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SEABIRD ECOLOGY IN THE NORTH SEA

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ABSTRACT

The numbers of all species of seabirds regularly occurring in the North Sea are presented and a brief account is given of the main processes affecting their population dynamics. Monitoring of breeding numbers and known trends, distribution at sea, and the patterns of movement of both breeding and non-breeding birds are described.

Feeding methods and foraging behaviour are discussed and methods for determining the diet of seabirds are critically examined. Quantitative methods for determining the amount of food taken, and the ecological energetics of seabirds are dealt with in some detail, including the problem of the availability of food to birds. Physical factors such as tide, weather and sea-state affect several aspects of seabird biology.

The relationship between seabird population and fish stocks and fisheries is of increasing importance and the major aspects of these are described and discussed in detail. Other impacts of man such as pollution by oil, chemicals and rubbish are also important. Predation by introduced mammals and also by the native larger gulls, and unintentional disturbance resulting from human recreation, can have serious effects on breeding colonies. In the south-eastern North Sea low-lying coasts are vulnerable to flooding and affected by land reclamation and coastal management.

INTRODUCTION

Seabirds form an important and visible component of the fauna of the North Sea. Species occur on the North Sea in different places, at differing times and for differing reasons and the components of each species population must be considered; accordingly in Table 1 the birds breeding on the coasts of the North Sea have been distinguished from those which breed elsewhere but use the North Sea during the non-breeding period, and from the immature prebreeding components of populations breeding around the North Sea. Immature birds wander more widely than adults and the youngest age-groups of native breeding populations may not return to the North Sea for one or more years.

The species using the area may be divided into those which feed primarily in the coastal zone (under 5 km from the coast), and pelagic species feeding farther offshore (Table 1). With the exception of some terns, most of the coastal birds feed on benthic fauna, and some, notably the gulls, also feed inland. In this review we include the sea-ducks and grebes, but exclude species which occur on the North Sea in only small numbers or intermittently.

Oceanic species (fulmar, storm petrel, Leach's petrel) range far from land to feed. These birds, all in the order Procellariiformes, have the capacity for reducing their food (often plankton) to a stomach oil that enables maximum energy to be carried at minimum weight. They are the only species found frequently far from land while breeding (TASKER *et al.*, 1985a; HALL *et al.*, 1987).

Several species dive and pursue their prey below the water surface. These include red-throated diver, Manx shearwater, gannet, cormorant, shag, guillemot, razorbill, black guillemot and puffin, and they require moderately clear water (as they hunt by eyesight) and moderate densities of relatively large prey (commonly fish over 5 cm) or very high densities of smaller prey.

Within the North Sea, the skuas parasitise or prey upon other seabirds; they require high densities of seabirds that will disgorge edible foods when attacked and thus are found with large numbers of other seabirds.

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1. BREEDING NUMBERS

The numbers of most seabird species breeding on North Sea coasts are now reasonably well known as most colonies have been counted within the 1980s (Table 2). The northern part of Britain (Fig. 1) is the most important area within the North Sea, in terms of both numbers of birds and diversity of species.

Some species are present at or near breeding colonies for much of the year, whereas others only visit for a relatively short period and spend the winter south of the North Sea (Table 1). Assessing numbers of seabirds passing through or wintering in the North Sea is very difficult (see section on movements).

An attempt can be made to estimate numbers of 'offshore' species present in the North Sea throughout the year using information gathered in wide-ranging surveys of their distribution at sea made in the 1980s (TASKER *et al.*, 1987). These surveys gathered information on densities of birds in 28 areas (Fig. 2) of the North Sea through the year. If the average monthly densities for each of these areas is multiplied by their respective surface-area, an approximate number of birds present at sea within the North Sea may be estimated. Information for four of the commoner species, gannet, guillemot, kittiwake and fulmar are presented in Fig. 3. These figures do not take into account numbers of birds present at a breeding colony or on the water nearby, so that the total number present in the North Sea during the breeding season may be more than double that recorded at sea. The coverage of the North Sea by these surveys was not even and further surveys are now being carried out by British, Norwegian, Danish and Dutch teams.

Peak numbers at sea often occur during migration periods; for example, the majority of gannets (Fig. 3a) move out of the North Sea in winter, adults return first in spring, and move onto their colonies shortly afterwards. Increasing numbers at sea following this probably indicate the return of immatures and an autumn peak in numbers is associated with the departure of both adults and juveniles from the colonies (TASKER *et al.*, 1985b). The number of guillemots at sea peaks in August (Fig. 3b), when all chicks and adults are at sea. At this time chicks are still being tended by the male parent, while the adults are flightless as they moult their flight feathers. There is probably also some immigration from guillemot colonies to the north and west of the

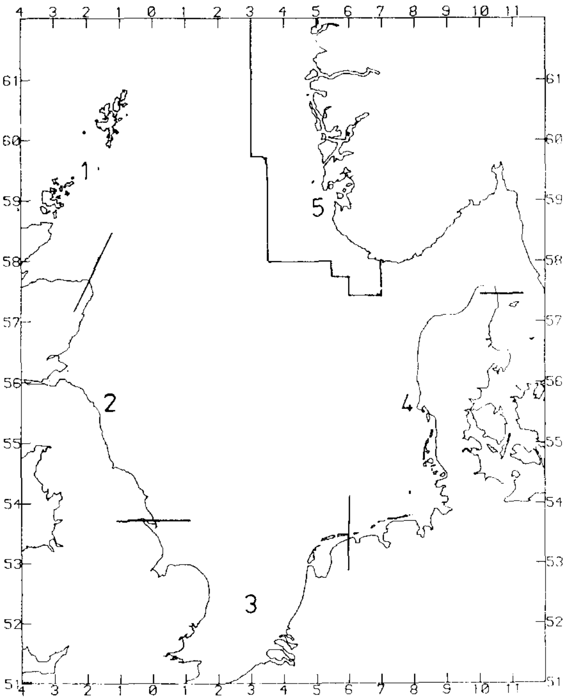


Fig. 1. The North Sea coast showing sections used for estimation of numbers of breeding birds (Table 2).

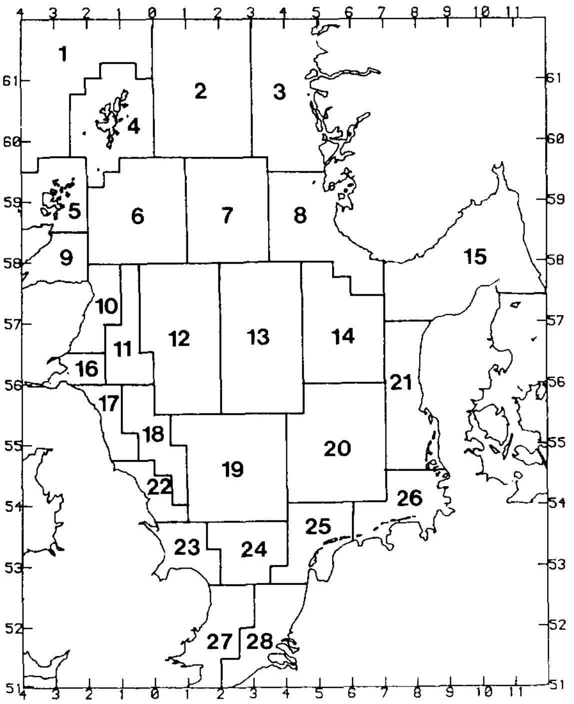


Fig. 2. Division of the North Sea into 28 areas for the estimation of numbers of birds at sea.

TABLE 1

The presence of commoner seabird species and their population components in the North Sea on a seasonal basis, and an indication of main feeding habitat (coastal (C) or offshore (O)).

	feeding		*month*		
species	*habitat*	*JFM*	*AMJ*	*JAS*	*OND*
Red-throated diver	C	++IB	IIBB	IIBB	++BB
Black-throated diver	C	++	+	+	++
Great northern diver	C	++	+	+	++
Great crested grebe	C	++		+	++
Fulmar	O	+IBB	+IIBB	IIBB	+IBB
Sooty shearwater	O			++	+
Manx shearwater	O		BB	++IBB	IB
Storm petrel	O		BB	++IBB	IB
Leach's petrel	O		BB	BB	IB
Gannet	O	B	IBB	+IIBB	B
Cormorant	C	IIBB	IIBB	IIBB	IIBB
Shag	C	IIBB	IIBB	IIBB	IIBB
Eider	C	++IIBB	+IIBB	IIBB	++IIBB
Long-tailed duck	C	++	+		+
Red-breasted merganser	C	+	+		+
Common scoter	C	++		++	++
Velvet scoter	C	++		++	++
Pomarine skua	O		+	+	++
Arctic skua	O		BB	+IBB	
Great skua	O		BB	+IBB	B
Little gull	C	+	+	+	+
Black-headed gull	C	++IIBB	+IIBB	+IIBB	++IIBB
Common gull	C	++IIBB	IIBB	IIBB	++IIBB
Lesser black-backed gull	C,O	B	+IBB	++IIBB	B
Herring gull	C,O	++IIBB	IIBB	IIBB	++IIBB
Glaucous gull	C,O	+			+
Great black-backed gull	C,O	++IIBB	IIBB	++IIBB	++IIBB
Kittiwake	O	IB	IBB	IIBB	IB
Sandwich tern	C	B	+IBB	+IBB	+B
Common tern	C		+IBB	+IBB	+B
Arctic tern	C	B	++BB	++IBB	+B
Little tern	C		+IBB	+IBB	
Guillemot	O	+IIBB	IIBB	+IIBB	+IBB
Razorbill	O	IB	BB	++IIBB	+IB
Little auk	O	++	+		++
Black guillemot	C	IIBB	IIBB	IIBB	IIBB
Puffin	O	BB	IBB	IIBB	BB

For species breeding around the North Sea: + = immigration by birds breeding elsewhere at a level 2-10 times the breeding population; ++ = immigrants at more than 10 times the breeding population. For non-breeding species: + = noticeable immigration, ++ = North Sea is important for this species. II = more than 2/3 of immatures from North Sea colonies present. I = 1/3 - 2/3 of immatures from the North Sea colonies present. BB = as II, but for breeding birds, B = as I, but for breeding birds.

North Sea (TASKER *et al.*, 1986a).

Numbers of birds occurring in the coastal zone (especially gulls, terns, divers and ducks), should be more easily estimated as many are within sight of land. Numbers in some sectors of the North Sea have been evaluated on a seasonal or monthly basis (*e.g.* Moray Firth, Scotland, MUDGE & ALLEN, 1980; Delta Region, Netherlands, SMIT & WOLFF, 1980; MEINNIGER *et al.*, 1984; SOVON, 1987; Denmark, JOENSEN, 1974; CHRISTENSEN, 1986, 1987; LAURSEN, 1987; LAURSEN & FRIKKE, 1987a, 1987b; LAURSEN *et al.*, 1987; MELTOFTE & FALDBORG, 1987; Germany, BUSCHE, 1980; KUSCHERT, 1981; KNIEF, 1982; KUSCHERT & WITT, 1985), but there has never been an attempt to examine changes in numbers of these species in the entire North Sea throughout the year.

Though densities of birds at sea have been estimated and mapped from month to month, the mobility of birds, their seasonal movements, and the fact that different populations (or population components) of each species may be present in different places at different times can make the interpretation of such data very difficult.

2. POPULATION DYNAMICS AND MONITORING

2.1. POPULATION DYNAMICS

With the partial exceptions of most gulls and terns, and sea ducks, seabirds are characterised by long life, delayed maturity and a slow breeding rate. These impose substantial constraints and determine important characteristics of their population dynamics.

Many species have mean annual survival rates of over

TABLE 2

Numbers of birds breeding on coasts of the North Sea, sections as in Fig. 1. Sources and data (TASKER et al., 1987). All counts are of pairs, with the exception of the auks (guillemot, razorbill, black guillemot, puffin), where individual birds are counted.

Species	*North Britain* 1	*East Britain* 2	*Southern Bight* 3	*Eastern North Sea* 4	*Scandinavia* 5
Red-throated diver	793	0	0	0	0
Fulmar	294128	12596	697	36	142
Manx shearwater	c.250	0	0	0	0
Storm petrel	low 1000s	0	0	0	0
Leach's petrel	low 1000s	0	0	0	0
Gannet	21648	22130	0	0	0
Cormorant	1483	703	18	0	18
Shag	13486	4563	0	0	1755
Arctic skua	2988	0	0	0	206
Great skua	7299	0	0	0	4
Black-headed gull	3455	15980	19272[1]	53781	36854
Common gull	15770	80	7790	6452	43240
Lesser black-backed gull	2583	2180	3255	15791	25502
Herring gull	41827	40445	24512	96293	34037
Great black-backed gull	9924	31	0	1	14480
Kittiwake	206606	199949	2571	3310	2991
Little tern	31	319	1070	912	3
Arctic tern	55951	5349	83	4712[2]	8634
Common tern	1157	1730	4378	14407	39815
Roseate tern	0	36	0	0	0
Sandwich tern	1122	5592	7644	14687	1502
Guillemot	507487	167609	0	4900	438
Razorbill	54537	18260	0	16	302
Black guillemot[3]	20847	3	0	0	2891
Puffin[4]	124289	79973	0	0	21695

Notes

[1] Numbers of black-headed gulls nesting on the coasts of North Holland are not known.

[2] There could be up to a further 1000 pairs of arctic terns on the Friesian islands.

[3] Black guillemot figures represent numbers counted at breeding sites in the pre-breeding period.

[4] A minimum number of individuals associated with colonies. At hole-nesting colonies, counts of burrows have been multiplied by two; at cliff colonies, the count represents maximum number of birds seen.

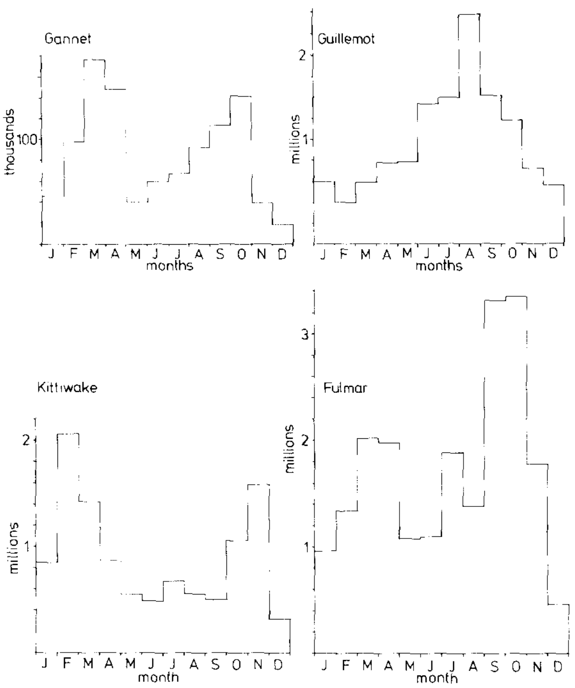


Fig. 3. Approximate numbers of a) gannet, b) guillemot, c) kittiwake and d) fulmar present at sea in the North Sea through the year. Estimates are derived from surveys detailed in TASKER *et al.*, (1987), when average densities for each of 26 sea-ares (Fig. 2) are extrapolated to give a total present. Areas 3 and 8 (off Norway) were not included due to inadequate survey. In sea-areas where there was inadequate survey for any one month, the mean density from surrounding sea-areas was used for extrapolation.

90%, resulting in overall mean adult lifespans of up to 35 years. These estimates depend on models which assume constant survival rates throughout adult life, and while this is biologically unlikely, attempts to demonstrate increasing mortality rates in old adults have largely failed, possibly for statistical reasons (BOTKIN & MILLER, 1974; BUCKLAND, 1982; DUNNET, 1982b; COULSON & WOOLLER, 1976).

Breeding rate is reduced not only by deferred maturity, but also by very small clutch sizes. Many species lay only one egg, (*e.g.* all Procellariiformes, most auks and the gannet), and may be unable to replace it if lost.

In many species young adults do not breed for the first time until several years old, the oldest being fulmars with a modal age of first breeding of 10 years for males and 12 for females (OLLASON & DUNNET, 1988). Within a species, age at first breeding is however highly variable and birds may begin breeding at younger ages in expanding colonies than in stable or declining colonies (HARRIS, 1984; PORTER & COULSON, 1987).

With delayed maturity, large numbers of seabirds are in the pre-breeding component of the population, and DUNNET (1982a) has estimated that prebreeding fulmars may be as numerous as breeding adults, and that in cliff-nesting auks pre-breeders may amount to about 30% of the adult population. These pre-breeders constitute a large and important reservoir of recruits to breeding populations, and their mobility and behaviour associated with finding and becoming established in breeding colonies are major challenges to our understanding of the population dynamics of long-lived seabirds.

Information on these biological parameters is readily available for almost all North Sea species (CRAMP & SIMMONS, 1977) and in much more detail in specialised accounts of the auks (NETTLESHIP & BIRKHEAD, 1985), the fulmar (DUNNET & OLLASON, 1978), the gannet (NELSON, 1978), and the kittiwake (COULSON & PORTER, 1985). Examples of these parameters are presented in Table 3.

2.2. NUMBERS AND TRENDS

2.2.1. BREEDING BIRDS

We have already presented data on the numbers of seabirds breeding around the North Sea (Table 2). Earlier estimates have varied considerably: from 2.56 million birds of 19 species (EVANS, 1973), 2.0 million (BOURNE, 1978) and 4.53 million (DUNNET, 1987). These estimates were all derived from actual counts made at colonies which attempted to record the numbers of birds breeding there. There are great difficulties in achieving this. Some species build a conspicuous and durable nest (*e.g.* kittiwake, gannet); others occupy natural hollows in which they may construct inconspicuous nests (*e.g.* fulmar, terns) others make no nest at all but lay the egg directly on rock ledges and only adult birds present can be counted; yet others nest in burrows and are active on land mainly at night (shearwaters, puffins); storms petrels nesting in boulder screes and largely nocturnal, are almost impossible to count. Thus the precision and accuracy of counts varies markedly between species.

The pioneer work in this area was carried out by the British Seabird Group, mainly in 1969 and 1970 for Britain and Ireland (CRAMP *et al.*, 1974). In recent years the Seabird Group and the Nature Conservancy Council have cooperated to re-count all British colonies for the Seabird Colony Register (LLOYD *et al.*, in prep.). Detailed mapping and counting have also taken place in Norway (RØV *et al.*, 1984) and on the German (BECKER & ERDELEN, 1987; TAUX, 1984, 1986), and Danish (DANIELSEN *et al.*, 1986) coasts. Most coastal breeding colonies have now been located and mapped, but herring and black-headed gulls, many of which nest inland, are not fully covered.

Monitoring programmes have been developed to detect and measure changes in the numbers of breeding

TABLE 3

Age at first breeding, clutch size and adult mean annual survival in certain North Sea seabirds.

	age at first breeding, years	*normal clutch size*	*mean annual survival rate of adults (%)*	*references*
Fulmar	9.2	1	97	DUNNET & OLLASON (1978) OLLASON & DUNNET (1978)
Manx shearwater	5-6	1	80-95	PERRINS et al, (1973)
Gannet	4-5	1	94	NELSON (1978)
Shag	3-4	1-6		CRAMP & SIMMONS (1977)
Herring gull	5.25	2-3	90-96	DROST et al., (1961) CHABRZYK & COULSON (1976) KADLEC & DRURY (1968)
Kittiwake	3-5	1-3	81-86	COULSON & WOOLLER (1976)
Arctic tern	3-5	1-2	87-91	GROSSKOPF (1964) COULSON & HOROBIN (1976)
Guillemot	3-7	1	94	BIRKHEAD & HUDSON (1977)
Razorbill	4-5	1	91	LLOYD & PERRINS (1977)
Puffin	4-5	1	95	ASHCROFT (1979)
Eider	2-3	4-5	93	S.R. BAILLIE (pers. comm.)
Common scoter	2-3	7-9	77	CRAMP & SIMMONS (1977)

TABLE 4

Trends during 1976-1986 in the numbers of seabird pairs breeding on the German, Dutch and Danish North Sea coast. Data from Germany come from 31 important seabird areas on the coast (see map in BECKER & ERDELEN 1987); unpubl. data for 1986 from Niedersachsisches Landes Verwaltungsamt, Landesamt fur den Nationalpark Schleswig-Holstein and Landesamt fur Naturschutz und Landschaftsplege Schleswig-Holstein. Data for the Netherlands from SOVON (1987), MEININGER (1986), SPAANS et al., (1987) and ROOTH (1985). Trends for Denmark (Ringkobing) in CHRISTENSEN (1986).

	Germany		*Netherlands*	*Denmark*
Species	*no. of breeding pairs in 31 areas, 1986*	*change 1976/1986*	*trend*	*trend*
Herring gull	41860	77%	+	+
Lesser black-backed gull	1610	693%	+	+
Common gull	1710	135%	+	+
Black-headed gull	28550	81%	+	+
Common/arctic tern	12130	22%	+	+
Sandwich tern	6650	-14%	(+)	(-)
Little tern	320	12%	+	-
Eider	320	187%	?	+
Fulmar	36[1]	620%		
Kittiwake	2630[1]	111%		
Guillemot	2450[1]	151%		
Razorbill	5[1]	150%		
Cormorant	177[2]	332%	+	+

[1] Breeding on Helgoland only

[2] Breeding at the Weser estuary only

seabirds in relation to specific perceived threats such as oil pollution (RICHARDSON *et al.*, 1981; MUDGE & ASPINALL, 1985; BENN *et al.*, 1987), and to describe national trends (COULSON, 1983; R.S.P.B., 1979; BECKER & ERDELEN, 1987). Fairly standardised monitoring procedures have evolved over the past fifteen years which take account of differences between species (EVANS, 1980; BIRKHEAD & NETTLESHIP, 1980). However, there remain substantial problems in designing the collection of relevant data (DUNNET, 1982a, 1982b; ROTHERY *et al.*, 1988) and in the statistical and biological interpretation of the results (ROTHERY *et al.*, 1988; HARRIS *et al.*, 1986; STOWE, 1982a; DUNNET *et al.*, 1979).

Increasingly it is being realised that changes in breeding numbers result from a variety of man-induced and 'natural' factors, and this has led to the collection of data on breeding rate and success, parental behaviour, and diet in addition to bird counts (RØV *et al.*, 1984; HEUBECK & ELLIS, 1986; HARRIS & MURRAY, 1981), but given the long adult life in most species, poor breeding is rarely clearly reflected in breeding numbers in the years immediately following.

In general, seabird populations in the North Sea have been increasing in recent decades, but in the last six years or so declines have been described for some species in some places, *e.g.* kittiwake in Shetland, and herring gull in much of Britain (LLOYD *et al.*, in prep.).

The analysis of trends from 1976–86 in seabird numbers breeding in the German and Dutch Wadden Sea shows steep increases in most species, and near stability in terns (Table 4). This increase began in the 70s (BECKER & ERDELEN, 1987; MOLLER, 1978; SMIT & WOLFF, 1980; Fig. 4), after two decades characterised by enormous decreases in tern populations, and by stability or slow growth in the numbers of gulls and eiders. In Denmark, during the last ten years the breeding populations of the eider have increased too, but the number of little terns declined dramatically (F. Danielsen, pers. comm.). There are also indications that the growth of the herring gull population in the Netherlands reached its peak during the mid 80s (SPAANS *et al.*, 1987).

Possible causes of these changes are discussed later.

3. DISTRIBUTION AND MOVEMENT AT SEA

The mobility of seabirds is important in many ecological contexts. Here we consider two main categories: movements by breeding birds from colonies around the North Sea, and movements throughout the year, by

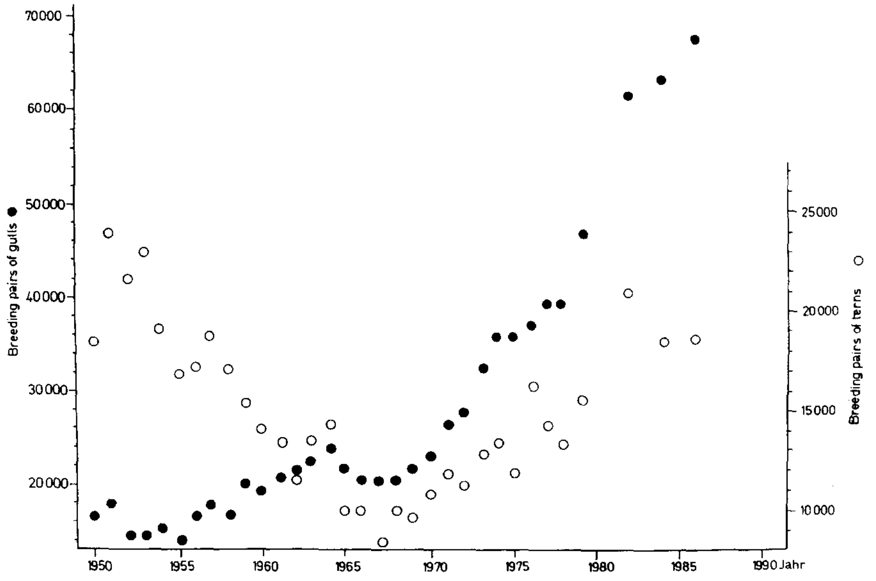


Fig. 4. 1950-1986 trends in the numbers of gulls (*Larus argentatus, L. fuscus, L. canus, L. ridibundus*) and terns (*Sterna sandvicensis, S. hirundo, S. paradisaea, S. albifrons*) breeding at 28 important sites in the German Wadden Sea coast. See BECKER & ERDELEN, (1987) for the location of the sites. For methods and data sources see TAUX (1984, 1986) and Table 4.

seabirds not associated with local breeding colonies. The different techniques for examining these movements are reviewed.

3.1. MOVEMENTS FROM BREEDING COLONIES

The feeding ranges of seabird species from their breeding colonies have been the subject of many discussions. Feeding ranges are important for many ecological studies, especially those on foraging behaviour, effects on food stocks, and vulnerability, for example in relation to oil pollution.

In the North Sea, PEARSON (1968) studied seabirds on the Farne Islands and estimated maximum feeding ranges on the basis of time spent away from the nest on foraging flights, and previously published estimates of flight speed. Sandwich, common and arctic terns and shags all had estimated maximum feeding ranges under 25 km, while those of kittiwakes were 55 km, and puffins 138 km. The main disadvantage to this approach is that it is difficult to determine how long a bird spent foraging, as opposed to commuting, while on the feeding trip. Measurements of flight speeds are subject to considerable variation, and wind and fish-carrying can have a considerable effect (PENNYCUICK, 1987; WEBB *et al.*, in prep. a). This method cannot identify the feeding areas or show how they change.

Analysis of returns or sightings of ringed breeders during the breeding season provides information on foraging range and feeding areas. For example, DUNNET & OLLASON (1982) showed that some fulmars move up to 600 km into the North Sea from their colony in Orkney. Recoveries of seabirds are more useful in determining more generalised movements and distribution patterns and are reviewed below.

In recent years direct observations from ships and aircraft have been made on the locations of feeding auks around colonies in the North Sea (Fair Isle, Shetland, BLAKE *et al.*, 1984; Flamborough Head, Yorkshire, WEBB *et al.*, 1985; Isle of May, Fife, WEBB *et al.*, in prep. b). These studies have shown considerable variation in the distribution of feeding birds at different times of day, and from day to day. Feeding areas may also differ between years (GASTON & NETTLESHIP, 1982). Advantages of direct observations are that a large sample of the population may be examined and specific feeding areas visited, allowing assessment of some of the factors controlling the availability of food. Diurnal rhythm of attendance at feeding sites can be described, but one disadvantage is that the feeding distribution of individuals cannot be studied.

Wider ranging surveys may be used to determine feeding ranges from colonies. In the northern North Sea, TASKER *et al.*, (1985b) found that gannets from Noss, Shetland fed almost entirely within 150 km of the colony, with the majority feeding at less than 50 km away (Table 5). These values can be compared with an estimate of 161 km, based on duration of feeding trips away from the colony on Bass Rock, E Scotland (NELSON, 1966), and an estimate of the same maximum feeding range obtained from a small sample of ring recoveries near Bonadventure Island, Canada (MOISAN & SCHERRER, 1973).

Direct observation of some species of inshore feeders may be carried out from land: EWINS (1986, 1987) has observed the feeding range and behaviour of black guillemots near Shetland.

The foraging ranges of gull species in the Wadden Sea area are described by SPAANS (1971) and VAUK & PRUTER (1987). Feeding ranges of terns in coastal waters are given by VEEN (1980) and BOECKER (1967): the species-specific feeding range in terns seems to correlate with body weight and with size of colonies and foraging groups. Maximum feeding range is about 25 km.

Marking techniques have been developed to track in-

TABLE 5

Densities, area and estimated total number of gannets in concentric circles of various radii (km) around Noss.

Radius (km)	*18*	*37*	*55*	*74*	*93*	*111*	*130*	*148*	*167*	*185*	
Average densities											
May/June	1.24	1.56	0.19	0.13	0.06	0.01	0.02	0	0	0	
July	1.62	0.65	0.24	0.11	0	0.06	0.21	0.11	0	0	
Area within circle (km²)	809	2039	2783	4034	5167	6526	4513	5620	6280	6770	
Total number within circle											Total
May/June	1003	3181	529	524	310	65	90	0	0	0	5702
July	1311	1325	668	444	0	391	948	618	0	0	5705

dividual birds. Four hundred guillemots were captured in colonies on Fair Isle and marked conspicuously with dye, but only 11 were seen at sea, all but one within 11 km of the dye-site (BLAKE *et al.*, 1984). The breeding status of some of these birds was uncertain and the sighting of three of them ashore at other nearby islands supported the suggestion that some were non-breeders. The trauma of handling may also have affected the birds.

Miniaturised radio-transmitters provide the opportunity to track birds away from their colonies. Within the North Sea, WANLESS *et al.*, (1988) and WANLESS & MORRIS (1988) have used transmitters to follow auks away from the colony, and to examine diving behaviour. However, such transmitters can alter the birds' behaviour, particularly their foraging ability (WANLESS *et al.*, in press), probably by reducing underwater streamlining (WILSON *et al.*, 1986). Such studies have been carried out on a small number of birds since the few radio frequencies available mean that large numbers cannot be followed individually.

There have been suggestions that birds might be followed away from colonies using active or passive radar devices, and satellite transmitters. Miniaturisation and development of these devices has yet to be completed.

3.2. GENERAL MOVEMENTS IN THE NORTH SEA

Most seabirds migrate or disperse outside the breeding season (Table 1). Such movements may take North Sea breeders to many areas of the North Atlantic, and in at least one case (arctic tern) as far as the Antarctic. The distribution and movements of these birds can be studied in several ways.

One of the oldest techniques has involved watching and counting seabirds moving past headlands or other prominent observation positions. At some times of year extremely large numbers of birds may be seen moving. In Britain there have been many studies (PETTITT, 1967), and records have been summarised for the whole coastline (JONES & TASKER, 1982). On continental coasts, a very large scheme of coordinated watching has been organised in the Netherlands, the data from which were analysed by CAMPHUYSEN & VAN DIJK (1983), with several more recent updates by other authors (STEGEMAN & WINTER, 1988). Off the coast of Denmark, many observations have been made from Blaavands Huk (MELTOFTE, 1979; RASMUSSEN, 1985; MELTOFTE & FALDBORG, 1987).

Observations from land have several disadvantages; the most obvious is that only those birds moving close inshore are recorded. In addition, several analyses have shown that numbers passing a point of land are affected by wind direction and speed (CAMPHUYSEN & VAN DIJK, 1983), relative location of weather systems (BLOMQVIST & PETERZ, 1984) and barometric pressure (JONES & ROWLEY, 1982). Severe weather in parts of the range of some of the coastal birds may cause hard weather movements, when large proportions of the population move in winter to milder areas, for example, between the Wadden Sea and England. These events can in some cases be recognized, but ignorance of movements further out to sea limits this technique severely. However, some inshore species tend to migrate along coasts; for instance, off the Netherlands the majority of common scoter moving down the eastern seaboard of the North Sea are visible from land (CAMPHUYSEN & VAN DIJK, 1983).

Watching from coasts may give a good indication of the size and phenology of movements and migrations, but not on how birds may be using an area of sea. In order to study this it is necessary to make observations at sea. Studies have been conducted since 1979 by a team based in Aberdeen, Scotland, whose observations have been reported by BLAKE *et al.* (1984), TASKER *et al.* (1987) and elsewhere. Observations were made mostly from ships, and occasionaly from aircraft. Methods of observation and recording are now becoming standardised (TASKER *et al.*, 1984). Within the North Sea, there are sufficient vessels to ensure wide coverage but some important areas are not visited regularly. To overcome this, vessels have to be chartered, at considerable cost. Seabirds in the Moray Firth were studied from one such chartered vessel by MUDGE & CROOKE (1986), and other studies have been carried out on specific concentrations of auks by TASKER *et al.* (1985d, 1986a). Separate studies have started recently off Norway, Denmark and the Netherlands, but few results have been reported so far.

Maps of seabird distribution in the North Sea have been prepared for all months and seasons of the year (TASKER *et al.*, 1987). Knowledge of movements of bird populations to and from the North Sea has improved also. As an example, Fig. 5 shows the distribution of razorbills in the North Sea at three times of the year. In the main part of the breeding season (April to June, Fig. 5a) most of the birds were found close to their breeding colonies in the north and west North Sea. A few concentrations occurred farther offshore, particularly in the southern North Sea, and these may be birds returning late to their colonies from southern wintering grounds. By August (Fig. 5b), all the razorbills have left their colonies and adult males accompany their single chick during the final phase of rearing at sea. At this time a very large congregation of birds occurs in the north-western North Sea off north-east Scotland, and very few are found in the eastern North Sea. On cruises to study this concentration in 1984 and 1985, TASKER *et al.*, (1985d, 1986a) found the numbers present to exceed the North Sea breeding population, indicating that movement into the area must be occurring, probably

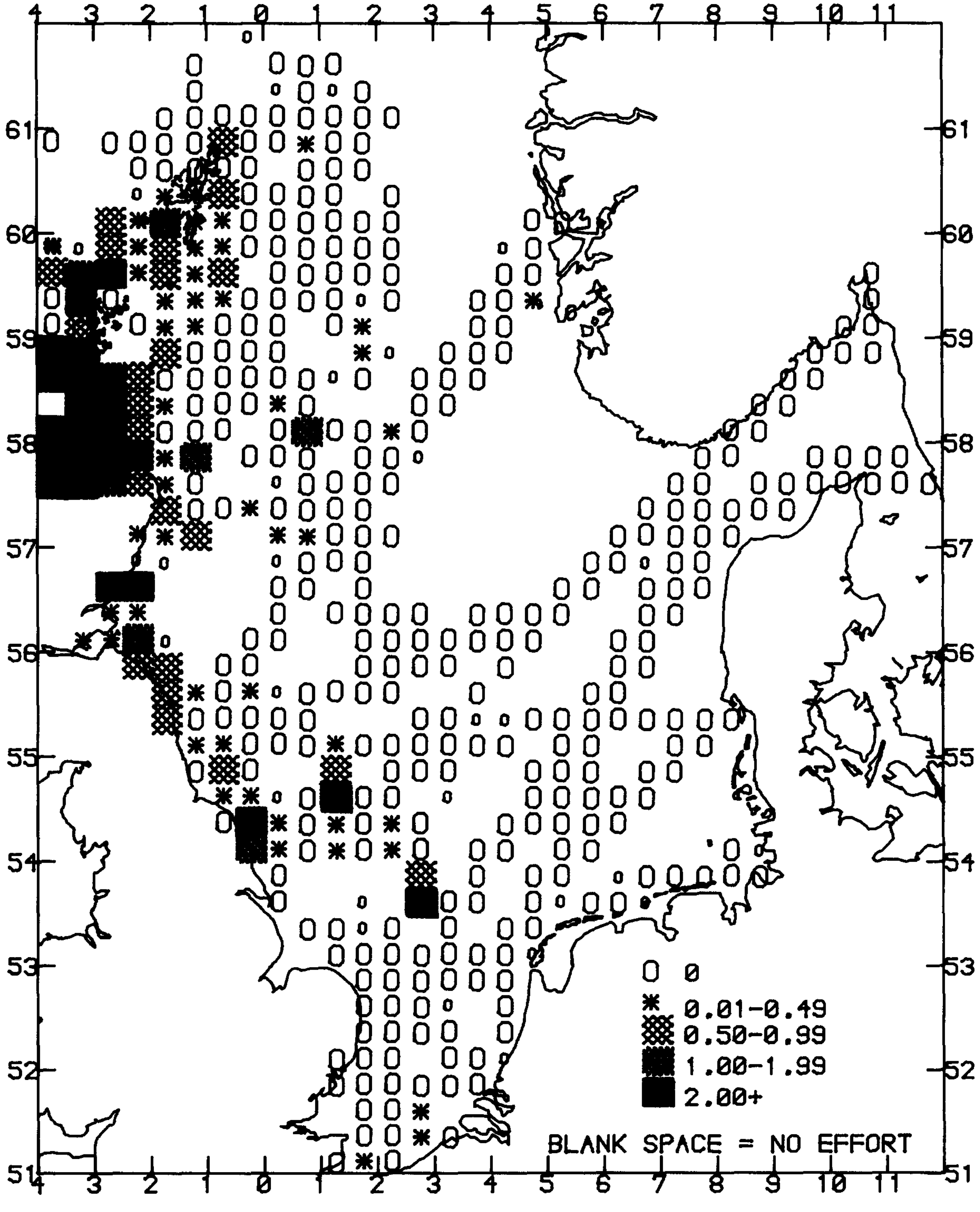
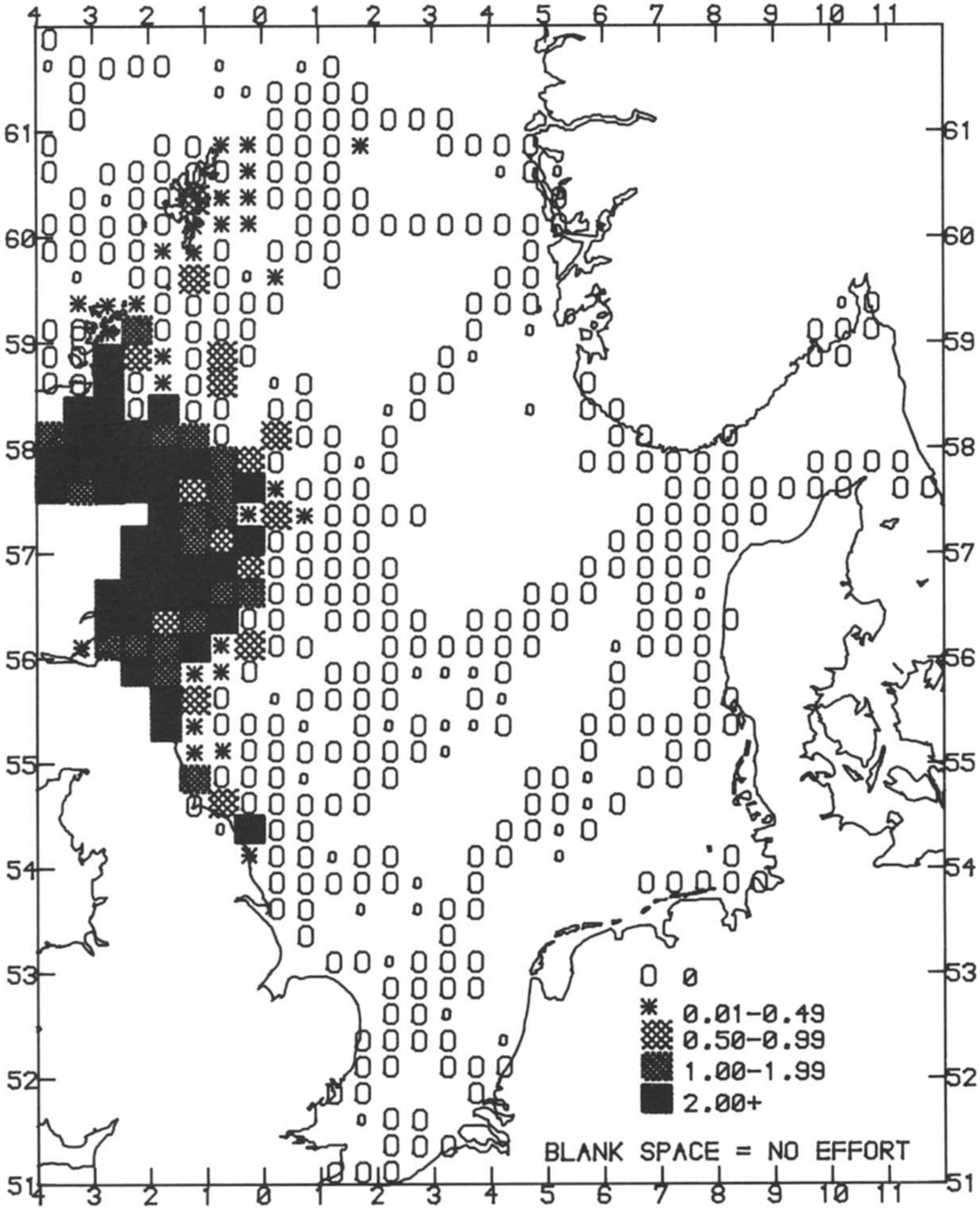
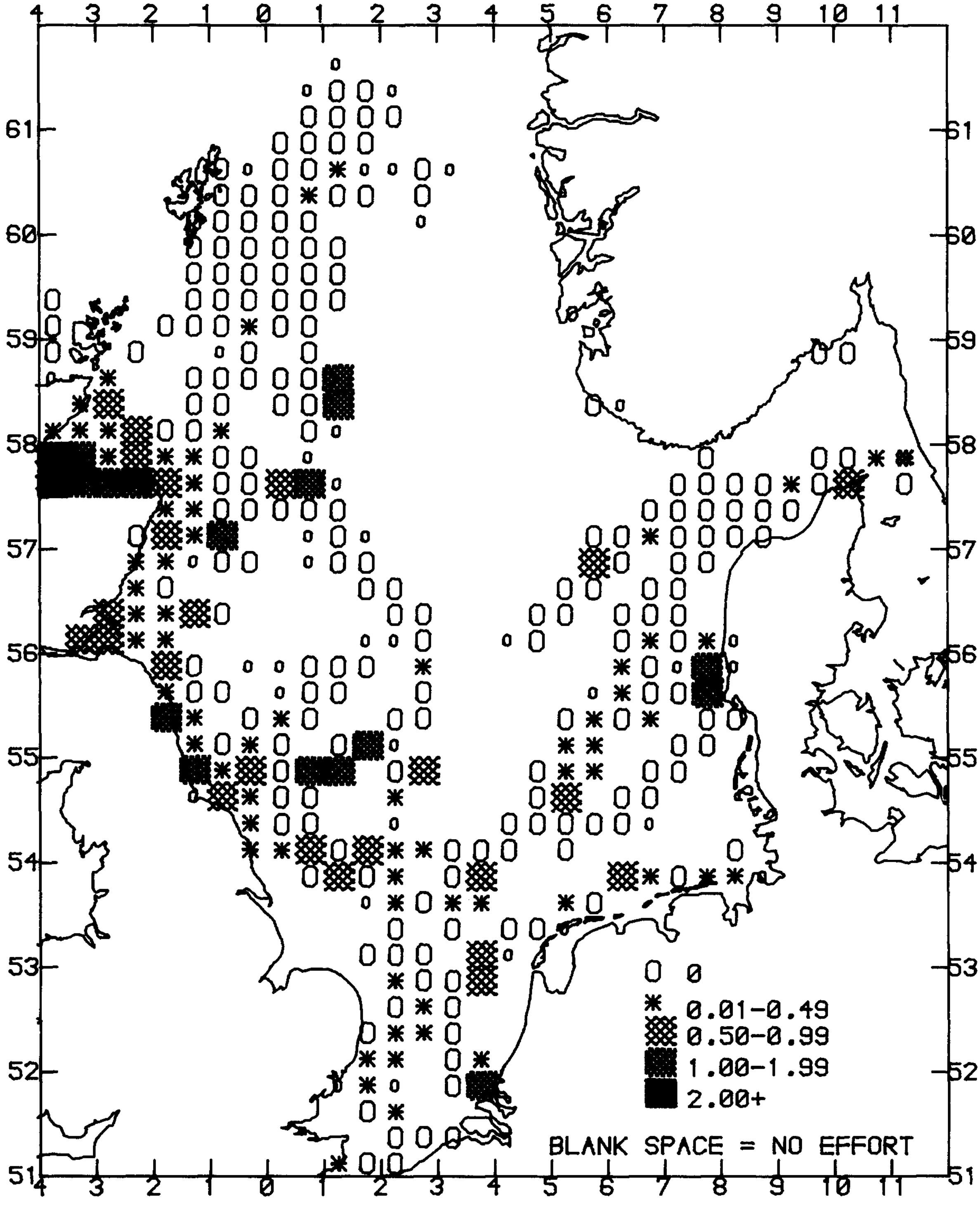


Fig. 5. Distribution of razorbills in the North Sea in a) April-June;



b) August and September;



c) November-January. Shading represents numbers of birds seen per km².

from colonies to the north and west of Scotland. In winter (Fig. 5c) razorbills may be found in all parts of the North Sea. Highest densities are found close to the colonies, but also in the southern Moray Firth, an area known to be important for one major prey species, sprat, at this time of year. Other evidence indicates that many razorbills move out of the North Sea at this time. Similar maps for all species are presented in TASKER *et al.* (1987).

This method of presentation has several limitations. Maps are compiled to illustrate average distributions for all years of survey, so that any year-to-year variations in distribution will not be detectable. TASKER *et al.* (1987) have analysed between-year variation in data for guillemots, and found this to be low. Daily or other short term variations in distribution will be missed also. The understanding of this important process, based on mobility of seabirds, requires development of remote sensing devices, but these are costly, and can be used on only small samples of any population.

The North Sea Bird Club collates records of seabirds seen off oil and gas platforms in the UK sector of the North Sea, but these are rarely systematic, *e.g.* ANDERSON (1988). TASKER *et al.* (1986b) observed seabirds feeding and sheltering around oil platforms, and found distinct regional differences in bird attendance.

There are several other methods by which seabird distribution and movements might be inferred. Recoveries or recaptures of ringed birds have been used for over 70 years in studies of bird migration. In one of the first analyses, THOMSON (1939) examined the distribution of recoveries of ringed gannets, and showed that they move southwards in winter, the mean distance varying with age. The British Trust for Ornithology is analysing the recoveries of seabirds from bird-marking schemes throughout Europe, with special reference to the North Sea and oil pollution.

Ringing recoveries have been used to calculate proportions of breeding populations remaining in the North Sea and proportions leaving but there are several potentially important biases. Birds may die or be recaptured through a variety of causes, and inevitably the distribution and intensity of these causes varies within the geographical range. Human causes of death (*e.g.* oiling, hunting, entrapment in fishing nets) are possibly the most variable, and the probability of a dead ringed bird being found by an interested person is far from uniform. In spite of these and other biases, ringing recoveries can provide a useful corroboration of other evidence for bird migration.

Biometric analysis of corpses of birds found on beaches may often give a clue to their origin through various known morphological variations in the breeding populations (JONES, 1985; JONES *et al.*, 1985). However, as with ringed birds found dead on beaches, it is often difficult to be sure where these birds died, and it is difficult to extrapolate from beach to offshore distribution.

Table 1 gives a general indication of the presence of seabird populations in the North Sea; Table 6 shows the location of North Sea breeding birds in the non-breeding period, using information derived from ringing recoveries and other methods.

4. FORAGING AND FOOD

4.1. FEEDING METHODS

ASHMOLE (1971) classified seabird feeding methods into six categories: 1. wing-propelled underwater swimmers; 2. foot-propelled underwater swimmers; 3. birds that plunge from the air using momentum to approach prey at high speed; 4. birds that feed while settled on the surface; 5. birds that feed when flying, capturing prey at or near the surface; 6. birds that obtain food by 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 7).

The auks stand out as being particularly specialised in feeding methods, though differing in details of feeding ecology (BRADSTREET & BROWN, 1985; PIATT & NETTLESHIP, 1985; SWENNEN & DUIVEN, 1977). Gulls show the greatest diversity of methods within and between species: differences between species are largely a function of body size and its implications for flight. Larger gulls are less agile in the air but more powerful and able to displace smaller species from food items (BRAUNE & GASKIN, 1982; HUDSON & FURNESS, 1988).

Many seabirds feed in flocks, and this is especially true of those that feed by plunge-diving on shoals of fish. One reason for the development of flocks over shoals is the apparent reluctance of fish shoals to split or disintegrate when attacked by predators. This is particularly a feature of the behaviour of sandeels (PITCHER & WYCHE, 1983), which are exploited by both diving and surface-feeding birds. Around Shetland, shoals of sandeels at the sea surface used to attract flocks of 50–500 seabirds; predominantly fulmars, great black-backed gulls, great skuas and gannets, with small numbers of herring gulls and lesser black-backed gulls. (For unknown reasons these surface shoals appear to have vanished in recent years). Occasionally these feeding flocks include kittiwakes, but these usually leave as numbers of larger seabirds increase. 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 (PORTER & SEALY, 1981), and age-related feeding performance (PORTER & SEALY, 1982).

It has generally been thought that the dark colouration of skuas, and some other solitary feeders or kleptoparasites is a form of crypsis or aggressive camouflage (FURNESS, 1987a) whereas white or black and white

TABLE 6

Locations of seabirds from populations breeding around the North Sea during the non-breeding period. Resident populations remain in the vicinity of their breeding colonies.

Species	*Location*
Red-throated diver	North Sea
Fulmar	North Sea, North Atlantic
Manx shearwater	off eastern seaboard of South America, some to southern oceans
Storm petrel	off south-western coasts of Africa
Leach's petrel	uncertain
Gannet	off western Africa to North Sea
Cormorant	resident and North Sea
Shag	resident
Arctic skua	off southern Africa
Great skua	south Bay of Biscay/Iberian coasts
Black-headed gull	North Sea, Ireland and France
Common gull	North Sea, Ireland and France
Lesser black-backed gull	France and Iberia
Herring gull	North Sea and inland
Great black-backed gull	North Sea
Kittiwake	North Sea and North Atlantic
Little tern	West Africa
Arctic tern	southern ocean
Common tern	tropical western Africa
Roseate tern	tropical western Africa
Sandwich tern	western Africa
Guillemot	North Sea with some to English channel
Razorbill	mostly North Sea, some movement to south and west
Black guillemot	resident
Puffin	North Sea

plumages characteristic of most flock-feeding plunge-diving seabirds are highly visible and signal the location of aggregations of prey at sea. Recent experiments with captive gulls given fish to catch in laboratory pools (GOTMARK *et al.*, 1986) showed that the rate of capture of fish, and rate per bird, were greater in a flock than for isolated individuals. This came about because fish startled by the plunge of one gull were more vulnerable to being caught by another gull, so that in the wild the feeding success of the first gull to locate the school may be enhanced when others are attracted.

Flocks of seabirds plunge-diving onto sandeels may continue to obtain fish for periods of 10–20 minutes on occasions, suggesting that the sandeels do not move out of reach of the diving birds. Whether their behaviour, and hence availability to seabirds, is largely dictated by the numbers and behaviour of predatory fish is unknown (but see SAFINA & BURGER (1985) for discussion of interactions between seabirds and predatory fish exploiting shoals of small fish). Marine mammals are comparatively rare in the North Sea; elsewhere in the world seabirds often exploit prey fish schools that have been disturbed by cetaceans.

4.2. DIET

4.2.1. METHODS OF STUDY

Methods of sampling seabird diets and statistical considerations regarding necessary sample sizes and presentation of data have recently been reviewed by DUFFY & JACKSON (1986). 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 of food being consumed, carried, fed to chicks, or dropped at colonies. All of these methods have their advantages and disadvantages. All can be used at breeding colonies during summer, but killing birds is usually the only practical method of studying the diet of seabirds in winter. The problem is aggravated by the fact that many 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 are likely to 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.

The diet composition may vary widely between localities, as found even for wide-ranging species such as the fulmar (FURNESS & TODD, 1984). Thus, obtaining an accurate picture of the diet of a seabird species throughout the North Sea would require regular (*e.g.* monthly) shooting of samples of at least 30–50 birds at a wide variety of localities. Furthermore, the diet of breeding and non-breeding components of the population may differ (FURNESS & HISLOP, 1981) and breeders often feed chicks on food with a higher calorific density than the prey they eat themselves (HARRIS & HISLOP, 1978; FURNESS & HISLOP, 1981).

Examination of the gizzard contents raises a further problem: different kinds of hard parts of prey remain in the gizzard for different lengths of time, while soft parts of prey may also vary in rates of digestion, though little is known about this (GALBRAITH, 1983; PARTRIDGE, 1986; DUFFY *et al.*, 1985a; LAUGKSH & DUFFY, 1986; WILSON *et al.*, 1985). Emetics have usually been found unsatisfactory for seabirds, and stomach pumps seem to be much more successful (DUFFY & JACKSON, 1986; GALES, 1987), but these difficulties may still apply though for many species only the contents of the proventriculus are retrieved, and hard remnants rarely accumulate there.

Cast pellets provide another source of information on diet. Gulls, terns and skuas regurgitate bones and other

TABLE 7

Feeding methods employed by seabirds in the North Sea. *** main and predominant feeding method, ** common feeding method, * rarely used feeding method.

Species	*Wing propelled underwater swimming*	*Foot propelled underwater swimming*	*Plunge diving*	*Surface settled feeding*	*Flying near-surface feeding*	*Klepto-parasitism*
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			**	**	*	
Glacous gull			*	***		
Greater black-backed gull			*	**	*	**
Kittiwake			*	*	***	
Arctic tern			***		*	
Common tern			***		**	
Roseate tern			***		*	**
Sandwich tern			***			
Little tern			***		*	
Guillemot	***					
Razorbill	***					
Black guillemot	***					
Little auk	***					
Puffin	***					

hard parts (*e.g.* otoliths and squid beaks) so soon after ingestion that regurgitated items have suffered little or no digestive breakdown. This may not be the case for some species of fish where otoliths are tiny and fragile. There is a probability that small otoliths may be voided through the intestine and only large otoliths are regurgitated. Great skuas regurgitate even the smallest sandeel otoliths in pellets, but great black-backed gulls void all sandeel otoliths in faeces while regurgitating otoliths from gadoids (HUDSON & FURNESS, 1988). JOHNSTONE *et al.* (1990) show that measurements of otoliths regurgitated by shags can give a very misleading estimate of the size of fish taken. Other seabird species regurgitate otoliths only after long periods in the stomach or void them in faeces. Otoliths obtained from auks by dissection of the gizzard and otoliths voided in faeces (*e.g.* by cormorants) may be eroded and provide biased information on the size and species of fish in the diet (TREACY & CRAWFORD, 1981; DUFFY & LAURENSON, 1983; DUFFY & JACKSON, 1986). Guides are available for the identification of otoliths of North Sea fish (HARKONEN, 1986) and squid beaks (CLARKE, 1985).

Fish carried by seabirds into colonies and dropped there, may also give a biased picture of the diet (ATWOOD & KELLY, 1984; BECKER *et al.*, 1987). Seabirds tend to drop more of the fish that are larger than average, or of species that are difficult to swallow (*e.g.* sticklebacks are dropped particularly often by common terns). During courtship-feeding, male terns tend to select larger fish to offer to their mate than they consume themselves (NISBET, 1973).

Fish being carried in the bill of adult birds (*e.g.* terns, auks) can often be identified by observation, and the size estimated in relation to the bill-length, and validated by obtaining the fish (FURNESS & BARRETT, 1985). However, since fish mass is proportional to the cube of fish length, slight errors in estimation of fish lengths result in large errors in estimated masses.

Where the above methods cannot be used, there may be applications of electrophoretic identification or immunological identification of prey proteins. However, electrophoretic methods do not work well if food samples are partly digested since banding patterns on gels become blurred and diffuse. Immunological methods have greater ability to identify semi-digested food remains precisely (CALVER, 1984; WALTER & O'NEILL, 1986; WALTER *et al.*, 1986) but suffer from the disadvantage that the range of prey thought to be in the diet must be used to test for the presence of each prey item expected; unexpected prey items cannot be detected or identified since immunological reactions can only be obtained against pre-prepared antisera for specific food items. This technique is also rather slow and expensive by comparison with direct studies of diet, but may be the only method available for some purposes.

4.2.2. SEASONAL PATTERNS

There is a marked seasonal pattern in the diet of great skuas in Shetland (FURNESS, 1987a); the proportion of sandeels is low early in spring, rises to a peak around June, then declines to a very low level in July/August. When sandeels are not available the skuas feed largely on discards from whitefish boats, and since fisheries statistics show that there is little seasonal variation in the quantities of fish discarded the seasonal pattern in the diet can be attributed to changes in the availability of sandeels. This is supported by observations made at sea (TASKER *et al.*, 1985c). Observations of gannet feeding behaviour at sea show a similar change in feeding with season in that species which again takes sandeels largely in May-June (TASKER *et al.*, 1985b). In the North Sea guillemot food changes from being predominantly sandeels in spring and summer to a more diverse diet in autumn and winter (BLAKE *et al.*, 1985; TASKER *et al.*, 1987).

4.2.3. PREY PREFERENCES

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 & BECKER, 1988) probably because fish prey have a higher calorific and protein content. Puffins grow best on a diet of oily fish, their preferred prey, such as sprats or large sandeels (HARRIS & HISLOP, 1978; HARRIS, 1984). Similarly, great skuas feed their chicks on sandeels in preference to other foods, 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).

Even within a prey species, quality can vary considerably. Capelin show large seasonal changes in water, lipid and protein content and show differences between age classes (MONTEVECCHI & PIATT, 1984), and 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 (FURNESS & BARRETT, 1985). Probably the seasonal changes in chemical composition of prey fish in the North Sea are rather less pronounced than those in Arctic fish, but selection by seabirds of nutritionally superior prey within fish species may occur.

4.3. ENERGETICS

4.3.1. METHODS OF STUDY

It is very difficult to study the foraging ranges over which breeding birds travel from their nest site and the distribution of foraging activity when they are at sea. Such information is essential for the measurement of the quantitative relationships between seabirds and their food stocks, which are fundamental both to the understanding of the role of prey depletion (if any), on breeding success and colony size, and the effects of seabird predation on the population dynamics of their food organisms. Major advances in this area have begun to be made as a result of technological developments. The location of seabirds at sea can now be determined by radiotracking so that foraging ranges can be determined, and often devices can be used to study diving and foraging activity.

Recent work with auks shows species-specific diving patterns and gives an indication of prey capture rates (WANLESS *et al.*, 1985) and the effects of these on the attendance of adults at their colonies (WANLESS & HARRIS, 1986). However, these workers showed that birds to which radio transmitters were attached behaved abnormally; guillemots given transmitters with external aerials spent longer at sea on each trip, made fewer trips and brought fewer fish to their chicks than did control birds or the unmarked mates of the birds with transmitters (WANLESS *et al.*, 1988). Hydrodynamic drag rather than the weight of the transmitter may be the major factor. Information derived from such methods must be interpreted with caution. Although heart-rate telemetry has been used to study the energy costs of activity in birds (BUTLER, 1980; HÜPPOP, 1987; KANWISHER *et al.*, 1978) there are large variations from bird to bird in the relationship between heart rate and metabolism. Heart stroke volume and oxygen content of the blood may also change independently of heart rate so that the relationship between heart rate and energy expenditure is not good, particularly at high metabolic rates (FURNESS & MONAGHAN, 1987).

Devices to monitor the duration of foraging trips, sizes of meals fed to chicks, numbers of dives per foraging trip, diving depths, swimming speeds, and time spent underwater, on the surface and in flight, have been developed based on principles of varying sophistication from tiny dye-filled plastic capillary tubes to the recording of data by satellite from electronic computer-transmitters (CAIRNS *et al.*, 1987; KOOYMAN *et al.*, 1982; PRINCE & WALTON, 1984; SIBLY & MCCLEERY, 1980, 1983; WILSON & BAIN, 1984a, b). Again, devices attached to seabirds may affect their behaviour; in some studies such effects have not been apparent (CAIRNS *et al.*, 1987) while others have found significant reductions in the foraging performance (WILSON *et al.*, 1986). Theoretical calculations based on aerodynamic theory may be of use in suggesting the size of devices that birds can carry without adverse effects (CACCAMISE & HEDIN, 1985) but such theoretical consideration has not yet been given to the problems of increased drag while diving.

4.3.2. BIOENERGETICS MODELLING

With a knowledge of the numbers of seabirds in a given area (whether a breeding colony and its surrounding sea, or a defined area of sea or ocean) and their activity budgets, it is possible to estimate their food consumption using generalised allometric equations for the energy costs of different activities in relation to body mass (NORSTROM *et al.*, 1986).

Early attempts to estimate energy requirements of seabirds (EVANS, 1973; FURNESS, 1978) concluded that they had a much greater food requirement than had previously been supposed, but also demonstrated that many parameters to which model outputs were sensitive needed to be refined in order to provide estimates with acceptable confidence intervals. Since these early attempts, numerous models have been developed (FURNESS & MONAGHAN (1987) and CROXALL (1987)). Recent models generally use more accurate and detailed allometric bioenergetics equations and provide more precise estimates, since they are based on much more detailed information on the energy costs of basal and existence metabolism (ELLIS, 1984) costs of foraging by flight (BAUDINETTE & SCHMIDT-NIELSEN, 1974; GABRIELSEN *et al.*, 1987), costs of diving foraging (GABRIELSEN *et al.*, pers. comm.), costs of incubation (CROXALL, 1982), and costs of moult (FURNESS & BURGER, 1988). We need more studies to validate the estimates of energy measurements using independent means of measuring energy expenditure by seabirds, for example using the labelled water technique (GABRIELSEN *et al.*, 1987). To date, no extensive test of this sort has been reported for seabirds in the North Sea but work is in progress (FURNESS; UTTLEY, pers. comm.). However, NAGY *et al.* (1984) obtained direct measurements of energy expenditure in penguins that were within 3% of the values predicted by the model of FURNESS & COOPER (1982); but see also the cautions of WEATHERS & NAGY (1982).

Energy cost relationships have been discussed by several authors, *e.g.* FURNESS & MONAGHAN (1987). The main constraints on the accuracy of current models are errors in estimates of the size of the seabird population in the study area, and uncertainties concerning the activity budgets while away from breeding colonies. However, information on both of these is improving. Translation of the energy requirements of seabirds into the amount of food consumed requires data on the composition of the diet and assimilation efficiency.

4.3.3. ENERGETICS OF FORAGING

DRENT & DAAN (1980) provided strong evidence to support an argument that mammals and birds can sustain work only to a metabolic ceiling of about four times the Basic Metabolic Rate (4 BMR). The physiological factors preventing a greater sustained metabolic rate are not known, nor do we know if or how this ceiling may vary between species. Birds can exceed a metabolic rate of 4 BMR in the short term, but in order to do so they need to draw on body reserves. For most seabirds, energy expenditure of adults is greatest during chick-rearing. When the food requirements of the chicks are high, adults spend much of their time foraging, which may increase their energy requirements above 4 BMR as a daily average expenditure. Further work is needed to investigate these matters since they may set limits to the activities of seabirds with energetically-expensive foraging behaviours.

Costs of foraging vary considerably in different seabirds. Species adapted to gliding flight (*e.g.* fulmar) can sustain continuous foraging in normal environmental conditions without exceeding a ceiling of 4 BMR. For some small species with low wing loadings, adapted to slow and highly efficient flapping flight (*e.g.* terns), energy costs of flight may not be much above 4 BMR, but in contrast, the energy costs of underwater swimming (pursuit diving) and of continuous flapping flight by seabirds with high wing loadings such as auks, shags, cormorants, divers and seaducks, greatly exceed 4 BMR (BAUDINETTE & SCHMIDT-NIELSEN, 1974; GABRIELSEN *et al.*, 1987, pers. comm.). It may be essential for these species to spend periods resting to reduce their average daily energy expenditure to a sustainable level. It is well known that many seabirds, particularly larger species such as the shag (PEARSON, 1968) do spend prolonged periods each day 'resting' in the vicinity of their nest. The presence of an 'off duty' adult near its mate who is guarding the nest does not necessarily imply that the birds have 'spare' time that they could devote to foraging.

Most seabirds lose weight during the breeding season, some especially during chick-rearing (HARRIS & WANLESS, 1988). However, the significance of weight loss is unclear. Immature great skuas lose weight during the breeding season just as breeders do (FURNESS, 1987a) and immature herring gulls show the same pattern of weight loss in summer as shown by breeding adults (COULSON *et al.*, 1983). The rapid rate of weight loss in kittiwakes at a particularly successful breeding colony in north Norway showed no significant differences between adult that had lost their eggs, birds with broods of small chicks or large chicks or between birds with different brood sizes (FURNESS & ANDERSON, unpubl.). Weight loss during the breeding season may therefore not be a sign of stress, but an adaptive strategy. Weight loss will reduce the costs of foraging since lighter birds expend less energy in flight than do heavier birds of the same wing area (NORBERG, 1981). Alternatively, weight loss in summer may represent the metabolising of reserves held during winter as an insurance against periods of severe weather.

Breeding seabirds may be constrained in their foraging by time restrictions too (RICKLEFS, 1983). In many species (*e.g.* kittiwake, gannet, skuas) the nest is normally attended by at least one adult throughout the laying, incubation and chick-rearing periods. In species with a high degree of sexual dimorphism in body size there may be a tendency for one sex to take the bulk of nest attendance duties while the other sex does most of the foraging. For example, in skuas breeding females spend little or no time foraging and are fed by the males (FURNESS, 1987a). However, severe food shortage may lead to a breakdown of the normal pattern and both adults may have to forage leaving the nest unattended. This can lead to increased loss of chicks to predators or to thieving of nest material by neighbours (NELSON, 1978; FURNESS, 1987a).

It can be predicted that seabirds, being long-lived as adults but with relatively low reproductive rates, should not invest effort in breeding to levels that will reduce their future survival prospects. Thus birds may elect not to attempt to breed in years when food availability is greatly below normal. Changes in breeding numbers at seabird colonies from year to year often seem to exceed the changes that would be expected on the basis of adult mortality alone, and so breeding numbers may provide a measure of changes in fish stocks providing that the availability of fish to seabirds remains constant with changes in stock size.

4.4. EFFECTS OF FOOD AVAILABILITY

In seabirds, incubation rhythms, chick growth, mortality and breeding success depend on the food available during the breeding season (BIRKHEAD & FURNESS, 1985; BARRETT *et al.*, 1987; ANKER-NILSEN, 1987). Due to great spatial and temporal variations in food availability and breeding success (HARRIS & HISLOP, 1978; BARRETT *et al.*, 1987; BECKER & FINCK, 1985; BECKER *et al.*, 1987), investigations need to cover several breeding seasons and habitats. Such investigations are rare due to problems of logistics and cost. It is extremely difficult to study the abundance and availability of even the most important prey, and most studies depend on indirect evidence, and sometimes circular argument.

Terns are particularly sensitive to local changes in food availability because they spend most of the day foraging when rearing chicks, and have to feed fairly close to the colony. During the years 1981–87, the breeding success of common terns on the Wadden Sea island of Minsener Oldeoog varied from 0.0 to 1.6 chicks fledged per clutch. Nest position, density, date of clutch initiation, flooding and predation (with the exception of rat damage in 1987) were no more than minor influences on reproductive success, compared with the decisive influences of weather and food availability (BECKER & FINCK, 1985, 1986, unpubl.).

Food selection by common terns at Minsener Oldeoog was studied by comparing dropped prey items, the contents of pellets found near nests and the food offered to the chicks (automatic filming) with the results of fishing trawls made nearby (BECKER *et al.*, 1987; FRANK *et al.*, 1988). The information gathered by these methods suggested that food supply was poor during 1984 and 1985 but abundant in 1986, due in particular to increased sandeel stocks (FRANK, in prep.). Significant differences were observed between study sites and years: whereas clupeids, flatfish or crustaceans dominated the diet in Wadden Sea colonies, sticklebacks caught in inland waters were important prey at coastal colonies (BECKER *et al.*, 1987). For some fish, trends in the frequency of occurrence as prey corresponded to abundances as indicated by trawling, suggesting that the birds could provide relative indices of the stocks of at least some fish.

Research is still needed to determine the relative sensitivity of different aspects of seabird biology to changes in food availability. Some data are now available for Shetland seabirds in relation to Shetland sandeels (HEUBECK, 1989).

4.5. EFFECTS OF PHYSICAL FACTORS

4.5.1. TIDAL EFFECTS

Direct observations in the Wadden Sea area, and the study of incubation shifts, have shown that gulls feeding on the coast have tide-dependent foraging behaviour. Herring gulls are away from their colonies foraging for 1.5 to 2 hours before and after low tide when the tidal flats containing their main food, mussels (*Mytilus edulis*), are exposed, and maximum numbers are present at the colony for two hours before and after high tide. DRENT (1970) showed that herring gulls leave their colonies in different directions at different stages of the tide, suggesting the use of different feeding areas. Accordingly the activities and directions of feeding flights display a tidal pattern (BECKER, 1984). Black-headed gulls breeding on the Wadden Sea islands show a similar tidal rhythm of foraging (VEEN, 1977).

The tide also dictates the timing of foraging by piscivorous birds in the Wadden Sea. At Engelsmanplaat, common and arctic terns feed most actively on fish early in the morning, just prior to sunset, and from 2 h after high tide to low water (MES & SCHUCKARD, 1976). Highest counts of terns at the nest were made just before high tide (BOECKER 1967; CONRAD, 1979). At Wangerooge BOECKER (1967) found the highest feeding rates 2 hours after low water. In addition to taking marine prey, common terns breeding on the mainland coast fly inland to feed from fresh water (BECKER *et al.*, 1987); they do this mainly at high tide when food availability is reduced in the Wadden Sea (BECKER *et al.*, unpubl.). DUNN (1975) reporting on common terns fishing off the east coast of England, recorded their greatest foraging success during hours of low water. In Shetland, arctic terns showed greatest feeding activity in areas where strong tidal currents were flowing (FURNESS & MCKEE, unpubl.).

SLATER (1980) demonstrated that guillemots showed a tidal rhythm of feeding activity in Orkney, but such rhythms do not seem to occur at most colonies and the Orkney pattern may be a consequence of the unusually strong tidal currents and shallow seas in which many Orkney guillemots feed.

Many seabirds show diurnal rhythms in foraging behaviour, typically but not always having a large peak of feeding activity shortly after sunrise (NETTLESHIP & BIRKHEAD, 1985; HARRIS & WANLESS, 1986; FURNESS, 1987a). Many petrels feed also by night when plankton and associated predators tend to be nearer the surface.

Effects of physical factors seem least evident among the largest and most pelagic seabirds, although these seabirds may show strong associations with frontal systems where prey is concentrated by converging water masses (HANEY & MCGILLVARY, 1985; PINGREE & GRIFFITHS, 1978). Food availability can be influenced by weather factors (DUNN, 1973, 1975; TAYLOR 1983; BECKER *et al.*, 1985a; BECKER & FINCK, 1985). In the spring of 1983 heavy rainfall on the days preceding egg-laying was correlated with a temporary reduction in clutch size, egg size and breeding success in the middle of the egg-laying period of common terns at Minsener Oldeoog. In all probability, the rain had reduced the availability of food and thereby limited the quantity of fish that male common terns could feed to their mates during courtship feeding (BECKER *et al.*, 1985a).

Rain, high winds and low temperatures affect the feeding success of adult terns, and thus indirectly affect the chicks leading in some cases to chick mortality (VEEN, 1977; LANGHAM, 1972; DUNN, 1975; BECKER & FINCK, 1985). On Minsener Oldeoog the feeding rate of common terns decreased in winds upwards of 20 knots (FRANK & SPECHT, unpubl.).

TASKER *et al.* (in prep.) found associations between seabird distributions at sea and seabed sediment type.

4.6. RELATION TO FISH STOCKS

ASHMOLE (1963) suggested that seabird colony size may be determined by competition for food close to the colony leading to prey depletion, and that foraging range would increase as the colony size increased.

There is indirect support for these ideas from observations of colony distributions and sizes around Scotland (FURNESS & BIRKHEAD, 1984) and from evidence that birds in larger colonies have lower breeding success (BIRKHEAD & FURNESS, 1985; HUNT *et al.*, 1986). A particular problem is that available data on the age structure, size and productivity of fish stocks are gathered on a large spatial scale and at times of year related to fisheries, and are often not appropriate to the assessment of the effect of consumption by seabirds. Fisheries may operate on the entire stock of fish, or throughout the North Sea, whereas predation by breeding seabirds is usually confined within some tens of km from their colonies, and may be similarly concentrated at sea at other times of year. Measured densities of seabirds feeding around breeding colonies in summer are generally one or two orders of magnitude greater than densities at sea during winter (Table 8) suggesting a very much greater impact of localised predation in summer around colonies. To demonstrate that seabirds deplete food stocks close to their colonies would be difficult and expensive, and this critical test of ASHMOLE model has not been achieved. However, BIRT *et al.* (1987) measured fish population densities at various distances from two large cormorant colonies, and found that they were significantly lower close to the colony than they were beyond the foraging range of the breeding cormorants.

FURNESS (1978) estimates that seabirds breeding at the largest colonies in the North Sea, such as Foula in Shetland, may consume about 20–30% of the local annual production of small fish (predominantly the non-migratory sandeel), whereas in the whole North Sea seabirds consume around 5–15% of the annual production of small pelagie fish (TASKER *et al.* 1989).

In the North Sea, sandeels are one of the most important prey of many seabirds during the breeding season, and are now subject to industrial fishing. According to BAILEY & PARRISH (1987) 'Estimation of the size of sandeel populations presents major problems because of their life history. They are not amenable to estimation by surveys of eggs or larvae because their eggs are spawned on or in the sand and because, by the time the larvae hatch into plankton, considerable but unknown mortality may have taken place. As adults, they swim too close to the sea bed for acoustic estimation. As a result, no reliable estimates have been made of the size of unexploited stocks in the seas around Scotland. Estimation of stock size is also of dubious reliability using conventional assessment techniques, *i.e.* those dependent on accumulated catches through the life of each cohort (virtual population analysis)'. It may be added that sandeel distribution is extremely patchy, dependent on suitable areas of sandy bottom, and catch-per-unit- effort statistics are inappropriate for such shoaling species, particularly since they also reflect improvement in the fishermen's knowledge of good areas for catching sandeels gained over the early years of the fishery (FURNESS & HISLOP, 1981) and show influences of changes in the composition of the industrial fleet.

Studies of breeding numbers, breeding success and diets of seabirds have shown close correlations with the abundance and availability of fish species off southern Africa (CRAWFORD *et al.*, 1983, 1985; DUFFY *et al.*, 1985b) and in the North Pacific (SPRINGER *et al.*, 1984, 1986). So far, there have been no detailed studies of this aspect in the North Sea. However, the value of seabirds as indicators of trends in the size and composition of sandeel stocks may be worth consideration. Sandeels are the preferred prey of many seabirds, particularly for feeding to chicks. Seabirds that feed almost exclusively on sandeels are most likely to exhibit changes in breeding biology that mirror changes in sandeel stock size and composition; seabirds that feed on sandeels of a particular size may give particularly precise indications of changes in recruitment or of the abundance of older age classes of fish, *e.g.* arctic terns and puffins seem to select small (0 and 1 group) whereas guillemots take rather larger sandeels. Changes in tern or puffin biology may be reliable indicators of poor sandeel recruitment. Many seabird species feed on a varied diet, including sandeels, and these may not be good indicators of fish stocks. However, the abundance of sandeels in the diet of generalist feeders like

TABLE 8

Densities of seabirds around colonies during the breeding season and in winter in the North Sea. Data from TASKER et al. (1987) and BLAKE et al. (1984).

Species	*Colony area*	*Numbers per km²*	*Numbers per km² in North Sea in winter*
Gannet	<37 km from Noss	1.5	0.04
Gannet	Inshore near Bass Rock	1.0	0.04
Razorbill	Orkney and Shetland	0.3	0.05
Puffin	Orkney and Shetland	1.7	0.05
Guillemot	Fair Isle	30	1.6

fulmars and great skuas in Shetland may reflect changes in relative availability of sandeels to these birds, both within a season and from year to year (FURNESS & HISLOP, 1981; FURNESS, 1987a; FOWLER & DYE, 1987).

5. IMPACTS OF MAN

5.1. POLLUTION

Pollution of many kinds, and derived from many sources, has been a cause of concern to those interested in or dependent upon the North Sea for many years. Recent incidents include large mortalities of seabirds due to oil pollution at sea, the catastrophic reduction in populations of the common seal due to a virus infection but associated in the minds of many with chemical pollution, and reductions in numbers of terns in the southern North Sea as a result of the accumulation in birds of pesticides discharged into the sea. These and many other aspects of pollution in the North Sea have been reviewed in SALOMONS *et al.*, (1988), in which BOURNE & VAUK (1988), provide a chapter dealing specifically with birds, and cite over 100 relevant references. Seabirds are especially vulnerable to pollutants when concentrated at and near breeding colonies in spring and summer, and also in feeding and moulting areas at other times of year. The distribution of breeding colonies is well known and concentrations of birds throughout the North Sea have been mapped in detail by TASKER *et al.*, (1987) and summarised to show concentrations vulnerable to oil pollution (and therefore to other pollutants) by TASKER & PIENKOWSKI (1987).

5.1.1. OIL POLLUTION

Oil spilt at sea has caused the contamination and death of large numbers of seabirds in most seas of the world for more than eighty years. Many papers have been published on the effects of oil pollution on seabirds in the North Sea and elsewhere, covering sub-lethal effects as well as catastrophic mortalities associated with particular accidents. There are several recent comprehensive reviews (BOURNE, 1968, 1976; RSPB, 1979; DUNNET, 1982b, 1987; CLARK, 1984; BOURNE & VAUK, 1988). The development of production from the oil and gas fields in the North Sea has not resulted in the feared increase in bird mortality (DUNNET, 1987) but seabirds continue to die, sometimes in large numbers, as a result of contamination from oil slicks often of unknown origin: for example, 69,000 birds may have been killed by oil in the eastern North Sea in the winter of 1980–81 (BAILLIE & MEAD, 1982). Evidence for particular incidents, and from chronic oil pollution is obtained from Beached Bird Surveys which were conducted, in winter, on many stretches of the North Sea coastline (STOWE, 1982b) but are now discontinued as an international programme. Data from the more recent surveys show a reduction in the numbers and proportion of dead birds on British beaches which have been killed by oil, but an increase on southeast North Sea coasts. DUNNET (1982b) has shown that for some species the large numbers of birds found oiled in winter may constitute a small proportion of the expected natural mortality, (Table 9), and that the processes of recruitment of new breeders from the large reservoir of pre-breeding birds make it very difficult to identify local consequences of even large winter mortality incidents.

Interestingly, the International Council for Bird Preservation carried out a worldwide review of the status and conservation of seabirds (CROXALL *et al.*, 1984) and in his chapter on northwest Europe, EVANS (1984) does not identify oil pollution as the major threat to seabird numbers.

5.1.2. CHEMICAL POLLUTION

From 1964 to 1968 on the Dutch coast, effluents from a pesticides factory near Rotterdam - mainly dieldrin, telodrin, endrin and aldrin - caused enormous mortality in terns, herring gulls, eiders and other bird species (DUINKER & KOEMAN, 1978; ROOTH, 1980; SMIT, 1981). The consequence of this pollution was a steep decline in Dutch seabird breeding populations. Only female eiders were affected, associated with their marked weight loss during incubation, and their mortality diminished with increasing distance of the breeding site from the pollution source (SWENNEN, 1972). During the mid 1960s, in the German Wadden Sea, conspicuous decreases, or low population levels, were noted in most species of breeding seabirds, waders and ducks (BECKER & ERDELEN, 1987); these were probably a result of the pollution in the Netherlands. The elimination of the pollutant effluents (DUINKER & KOEMAN, 1978) and legal prohibitions of use and production of several toxic chemicals since the early 1970s have led to increased populations of many shore breeding bird species (SMIT & WOLFF, 1980; BECKER & ERDELEN, 1987).

Despite the potential value of seabirds in providing warning of changes in the environment adverse to the higher trophic levels of the community (NERC, 1983), very few North Sea studies are concerned with interspecific, intersite or year to year differences in contamination. A large number of stimulating but isolated results cannot be compared owing to methodological considerations such as methods of chemical analysis, selection of compounds, species and tissues, limited geographical coverage, and sample size (NERC, 1983).

Monitoring of levels of residues in British seabirds has shown there has been a decline in levels of DDE over recent years, particularly in comparison to the early 1970s (NEWTON *et al.*, 1985). Contamination by DDE

TABLE 9

Approximate estimates of the breeding and pre-breeding components of the populations of selected species of seabirds in Britain and Ireland, and the numbers dying per year, based on calculations and estimates of annual mortality rates (From DUNNET, 1982a).

	breeding birds (thousands)	*breeders dying annually* (thousands)*	*pre-breeding birds+ (thousands)*	*pre-breeders dying annually+ (thousands)*	*total dying annually (thousands)*
Guillemot	1458**	87	552	164	251
Razorbill	300**	27	128	38	65
Puffin	1400**	70	599	175	345
Fulmar	312++	9	335	86	96
totals	3470	193	1614	463	757

* From adult survival rates from Table 1.

\+ Based on 30% fledging success, 50% mortality in first year, 16% annual mortality until breeding (MEAD & BAILLIE, 1981), and age at first breeding from Table 3.

** RSPB (1979) stat.

++ CRAMP et al. (1974).

was suggested as a cause of egg-shell thinning in gannets, shags and guillemots (PARSLOW & JEFFERIES, 1977), and a cause of reduction of the breeding success of great skuas (FURNESS & HUTTON, 1980). The recent increases in populations of these species indicate that any effects were not sufficient to reduce the populations. Experimentally raised levels of PCBs in puffins have been shown to have no demonstrable effect on breeding success or longevity in a study carried out on the Isle of May, Scotland (HARRIS & OSBORN, 1981). In recent years it appears that levels of organohalogen residues have fallen in most birds.

The levels and effects of pollutant residues on top marine predators has recently been reviewed in the United Kingdom (NERC, 1983). In the offshore bird community, residues have been monitored in eggs of gannet and guillemot collected around the British Isles since the early 1970s. Early results revealed high geographical variation in levels of pollutants, with birds in the North Sea generally having lower levels than birds in the Irish Sea (PARSLOW & JEFFERIES, 1975). The higher levels of residue were generally associated with coastal industry and conurbations, rather than with sources further inland. More recent monitoring results have shown a decline in residue levels in guillemot eggs. For gannet eggs, DDE and HEOD residues are now much lower than in the early 1970s. Levels of metals in offshore birds have been examined in several areas. Very high levels of cadmium have been found in fulmars and other seabirds; however high levels have been found in some (presumably) relatively unpolluted areas, such as St. Kilda, with lower levels in the North Sea. There is evidence that fulmars can tolerate high levels of cadmium in their bodies. Mercury levels have been monitored in gannet eggs, these have changed little since the 1970s. In puffins from the Isle of May, levels of metals are generally low (OSBORN, pers. comm.).

BECKER *et al.* (1985b, c) describe the contamination of eggs of seven species originating from seven regions along the German North Sea coast in 1981. Terns had the highest residue levels (HEIDMANN *et al.* (1987)). The compounds found in greatest quantity were no longer insecticides but industrial chemicals, such as PCBs, HCB and mercury, a trend which is confirmed by other recent studies (FURNESS & HUTTON, 1980; BECKER *et al.*, 1988; BERGSTROM & NORHEIM, 1986; HEIDMANN *et al.*, 1987). Regional differences were found in nearly all species; eggs from birds breeding on the Elbe estuary contained distinctly larger quantities than those from the other regions, associated with the heavy pollution of the river Elbe.

Significant local differences clearly show that migratory species, such as terns, can also be indicators of site-specific environmental pollution in their breeding area (BECKER *et al.*, 1985b). According to these results, seabird populations breeding and feeding in the inner German Bight are particularly threatened by toxic residues, and it is here that important numbers of terns breed, and also kittiwakes and guillemots on the one and only cliff in the whole Wadden Sea area, on Helgoland. However, as most seabird populations have recently increased in the Wadden Sea, toxic residues do not seem to have adverse effects at the present time.

For inshore species, data are available from the southeast North Sea, and Britain. High concentrations of organohalogen compounds have been found in several birds found dead or dying on German shores (KOEMAN & STASSE-WOLTHUIS, 1978). VAUK & LOHSE (1977) investigated the levels of DDE and PCB in German seabirds, and found some particularly high levels in gull fat, these residues were found to increase in concentration with age, and may lead to a reduction in lifespan for some birds. OSBORN (unpubl.) has also recorded high levels of PCB in the fat of herring gulls on the Isle of May, Scotland.

High levels of dieldrin have been found in eiders and red-throated divers and raised levels were also detected in cormorants and shags. Massively raised levels of copper and mercury have been recorded for eiders; these birds feed on large invertebrates which also can accumulate high concentrations of metals. The effects of these metals and residues are more difficult to establish. There are a few fatal poisoning incidents such as that probably caused by methyl lead on the Mersey and other smaller incidents. The toxicity and sub-lethal effect of most metals remains unexamined and unknown for most birds. Damage of kidney tubules due to cadmium has been found in fulmars (NICHOLSON & OSBORN, 1981). Raised levels of contaminants may have contributed to the death of birds in a large scale mortality incident in the Irish Sea in 1969; however starvation was probably the primary cause (HOLDGATE, 1971).

5.1.2.1. TRENDS IN CONTAMINATION

In 1986 analyses for pollutants in the eggs of common terns, herring gulls and oystercatchers were repeated in four regions of the German coast (BECKER *et al.*, 1988). Intersite and interspecific differences were again found, but compared with 1981, lower levels of HCB and DDT were found and all species of PCBs in common terns, and of PCBs and mercury in herring gulls. The decline of DDT in seabirds up to 1981 (BECKER *et al.*, 1985b) continued, as it did in Baltic Sea guillemots (OLLSON & REUTERGARDH, 1986) and in herring gulls in South Norway (BERGSTROM & NORHEIM, 1986). The sharp reductions of HCB values since 1981 are probably due in part to the legal prohibition of its use in agriculture in the Federal Republic of Germany which came into effect in that year. Similar decreases in contamination levels of other industrial chemicals, were reported by BERGSTROM & NORHEIM (1986). Nevertheless, it would be premature to claim a general decrease in the known toxic contaminants in seabirds, since large year-to-year fluctuations of mercury and lindane residue levels came to light (BECKER *et al.*, 1988). Furthermore the mercury concentrations in 1985 with a mean of more than 11 ppm caused considerable alarm. Hence to detect and recognize trends in contamination, continuous monitoring over a larger number of years is necessary, especially in the recognized pollution black spots such as the German Bight. There, a three-year monitoring project started in 1987 on common terns and oystercatchers.

5.1.3. PLASTICS

Waste plastic on the sea surface directly affects seabirds in two ways; it may cause entanglement or it may be ingested. Both often lead to death (see reviews by AZZARELLO & VAN VLEET, 1987; LAIST, 1987). The North Sea appears to have increasingly large amounts of waste plastic, but its distribution has not been mapped in detail (DIXON & DIXON, 1981, 1983). In some areas, the density of plastic spherules on the ocean surface, first reported by CARPENTER & SMITH, (1972), has been estimated using tow nets, and has been found to be around 1000–8000 spherules km^{-2} in most major seas and oceans (MORRIS, 1980; WONG *et al.*, 1974; PRUTER, 1987). Levels in the North Sea have not been reported, but given the partly closed nature of the water mass and the extensive industrial production of plastics at sites on the east coast of Scotland and England, in the Netherlands and West Germany, levels of waste plastic spherules are likely to be particularly high. Surveys of beached plastic indicate that considerable quantities are dumped at sea (VAUK & SCHREY, 1987), or derived from river discharges and from coastal inputs (PRUTER, 1987).

Most ingested plastic is in the form of spherules, the raw material from which user-plastic items are produced (DAY *et al.*, 1985), although large seabirds, such as fulmars, may also swallow a wide variety of plastic products or fragments: recorded stomach contents include condoms, toothpaste tube tops, fragments of plastic bags, cups and fishing line (BOURNE, 1976; VAN FRANEKER, 1985; ZONFRILLO, 1985).

5.1.3.1. ENTANGLEMENT IN DISCARDED NETS

Fragments of fishing nets or lost drift nets ('ghost nets') pose a particular entanglement hazard (BOURNE, 1977; PIATT & NETTLESHIP, 1987).

In the North Sea, gannets more than any other seabird get entangled in floating fragments of net. An estimated minimum of 2.6% of live gannets seen from Helgoland were entangled in fragments of fishing gear and 29% of dead gannets found at Helgoland died as a result of entanglement in plastic (SCHREY & VAUK, 1987). However, part of the entanglement problem arises because gannets often make use of net fragments and floating plastic waste as nest-building material. NELSON (1978) estimated that two-thirds of gannet nests at some colonies contained plastic, and as a result some chicks become entangled and die or lose a leg through constriction of blood vessels. Adult and chick mortality due to entanglement have not been quantified, but the present levels are clearly insufficient to stop the current population increase of gannets.

5.1.3.2. INGESTION OF PLASTIC

Plastic spherules were first recorded in the stomach contents of seabirds in the early 1970s (ROTHSTEIN, 1973; BOURNE, 1976; AZZARELLO & VAN VLEET, 1987). Most studies of ingested plastic have involved small numbers of birds, found dead, collected at sea or at colonies, but generally of unknown age and breeding status, which impairs interpretation of the results. It is generally assumed that seabirds ingest plastic mistaking it for food, and that ingested plastic is likely to be harmful.

Accumulation of plastic in the gizzard is predominantly found among Procellariiformes, whereas other seabirds regurgitate indigestible material including plastic (FURNESS, 1985a; AZZARELLO & VAN VLEET, 1987). The only species for which the quantity of plastic in the gizzard has been measured over a period of years is the fulmar (BOURNE, 1976; FURNESS, 1985a; VAN FRANEKER, 1985). Birds collected at nests in Shetland in 1983 contained very similar amounts of plastic to those collected dead on beaches in the Netherlands between 1982 and 1984 (Table 10) but both samples contained about ten times as many plastic fragments as the sample shot at sea in the early 1970s by BOURNE (1976). Although the breeding origins of two of these samples is unknown and the gizzards were inspected by different workers, the data suggest a rapid increase in plastic pollution in the North Sea over the last two decades.

Most investigators suggest that ingested plastic is likely to block the intestine or injure the wall of the alimentary tract; depress hunger by causing stomach distension; reduce the functional volume of the gizzard leading to a slower rate of food processing, and/or a reduced assimilation efficiency; increase intake of organochlorines absorbed to pellet surface; cause intake of toxic antioxidants, colourants or plasticisers.

The last two ideas have never been tested. Physical damage to the digestive system (generally extensive ulceration) has been demonstrated (BOURNE, 1976; FRY *et al.*, 1987; ZONFRILLO, 1985) and may be a serious problem since the chances of damaged individuals surviving to be sampled by ornithologists may be low. Although several studies have suggested that body fat deposits or body mass may decline as a consequence of high plastic burden, suggestive correlations measured for small samples of birds generally failed to reach statistical significance (DAY, 1980; CONNORS & SMITH, 1982; FURNESS, 1985a, b) while RYAN (1987) and FRY *et al.* (1987) found no relationship between plastic burden and body condition in three procellariiform species. Further work is needed on the effects of ingested plastic on the feeding of adult petrels and on the growth of petrel chicks. In the North Sea the fulmar seems most likely to be affected by ingested plastic, although at present its population is increasing.

5.2. FISHERIES

Without a clear understanding of the ways in which seabird numbers are regulated it is difficult to know what impact fishery activities may have on seabird populations through effects on food supplies. However, three effects seem likely: (i) fisheries increase food availability to some seabirds by discarding waste offal and fish on the sea surface; (ii) fisheries may reduce fish stocks and thus reduce food availability to some seabirds, though in the North Sea most fisheries have in the past been directed at large predatory fish (cod, haddock, whiting etc) adults of which are not eaten by any seabirds; (iii) exploitation of certain fish stocks may lead to changes in community structure that can be beneficial to seabirds. Thus the response of seabirds to fishing activities can be complex. The history of North Sea fisheries with regard to their effects on seabirds has been reviewed by FURNESS (1982, 1987b).

Seabirds can become entangled in nets where drift netting for large fish is extensive; serious seabird mortality incidents have been reported from Newfoundland (PIATT & NETTLESHIP, 1987), from the Pacific Ocean (LAIST, 1987), from north west Norway (VADER & BARRETT, pers. comm.) and from the west coast of Ireland (MERNE, pers. comm.). In all these cases fishermen tended to hide or sink dead entangled seabirds and the death rate is likely to be higher than it appears. In several cases it may have led to immediate decreases in breeding numbers of auks in the vicinity of trapping areas. In the North Sea such netting is very limited, but could affect auks in north east England.

Few seabirds become entangled in trawl or seine nets,

TABLE 10

Numbers of fragments of plastic in the gizzard of fulmars.

Locality	*Reference*	*Year of sampling*	*Birds collected*	*Status*	*Mean number of plastic items*
North of Scotland	BOURNE, 1976	1969-74	36	at sea	<1.2
Netherlands	VAN FRANEKER, 1985	1982-84	65	dead on beach	11.9
Shetland	FURNESS, 1985	1983	13	from nests	10.6

or drown in lobster traps. Gannets may plunge dive after fish in nets and can break their bill as a result (HARTWIG *et al.*, 1985). Most of the few ringed birds recovered in lobster traps are juveniles that have recently become independent, and have not learnt the skills of foraging (GALBRAITH *et al.*, 1981). Bag nets and fly nets fixed along shores to intercept migrating salmon off the Scottish coast frequently capture auks in the vicinity of their colonies (MELVILLE, 1973) but there is no evidence that local breeding numbers are affected over the years.

5.2.1. FISHERIES FOR GADOIDS, FLATFISH, HERRING AND MACKEREL

LUNDBECK (1959, 1960, 1962) showed that the biomasses of gadoids and flatfish in the North Sea declined considerably in the 1890s and he attributed this to over-exploitation by the greatly increased power of fishing fleets. Effects of overfishing can be seen in increased growth rates of haddock and whiting and reduced age at maturity of cod (HEMPEL, 1978). Industrial fishing for immature herring and mackerel in the 1960s drastically reduced these stocks (HEMPEL, 1978) and the effect of these fisheries have been modelled by ANDERSEN & URSIN (1977) who predicted an increase in sandeels as one response. Such an increase has been observed (SHERMAN *et al.*, 1981). Reduction in numbers of large predatory fish early in the 20th century may also have allowed an increase in sandeels, one of their main prey, although no data exist to demonstrate this. Overfishing reduces the average size of fish in the population, which may result in a larger proportion of the stock being within a size range that can be exploited by seabirds.

Over much of the 20th century numbers of many seabirds breeding around the North Sea have increased, while almost all species increased during the 1960s–70s (CRAMP *et al.*, 1974), and part of this increase may be due to an increase in the stocks of sandeels and other small fish coincident with over-exploitation of whitefish, herring and mackerel (FURNESS, 1982, 1987b).

5.2.2. SANDEEL FISHERIES

Most sandeel fishing in the North Sea occurs in central areas well away from seabird breeding colonies, but the fishery developed around Shetland in the 1970s harvests sandeels from areas very close to some of the largest seabird breeding populations of the North Sea. These seabird populations could be threatened if the fishery led to a reduction in the stocks of sandeels or a change in their dispersion or behaviour. (Mass mortalities of seabirds as a consequence of over-exploitation by industrial fisheries has been apparent off Peru and south Africa (FURNESS, 1982)). The seabirds most at risk are species with specialized diets, surface feeding habits, specialized and inflexible feeding behaviour, limited foraging ranges, limited ability to increase foraging time, energetically expensive food-searching methods, and low tolerance of temporal fluctuations in food availability (FURNESS & AINLEY, 1984). Clearly certain North Sea seabirds show many of these characters; terns, kittiwakes, arctic skuas and some alcids, perhaps particularly the puffin which makes only shallow dives.

Around Shetland, industrial fishing for sandeel occurs from March to September, catching predominantly 1 to 3 year old fish early in the season and, after July, almost exclusively 0-group sandeels. Catch-per-unit-effort (CPUE) data cannot be used to indicate changes in the size of sandeel stocks over the years since the CPUE shows a progressive increase over the first years of the fishery, typical of new fisheries, as fishermen learn where best to fish. However, CPUE is clearly bimodal within each year (FURNESS & HISLOP, 1981) suggesting that the availability of different age classes changes seasonally. Since about 1983 the production of young sandeels around Shetland has been low, but it is not known why. Shetland populations of arctic terns have suffered almost total reproductive failure in recent years, and kittiwake breeding success has been erratic (MONAGHAN *et al.*, 1989; HEUBECK, 1989) while the numbers of breeding arctic terns, kittiwakes and arctic skuas have declined at Foula, a major Shetland colony (FURNESS, 1987b). It is thought that puffins failed to rear young at the enormous colonies on Foula in 1986 and 1988 (CALDOW, pers. comm.) and at Hermaness in 1987 and 1988 (MARTIN, pers. comm.) as very few adults were seen carrying fish in late July when chicks should have been receiving regular feeds.

Unfortunately, the causes of the decline in Shetland sandeel stocks is unknown. The size of the spawning stock may not have declined, although production of young sandeels certainly has. The levels of natural mortality of sandeels are unknown and will certainly vary between years as seabird predators at least will tend to consume a higher proportion of the stock when stock size is small. There is an urgent need for a large scale research programme into the biology of sandeels, their behaviour and role in the marine ecosystem, and this will require the cooperation of fish biologists and ecologists specialising on predation.

5.2.3. DISCARDED FISH AND OFFAL

Although ornithologists have speculated that offal and fish discarded from fishing vessels may have caused the explosion of the fulmar population in the North Atlantic and North Sea (FISHER, 1952), no studies of the exploitation by seabirds of waste at fishing boats were undertaken in the North Sea until the 1980s. Observations by the Seabirds at Sea Team showed that fulmars, large gulls, gannets and great skuas each associated

TABLE 11

Quantities of offal and fish discards from white fish and Norway lobster boats estimated to be discharged into the North Sea in 1982 (from ICES data, see text), together with estimates of the numbers of fulmars and gulls that could be sustained through the year by these food supplies, assuming that offal was consumed only by fulmars and discarded whole fish only by large *Larus* gulls.

ICES fishing area	*Offal discarded (tonnes)*	*Whitefish discarded*		*Scavenging seabirds that could be fed throughout the year*	
		Whitefish boats (tonnes)	*Nephrops boats (tonnes)*	*fulmars (offal)*	*gulls (discards)*
Northern North Sea	40,000	41,000	3,000	620,000	310,000
Central North Sea	34,000	30,000	8,800	530,000	277,000
Southern North Sea	9,700	5,300	10	150,000	38,000

closely with fishing boats at certain times of year (TASKER *et al.*, 1985a, 1985b; 1987). Gannets appear to make extensive use of discarded whole fish, especially early in the season when the birds first return to breeding colonies. Great skuas appear to prefer sandeels, but utilise discards when sandeels are not available. Availability of discarded small whiting and haddock from vessels around Shetland may have been important in sustaining the large increase in breeding numbers of great skuas in Shetland (FURNESS & HISLOP, 1981; FURNESS, 1987a), while fishery waste may have altered seabird community structure in other parts of the world too (ABRAMS, 1985).

In the northern North Sea, fulmars are dominant at fishing boats and obtain almost all of the discarded offal (HUDSON, 1986). Gannets, great skuas and large gulls take whole fish discards, selecting those they are best able to handle. Further south, herring gulls and lesser black-backed gulls predominate and kittiwakes become more numerous at fishing boats, while numbers of fulmars and great skuas are much lower.

Amounts of food made available to seabirds vary according to the fishing method. Whitefish and Norway lobster *(Nephrops)* boats provide most of the food available to scavenging seabirds at sea. Most discarded whole fish are small (10–25 cm) gadoids from Norway lobster boats or 25–30 cm gadoids from whitefish boats. Flatfish discards are usually ignored by seabirds if alternatives are available. Shetland boats in 1985–87 discarded approximately 30% of their catch (by volume), and Norway lobster boats discarded fish equal to about twice the quantity of *Nephrops* caught (FURNESS *et al.*, 1988). Quantities consumed by seabirds vary according to the sizes and species composition of discards and to the numbers and species composition of flocks of seabirds present, but generally about three-quarters of discarded fish from whitefish boats in Shetland and from Norway lobster boats off south Scotland are consumed by seabirds.

Quantities of offal discarded represent about 11% of the mass of gadoids and 6.5% of the mass of flatfish processed for market. From these data and ICES fisheries catch statistics it is possible to estimate the amounts of food made available to seabirds in sectors of the North Sea. From information on the calorific value of this material and the energy requirements of scavenging seabirds, it is possible to make a crude estimate of the numbers of scavenging seabirds that could be sustained through the year by these food supplies (Table 11) (FURNESS *et al.*, 1988). The numbers that could be supported by fishery waste seem to be considerably fewer than the numbers of scavenging seabirds present in the North Sea (see earlier) indicating that much of the diet of fulmars, large gulls and gannets must come from other sources.

Detailed studies of the foraging behaviour and interactions of scavenging seabirds at fishing boats when measured fish were experimentally discarded showed that gannets had the highest foraging success, which tended to be lower in smaller species with decreasing body size (HUDSON, 1986). Larger species tended to steal fish from smaller species, although gannets were not kleptoparasitic. The considerable competition resulted in the establishment of a dominance hierarchy with kittiwakes and herring gulls often being excluded from access to fish (HUDSON, 1986; HUDSON & FURNESS, 1988).

Since the minimum net-mesh size for whitefish boats in the North Sea is currently being increased in an attempt to reduce the amount of discarding of undersized fish (which are dead or moribund by the time they are discarded), it can be predicted that over the years the amount of waste made available to scavenging seabirds will progressively decrease. Also, the average size of the fish that are discarded will increase, which will accentuate the disadvantage that herring gulls, lesser black-backed gulls and great skuas suffer in competition with great black-backed gulls and gannets (HUDSON & FURNESS, 1988). In areas where seabirds scavenge predominantly from Norway lobster boats rather than from whitefish boats these changes will have no effect, since Norway lobster boats will continue to use small-mesh nets and to discard large quantities of 10–25 cm fish. However, it seems inevitable that more sensible management of whitefish fishing will adversely affect the food supplies of small scavenging seabirds in the North Sea, and this should be monitored.

5.3. PREDATORS

5.3.1. INTRODUCED MAMMALIAN PREDATORS

Ground nesting and even cliff nesting seabirds are very vulnerable to mammalian predators during the breeding season. Many colonies are established on islands which are inaccessible to terrestrial mammalian predators (LACK, 1968; SOUTHERN *et al.*, 1985). On the low lying German North Sea coast common terns, herring gulls, black-headed gulls and common gulls establish their nesting colonies near the outer edge of the tidal salt marsh, as far as possible from the dyke and from terrestrial predators (BECKER & ANLAUF, 1988a, b). Because seabirds in breeding colonies have insufficient defence mechanisms against terrestrial enemies, in particular nocturnal ones (SOUTHERN *et al.*, 1982), they suffer enormous losses of both breeding adults and their eggs or chicks. Predation sustained over a number of years may well lead to the abandonment of the breeding area (SOUTHERN *et al.*, 1985).

However, man, either deliberately or accidentally, has been responsible for introducing mammalian predators to islands. Three predators which greatly affect the seabirds of the Wadden Sea islands along the southern North Sea coast are the domestic cat (*Felis domestica*), the hedgehog (*Erinaceus europaeus*) and the brown rat (*Rattus norvegicus*). Their distribution is described by VAN LAAR (1981), and some effects have been documented by GROSSKOPF (1968), who reports on losses caused by marauding domestic and feral cats on Wangerooge. Breeding adult common and arctic terns were frequent victims of the cats, but cat control measures succeeded in reducing the losses. Hedgehogs prey especially on eggs and young. In the course of a few years hedgehogs on Amrum caused the loss of several hundred common and arctic tern clutches, and entire colony sites were abandoned (RUTHKE, 1962), and since their first appearance on Wangerooge in the sixties, hedgehogs have caused and are still causing heavy losses (GROSSKOPF, 1968). In Shetland they have also been recorded eating arctic terns eggs (UTTLEY, pers. comm.).

Brown rats are capable of inflicting particularly serious damage among seabirds, preying as they do on eggs, young and breeding adults (STEINIGER, 1956). STEINIGER (1956) and VAN LAAR (1981) list many Wadden Sea islands where rats occurred or occur, having reached them usually in brushwood used for stabilising the islands. This was the case on Norderoog, Scharhorn and Oldeoog. STEINIGER (1956) reports that on Norderoog between 1945 and 1947, 7000 to 9000 breeding birds, for the most part terns, and including the entire 1946 brood, perished. On Scharhorn the entire 1950- and 1954-broods of 3000 and 4000 breeding pairs of common terns respectively were destroyed (TEMME, 1967). The islands were cleared of rats by extensive and long-term poisoning programmes, hunting with dogs and digging out their burrows.

This extensive damage caused by mammals introduced on islands shows how vulnerable seabirds are on their breeding grounds. The fact that the seabirds in the Wadden Sea are concentrated in a small number of breeding areas (TAUX, 1986; BECKER & ERDELEN, 1987) makes the populations nowadays particularly vulnerable to large scale breeding losses. Thus one of the objectives of nature conservation must be that no non-native predators should be admitted, and secondly that everything possible should be done to detect animals, in particular brown rats, hidden in cargoes before they are brought onto islands. Once mammalian predators have become established on an island it becomes much more difficult and more expensive to protect seabirds. Furthermore it is questionable whether the infestation can be brought under control before the seabirds abandon the area as a breeding place.

Mink (*Mustela vison*) are farmed for their fur, and when they escape from captivity, readily become established in the countryside. In Norway they are thought to have caused declines in black guillemots and eider (BARRETT & VADER, 1984). Attempts have been made to establish farms in both Orkney and Shetland where feral animals would constitute a serious threat to seabirds. Such farms have now been banned from these islands.

5.3.2. LARGE GULLS

Herring gulls, whose numbers have increased possibly in response to the provision of additional food by man, may be significant predators on other seabird species. On Mellum, common terns breed in the immediate vicinity of a herring gull colony of more than 10,000 breeding pairs. Chick losses due to herring gulls grossed between 44% and 95% in 1979-1983 (BECKER, 1984, 1985, 1987). No more than 10 km away, however, on the island of Minsener Oldeoog, herring gulls played only a minor role as a predator on the common terns (predation losses due to short-eared owls (*Asio flammeus*) and brown rats were greater; BECKER & FINCK, 1985, 1986). These studies show that gulls can cause considerable local reductions in the breeding success of terns. But only when several colonies over a larger area are taken into consideration, does it become clear that egg and chick losses through predators represent no more than 15% of the eggs laid (five common tern colonies at the Jade, 1980–1986, BECKER (unpubl.)). The significance of these losses for the populations was overshadowed by other factors such as weather, food availability and, locally, flooding.

5.4. GULL CONTROL

Gulls have been a quarry of mankind for centuries. Eggs were collected, and gulls used to be trapped all the year round for food (VAUK & PRUTER, 1987). With the advent of protective legislation this exploitation largely stopped, and gull populations, especially herring gulls, expanded rapidly and enormously. Where they breed with or close to other seabirds they may displace them and cause major changes of habitat (DROST, 1952, 1954a, b, 1958; MÖRZER BRUYNS, 1958; GOETHE, 1961, 1964, 1970; SOBEY, 1976).

From the 1940s onwards herring gulls breeding on some North Sea coasts have been kept under control in the interests of nature conservation, and sometimes public health. The steps taken in Europe and the methods of control have recently been summarized by VAUK & PRUTER (1987), and for the Federal Republic of Germany by THIESSEN (1986) and BECKER & ERDELEN (1986, 1987).

The annual killings, which on the Isle of May between 1972 and 1977 led to a noticeable reduction of the herring gull breeding colony, lay between 36% and 65% of the breeding birds (on the average 46% (DUNCAN (1978)). At least 30% of a lesser black-backed gull colony have to be destroyed annually in order to achieve a permanent reduction at Abbeystead (WANLESS & LANGSLOW, 1983). The desired decrease of the population can only be brought about by long-term, annual and widespread action, which embraces all the important colonies, and this is quite impracticable. However, in the last few years herring gull numbers have declined dramatically over much of Britain at least, for no known reason.

Neither nest site competition nor the influence of gulls on the breeding success of other species has been at all well examined or documented (GLUTZ & BAUER, 1982; THIESSEN, 1986). As long ago as 1967 anti-gull measures in the Netherlands had been discontinued, and in the Federal Republic of Germany by the end of the 1970s since doubt had arisen as to its efficacy (GOETHE *et al.*, 1980).

In the Netherlands (GOETHE *et al.*, 1980; SMIT & WOLFF, 1980) and in the Federal Republic of Germany (BECKER & ERDELEN, 1987) terns increased their breeding population simultaneously with the gulls, immediately after the discontinuation of the measures against the gulls. Thus negative correlations between the numbers of terns and gulls during the 1950s and 1960s cannot be cause and effect because: tern populations increased in the 1970s when the gulls were experiencing their most rapid population growth (Fig. 4); terns declined in north Friesland where herring gulls are far scarcer than in Lower Saxony (see also THIESSEN (1986)); declines in tern populations were recorded in the main in areas which were not major colony sites for gulls; and negative trends in tern populations were independent of the presence of gulls (BECKER & ERDELEN, 1987).

On the Wadden Sea islands the decline of terns and other bird species which breed on sparsely vegetated sand areas, although often coinciding with an increase in gulls, is mainly a consequence of natural vegetation succession (BECKER & ERDELEN, 1987). Since gulls take over from terns in the succession, they appear to drive them out.

The extensive control operations in the large herring gull colonies of Memmert, Langeroog and Mellum in Lower Saxony have not led to the intended increase in breeding numbers of threatened bird species (BECKER & ERDELEN, 1987; THIESSEN, 1986). The campaign against the gulls has not achieved the reduction of the colony area on the Isle of May (COULSON *et al.*, 1982), nor the recovery of the breeding habitats for other species, nor a deterioration in the environmental conditions favourable for gulls (FRANK, 1986).

The destruction of breeding herring gulls can also have some undesired effects, for the thinning out of the colony affects regulating factors related to population density such as food competition and cannibalism (*e.g.* PARSONS, 1971; BERGMAN, 1982; DE WIT & SPAANS, 1984; SPAANS *et al.*, 1987), and facilitates the immigration of recruits (CHABRZYK & COULSON, 1976; DUNCAN, 1978). The results of the cull on the Isle of May were lower densities of breeding pairs and a smaller breeding population, which resulted in an improvement in the condition of breeding adults (increase in weight, wing length and egg volume) and lowered the age of first breeding (COULSON *et al.*, 1982). Such changes are capable of compensating for increased adult mortality due to culling. After many years of rapid growth there are signs since the mid 1980s, that the increase of herring gulls in Holland is coming to a halt (SPAANS *et al.*, 1987).

The consequence is that today, for the Wadden Sea area, the recommendation is to abandon gull control in large colonies and to limit population control measures to exceptional cases (THIESSEN, 1986; BECKER & ERDELEN, 1986, 1987; VAUK & PRUTER, 1987; SPAANS *et al.*, 1987). Thus it may be advantageous, for instance in order to maintain the positive spatial separation between tern and herring gull colonies, to suppress new colonies of herring gulls close to important breeding areas of threatened species. Such approaches must always be recognised as short-term responses to long-term problems.

5.5. BREEDING HABITATS

Not only the processes of nature, but also activities of man are responsible for changes in habitats for breeding seabirds, especially non-cliff-nesting species. In the Wadden Sea, for example rapid geomorphological and biological changes occur: sand banks and islands are formed, shift their positions and disappear (*e.g.* LUCK, 1976; EISMA, 1980). Thus Knechtsand island, Lower Saxony, emerged in the 50s, and in the 60s and 70s became an important breeding area for gulls and terns (WIETFIELD *et al.*, 1984). Little by little this high sand was washed away again: in 1983 the area above sea level was reduced from 9 to 1.4 ha, and today the island has nearly disappeared again. Alongside these developments biological successions take place which SCHÄFER (1954) and HARTUNG (1975) described for the island of Mellum, and which SMIT (1981) discusses, for various types of island, with particular reference to the effects on birds.

The preferred breeding sites of terns and most gull species are sandy areas and primary dunes on high sands or small barrier islands (SMIT, 1981). The breeding colonies of gulls accelerate natural plant succession through the effect of fertilization by their faeces. Thus the birds themselves contribute to the alteration of their breeding habitat (SCHÄFER, 1954; GOETHE, 1968; SOBEY & KENWORTHY, 1979). As the vegetation gets denser and taller, it is avoided first by little terns, arctic terns and plovers, and then in later stages of the development also by common and sandwich terns. Thus the decline of these species in many areas can be attributed mainly to habitat change (*e.g.* for terns, Wangerooge (GROSSKOPF, 1962, 1968); Scharhorn (TEMME, 1967); Minsener Oldeoog (RITTINGHAUS, 1979); Knechtsand (WIETFIELD *et al.*, 1984; GLUTZ & BAUER, 1982). With the further advance of plant cover, herring gulls, too, begin to avoid such areas (BECKER & ERDELEN, 1986).

With these habitat changes, areas for breeding terns have become scarcer, whereas those for other species such as gulls have increased (BECKER & ERDELEN, 1987). Coastal stabilization and land reclamation measures resulted in increased coastal stability, inhibiting the development of high sands and drifting dunes (*e.g.* LUCK, 1976; JOENJE *et al.*, 1976; DIJKEMA *et al.*, 1980; EISMA, 1980; DIJKEMA & WOLFF, 1983).

Few new breeding sites for bird species adapted to sands and primary dunes have developed. Exceptions are Knechtsand Island and the enlargement of Minsener Oldeoog through the depositing of sand dredged from the Jade. Both have become important breeding areas (RITTINGHAUS, 1979; BECKER & ERDELEN, 1987; TAUX, 1984, 1986).

The terns' habitats are further threatened by human recreation, especially on the eastern end of the East Frisian Islands, where extensive sand flats are situated. Disturbance of terns during colony formation and the breeding period by man has not yet been controlled through the establishment of the Niedersachsisches Wattenmeer national park. If the future of the tern species' populations in the Wadden Sea area is to be secured, it will be essential to protect sandy areas against human disturbance, to create appropriate breeding habitats (see the example of Minsener Oldeoog) and to introduce biotope management. Similar problems exist elsewhere around the North Sea for terns and gulls.

Flooding is a major hazard to seabirds breeding on the low-lying island and salt marshes along the Wadden Sea, and other North Sea coasts. This is especially true for terns which build their nests only a few cm above mean high water level (*e.g.* GLUTZ & BAUER, 1982; VEEN, 1977; BECKER & ANLAUF, 1988b). Between 1951 and 1965 there were only six years in which common and arctic terns breeding on the island of Wangerooge did not suffer considerable losses: in two years where high water exceeded 1 m above mean high water level, breeding failed totally (GROSSKOPF, 1968). The decrease in tern populations of the flood-prone areas of Wangerooge in the 1960s and 1980s (BECKER, unpubl.) is probably a result of heavy breeding losses caused by flooding, and there are other examples.

Terns and gulls are specially adapted to minimize losses through flooding. On the tidal salt marshes they colonize the highest sites at the water's edge (BECKER & ANLAUF, 1988b), and if they suffered losses due to flood, tended to select more elevated areas for replacement clutches or for their colony site in the following year. During or after a flood common terns are capable of rolling their own or other eggs back into the nest; they are able to build a new nest under those eggs which have been swept away (BECKER, unpubl.); they dig out eggs which have been silted over (RITTINGHAUS, 1979) or they reinforce and raise their nests (GOETHE, 1939; BECKER, unpubl.; GLUTZ & BAUER, 1982; MONTEVECCHI, 1978; BURGER, 1980; BURGER & SHISLER, 1980). A further adaption in the common tern is the prompt production of a replacement clutch by a large proportion of the breeding colony, 9–14 days after losing eggs or chicks in floods (BECKER & ANLAUF, 1988b). Twice in 1987 all clutches in Augustgroden were destroyed by flooding. This led to three laying cycles in which almost the entire common tern colony participated; even their third attempt to breed was in the end thwarted by another flood at the end of July (BECKER, unpubl.).

Since 1978 tidal flood disasters occurred more frequently than before (BECKER & ANLAUF, 1988b), and were associated with greater wind forces and higher mean high water levels. These might relate to the rise in mean sea level which since 1970 has been increasing much more quickly (60–70 cm per century) than during the last 100 years (25 cm). Predictions of future rises vary between 0.56 and 3.45 m by the year 2100 (LUCK, 1976; VEENSTRA, 1980). Should this eventuate the flood hazard to species of terns, gulls and waders will increase to such an extent that even the above mentioned adaptions to occasional flooding will cause to be effective.

Because of the frequency of high wind velocity in the Wadden Sea another serious mortality factor for terns breeding on high sands is the smothering of clutches or chicks through sand drift (GLUTZ & BAUER, 1982). Little and common terns rapidly re-excavate their eggs (GOETHE, 1932; MARPLES & MARPLES, 1943; RITTINGHAUS, 1979), but their young quickly perish when sanded over. There are unfortunately no exact data for the extent of sand drift losses. According to GOETHE (1939) all 46 clutches of little terns breeding on Mellum in 1926 were destroyed by sand drift, and SCHULZ (1947) reports that in the years 1941 and 1942 common tern broods were also lost.

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APPENDIX

SCIENTIFIC NAMES OF SEABIRDS

GAVIIDAE

Gavia stellata	(Pontoppidan)	Red-throated Diver
Gavia arctica	(Linnaeus)	Black-throated Diver
Gavia immer	(Brünnich)	Great Northern Diver

PODICIPEDIDAE

Podiceps cristatus	(Linnaeus)	Great Crested Grebe

PROCELLARIIDAE

Fulmarus glacialis	(Linnaeus)	Fulmar
Puffinus griseus	(Gmelin)	Sooty Shearwater
Puffinus puffinus	(Brünnich)	Manx Shearwater

HYDROBATIDAE

Hydrobates pelagicus	(Linnaeus)	Storm Petrel
Oceanodroma leucorhoa	(Vieillot)	Leach's Storm Petrel

SULIDAE

Sula bassana	(Linnaeus)	Gannet

PHALACROCORACIDAE

Phalacrocorax carbo	(Linnaeus)	Cormorant
Phalacrocorax aristotelis	(Linnaeus)	Shag

ANATIDAE

Somateria mollissima	(Linnaeus)	Eider
Clangula hyemalis	(Linnaeus)	Long-tailed Duck
Melanitta nigra	(Linnaeus)	Common Scoter
Melanitta fusca	(Linnaeus)	Velvet Scoter
Mergus serrator	Linnaeus	Red-breasted merganser
Mergus merganser	Linnaeus	Goosander

STERCORARIIDAE

Stercorarius pomarinus	(Temmick)	Pomarine Skua
Stercorarius parasiticus	(Linnaeus)	Arctic Skua
Catharacta skua	(Brünnich)	Great Skua

LARIDAE

Larus minutus	Pallas	Little Gull
Larus ridibundus	Linnaeus	Black-headed Gull
Larus canus	Linnaeus	Common Gull
Larus fuscus	Linnaeus	Lesser Black-backed Gull
Larus argentatus	Pontoppidan	Herring Gull
Larus glaucoides	Meyer	Iceland Gull
Larus hyperboreus	Gunnerus	Glaucous Gull
Larus marinus	Linnaeus	Great Black-backed Gull
Rissa tridactyla	(Linnaeus)	Kittiwake
Sterna sandvicensis	Latham	Sandwich Tern
Sterna hirundo	Linnaeus	Common Tern
Sterna paradisaea	Brünnich	Arctic Tern
Sterna albifrons	Pallas	Little Tern

ALCIDAE

Uria aalge	(Pontoppidan)	Guillemot
Alca torda	Linnaeus	Razorbill
Cepphus grylle	(Linnaeus)	Black Guillemot
Alle alle	(Linnaeus)	Little Auk
Fratercula arctica	(Linnaeus)	Puffin