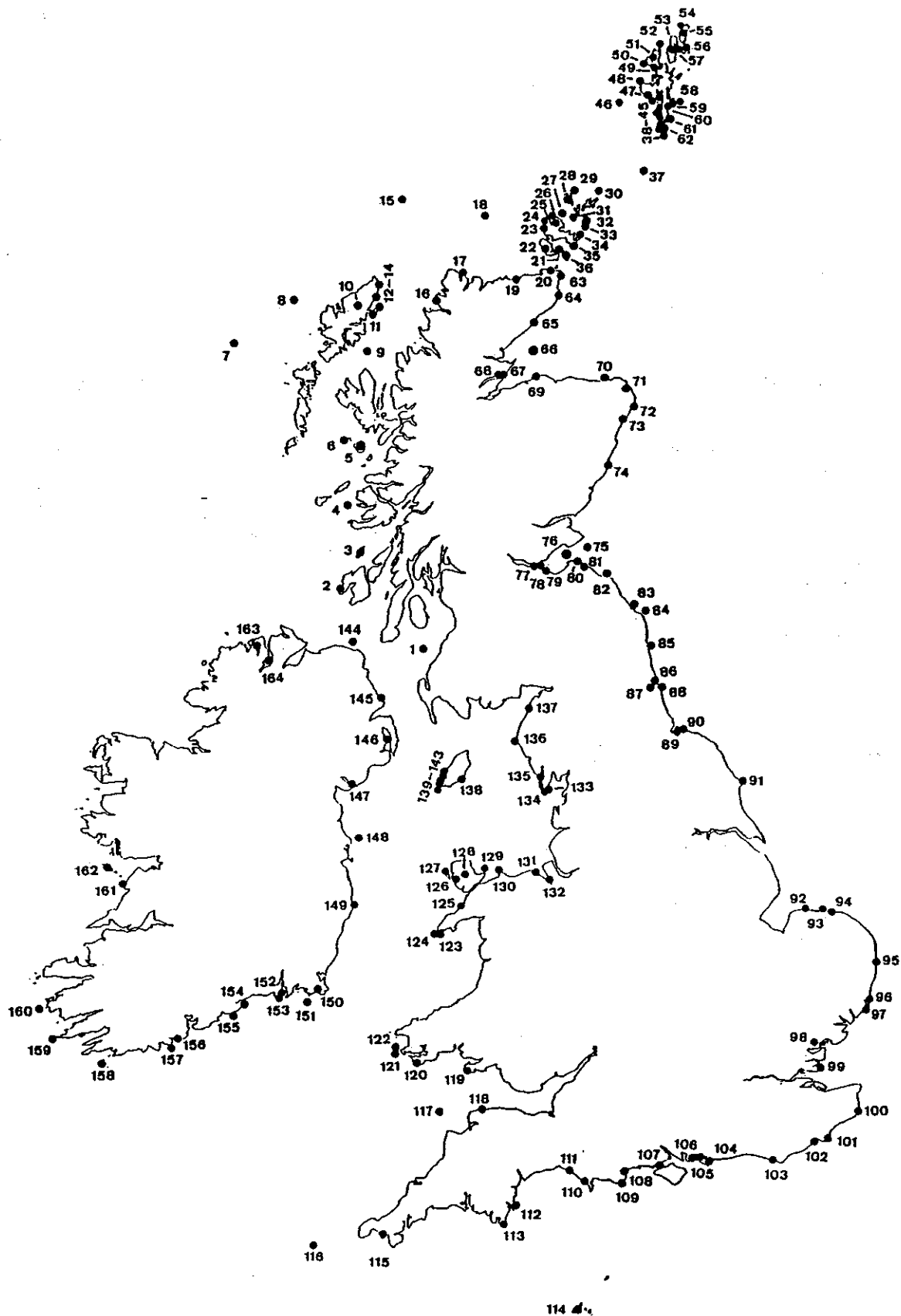


Figure 6.1 Colonies of kittiwakes and other seabirds in the JNCC database that have been monitored for seabird breeding success and other parameters.

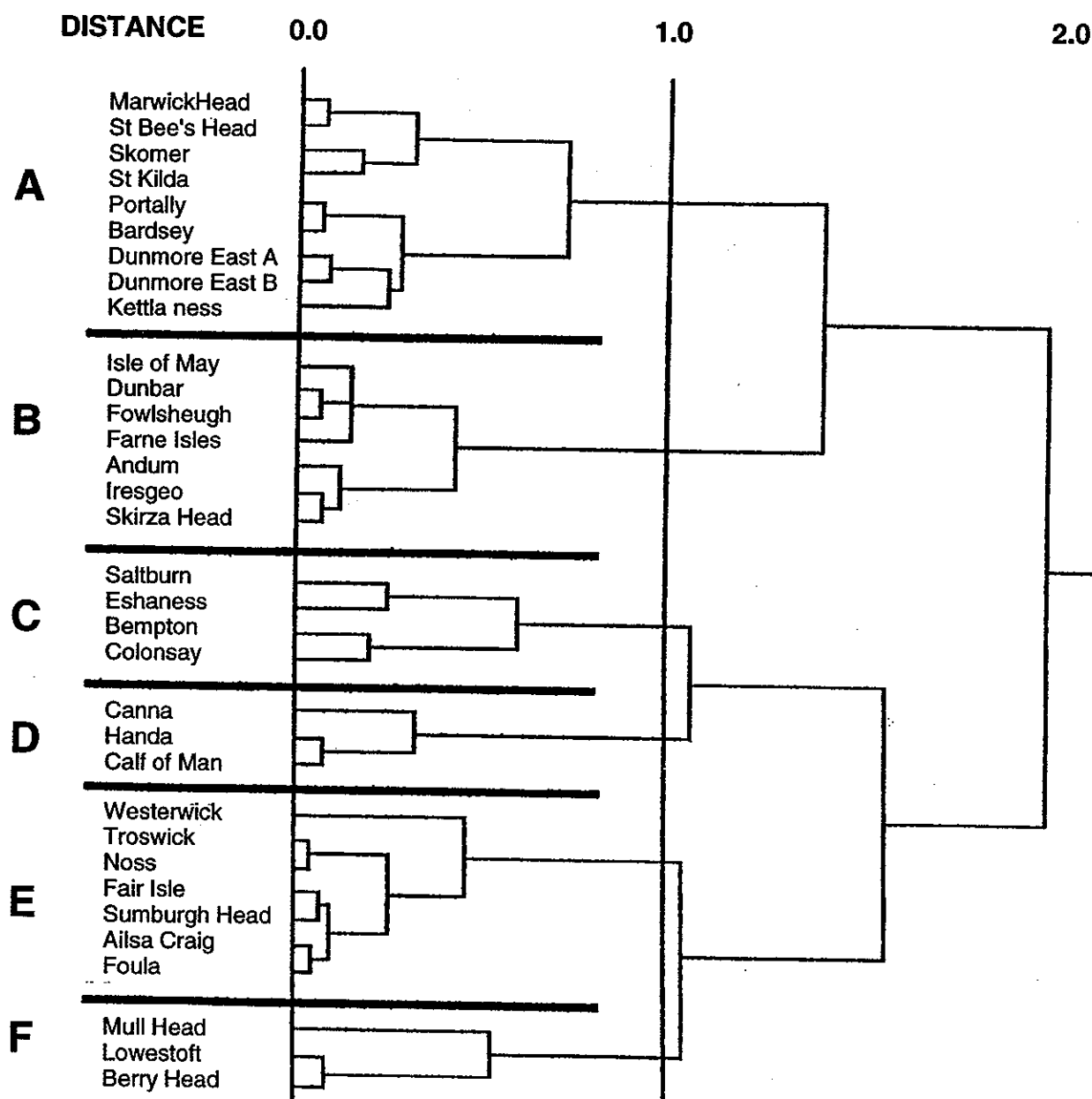


Figure 6.2 Dendrogram of kittiwake colonies showing similarity (concordance) in patterns of interannual variation in production of young. See Figure 6.3 for a map showing the locations of colonies classified into the different groupings.

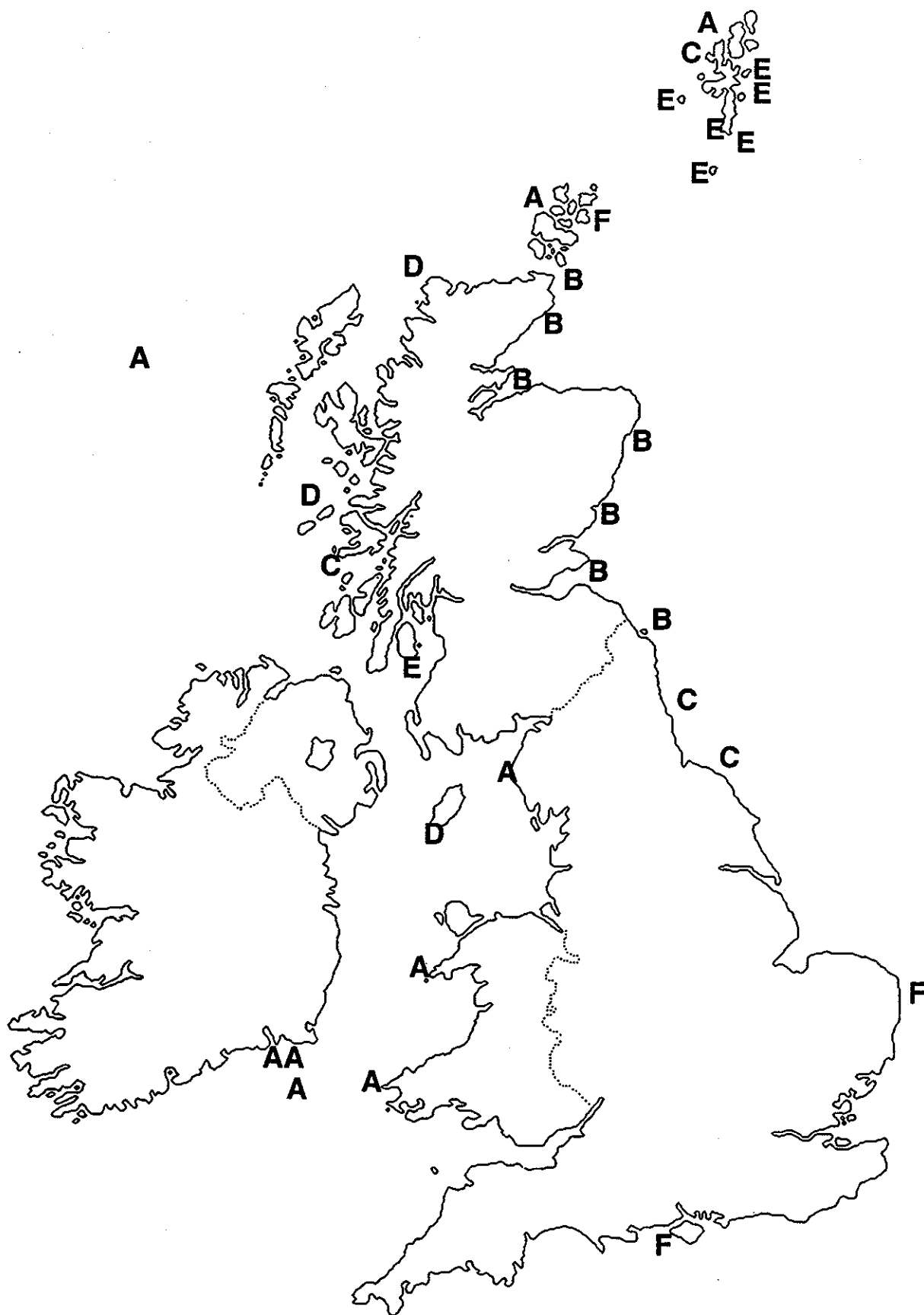


Figure 6.3 Locations of kittiwake colonies that clustered together on the basis of similarity in interannual variation in reproductive success, showing the tendency for colonies showing the same pattern of interannual variations to be predominantly from the same geographical region.