MULTI-SPECIES FEEDING ASSOCIATIONS IN NORTH SEA SEABIRDS: JOINTLY EXPLOITING A PATCHY ENVIRONMENT

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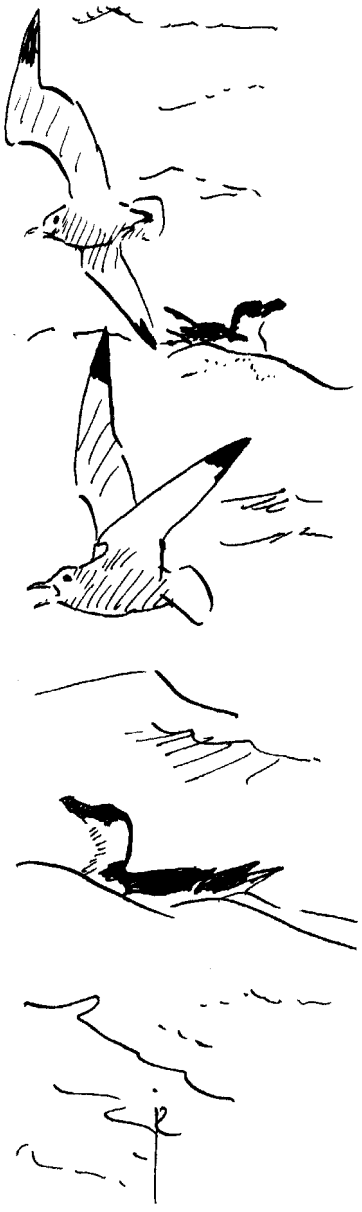

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We studied the foraging distribution and the formation of multi-species feeding associations of seabirds and marine mammals off the British east coast. The local top-predator community comprised *c.* 34 species of seabirds, two pinnipeds and eight cetaceans. It appeared that multi-species feeding associations (MSFA's) , with rather low species richness and diversity, were commonly formed around fishing vessels, were attracted by or otherwise associated with cetaceans (MSFA's with a generally low but more variable species richness and moderate diversity) and occurred over natural resources, apparently mainly fish shoals (MSFA's with the highest species richness and diversity). Small, short-lived MSFA's were the commoner type, particularly those over natural prey (sandeels and small clupeoids). Black-legged Kittiwakes *Rissa tridactyla* acted as catalysts in these flocks, Common Guillemots *Uria aalge* and Razorbills *Alca torda* as diving producers, apparently driving up fish towards the surface. The specific role of all other species joining in is described in general terms. Typical associations with marine mammals were those in which the cetaceans (mainly White-beaked Dolphins *Lagenorhynchus albirostris* and Harbour Porpoises *Phocoena phocoena*) operated as 'beaters' for Northern Gannets *Morus bassanus* and Black-legged Kittiwakes.

The functioning of MSFA's is decribed from two angles. First of all, MSFA's are prominent phenomena on the sea surface, guiding seabirds using visual cues for food finding. Secondly, perhaps more importantly, the differentiation of feeding methods deployed in MSFA's may facilitate seabirds to reach prey that would otherwise be unavailable for them. It is suggested that the frequent associations of Kittiwakes and auks are the most sustainable system, because commensalism is the underlying mechanism rather than competition. The participation of scroungers in these flocks (Herring Gulls *Larus argentatus* as common nearshore examples) normally ruined the MSFA formation in no time. Usually, a MSFA would usually collapse as soon as the auks gave up their synchronised feeding activities. This underlines the essential role of Alcidae in these formations. The MSFA's are common and prominent in the North Sea and they deserve further study in the context of when interspecific relationships and the structuring of seabird communities.

Key words: *Rissa tridactyla* - *Alca torda* - *Uria aalge* - *Morus bassanus* - *Larus argentatus* - *Phocoena* - *Lagenorhynchus* - *Balaenoptera* - feeding - multi-species feeding associations - patch exploitation - commensalism - sandeels

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INTRODUCTION

Ship-based surveys in the North Sea conducted since the late 1970s, have resulted in a considerable amount of data on the distribution of seabirds at sea (Tasker *et al.* 1987; Camphuysen & Leopold 1994; Skov *et al.* 1995; Stone *et al.* 1995). The data have been used first and foremost to identify areas that are particularly vulnerable for surface pollutants such as oil (Carter *et al.* 1993; Skov & Durinck 1992; Webb *et al.* 1995). Foraging distributions and particularly the foraging strategies of seabirds in the North Sea have so far received very little attention. This is odd, given that the ecology of seabirds at sea appears relevant to help explain phenomena like seabird wrecks, recruitment failures and trends in adult survival (Blake 1983, 1984; Swann *et al.* 1989; Camphuysen 1990; Dunnet *et al.* 1990). Such knowledge is critical to develop a responsible fisheries management (Bailey 1991; Bailey *et al.* 1991; Gislason 1993; Anon. 1994; Furness & Tasker 1997).

In a recent research project (Modelling the Impact of Fisheries on Seabirds, MIFOS), conducted off the British east coast in 1997 and 1998, it was necessary that feeding or foraging seabirds could be separated from (presumably) non-feeding individuals. Standard recording methods were slightly modified to achieve this. It appeared that foraging and feeding concentrations could be easily located and described in detail. Another finding was that seabirds commonly gathered in flocks to feed and often formed multi-species feeding associations (MSFA's). These findings triggered the analysis of a much larger data set, including re-coded older data (1987-96), and inspired the analysis presented here.

Many foraging seabirds search for underwater prey from above the water and, without further cues, prey are usually not detected from a distance (Eriksson 1979). MSFA's may play an important role in the visual food-finding of seabirds. Studies of MSFA's along the American west coast have shed light on the composition, structure and dynamics of such flocks (Sealy 1973; Hoffman *et al.* 1981; Porter & Sealy 1981; Duffy 1983; Haney *et al.* 1992; Maniscalco 1997), and on the specific role of certain species in mixed-species assemblages (Bayer 1983; Grover & Olla 1983; Chilton & Sealy 1987; Hunt *et al.* 1988; Mahon *et al.* 1992; Mills 1998; Ostrand 1999). Apparently, many MSFA's were formed by surface feeding or shallow plunging seabirds over concentrations of prey driven to the surface by underwater predators (e.g. predatory fish, cetaceans, seals or seabirds). These observations suggest that these flocks may also represent an important behavioural mechanism in the exploitation of resources of food that are 'normally' out of reach for surface feeding seabirds.

In this paper we describe and discuss what the attraction or potential benefit might be for MSFA participants to operate in multi-species feeding assemblages and how and what, if any, common resources are exploited in the commonest types of these flocks. We use field data collected between 1987 and 1998 in late summer off the English and Scottish east coast to describe the foraging distribution of seabirds and to examine where and when MSFA's are most apparent. Using recent literature on seabird flocks, we will show how the commoner types of MSFA could best be classified. How MSFA's are formed, which species normally participate, and what the specific role is of participants in the commoner forms of MSFA's is addressed by using field observations of the authors during dedicated observations in 1997 and 1998, supplemented by re-coded earlier data.

STUDY AREA AND METHODS

This study covers the north-western North Sea (54-59°N; 4°W-2°E; Fig. 1), an area with very large numbers and a great variety of seabirds (Lloyd *et al.* 1991; Skov *et al.* 1995) and only late-summer surveys were analysed (July - September, 1987-98 data). Ship-based surveys were conducted using strip-transect counts, which were developed as a standard for the North Sea (Tasker *et al.* 1984). Counts were conducted outside, from the top-deck of the ship during steaming by one or

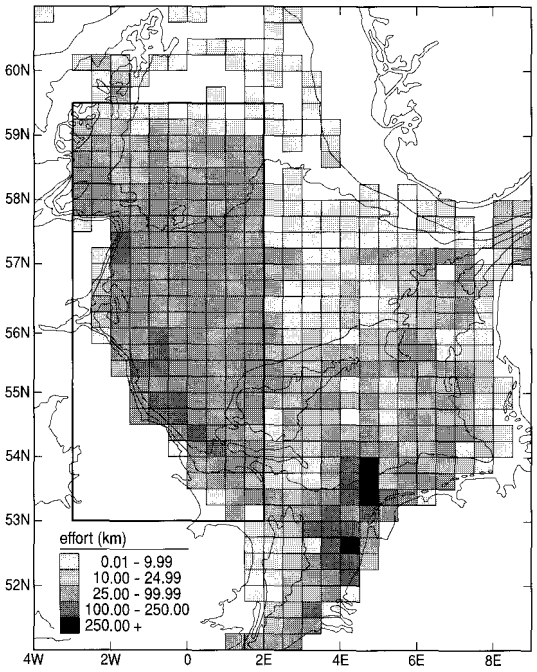

Fig. 1. Observer effort (km^2 surveyed) per quarter ICES square (15' latitude x 30' longitude) and study area off the Scottish east coast, July-September, 1987-98 (data NIOZ, IBN-DLO, CSR *Consultancy*).

two observers, operating a 300 m wide transect on one side and ahead of the ship. Birds were normally discovered with the naked eye and identified by using binoculars. Standard counting units were 10-minute periods and all swimming birds or birds touching the water within the transect were used to calculate densities (n km^{-2}). Simultaneously, a 180° scan of the area ahead of the ship was used to record scarcer species and marine mammals, again following methods described in Tasker *et al.* 1984). The scan was used to enlarge the sample of feeding frenzies and multi-species feeding associations, but data of which were not used to calculate densities. Since 1997, survey methods were modified, so that also the behaviour of seabirds was recorded, coded and stored into the database. Older data needed to be re-processed, so that details of foraging behaviour in the observed seabirds, as they were scribbled on the margins of the original recording forms, could be entered into the database.

Following the descriptions of Ashmole (1971) we recognised nine types of feeding behaviour (Table 1). Aerial pursuit was typical for kleptoparasites such as skuas Stercorariidae, dipping or

Table 1. Foraging behaviour recorded during recent ship-based surveys (basically following Ashmole 1971), and overall classification used in this study.

behaviour shortname	description	classification
aerial pursuit	stealing prey from other birds, or killing other birds	surface feeding
scavenging	picking up prey behind fishing vessels	surface feeding
dipping	picking up prey while airborne or pattering	surface feeding
surface seizing	picking up prey while swimming at surface or scavenging at corpse of bird or (marine) mammal	surface feeding
shallow plunging	catching prey by shallow plunge dive, birds remain visible (<2m depth)	shallow plunging
deep plunging	catching prey by deep plunge dive, birds shortly disappear under water (2-20m depth)	deep plunging
pursuit plunging	catching prey by deep pursuit dive started from the air	deep plunging
pursuit diving	catching prey by deep diving from the surface, either feet- or wingpropelled	deep diving
searching	circling seabirds, head down in flying terns and Gannets, underwater peering auks	

Table 2. Three types of MSFAs (following Hofmann *et al.* 1981) and five forms of associations between cetaceans and seabirds (following Pierotti 1988a).

Multi-species feeding associations	(Hoffman *et al.* 1981)
Type I	small, short-lived flocks over tightly clumped prey
Type II	larger and longer-lasting flocks formed over prey that apparently do not act as cohesive units
Type III	very large flocks formed where local water-mass discontinuities involved downwelling, concentrating zooplankton and small fish
Forms of association between seabirds and marine mammals	**(Pierotti 1988a)**
Type A	birds and mammals that occur in close proximity to one another, but do not appear to interact
Type B	cetaceans and birds that seem to be attracted to the same resource, but do not show any positive attraction to each other
Type C	birds that appear to be actively drawn to marine mammals because of the foraging activities of the mammals drive or otherwise force prey to the surface where birds have access to a resource that would otherwise be unavailable
Type D	birds scavenging by-products of marine mammals (e.g. scraps of prey, faeces)
Type E	marine mammals as predators of seabirds; birds showing avoidance behaviour

pattering was mainly observed in small gulls *Larus* and *Rissa* and storm petrels Hydrobatidae. Surface seizing included pecking of small prey at the surface as well as scavenging carrion (mainly Northern Fulmars *Fulmarus glacialis* and large *Larus*-gulls). Pursuit plunging was typical for shearwaters *Puffinus*, although it occasionally occurred in the larger auks. Surface plunging was mainly restricted to terns *Sterna* and small gulls, while deep plunging was more typical for Northern Gannet *Morus bassanus*. Pursuit diving in auks, cormorants *Phalacrocorax*, and divers Gaviidae needed to be distinguished from escape behaviour and particularly this form of feeding behaviour required an extra observer on board. Scavenging at fishing vessels is a form of feeding not listed by Ashmole (1971), while we also added 'actively' searching for prey (head down and often circling of Northern Gannet, gulls and terns, underwater peering in auks). The seabird community was divided in four major groups: surface feeders (aerial pursuit, dipping, surface seizing/pecking), shallow plunge divers, deep plunge divers (including pursuit plungers) and pursuit divers. Scavenging seabirds at fishing vessels, or birds clearly interested in or otherwise associated with nearby fishing vessels were treated separately.

All birds, whether swimming or flying, that operated 'together' or stayed tight in a particular area or in a particular movement were marked as distinct 'flocks'. Flocks comprising more than one species were named 'multi-species (feeding) associations' (MSFA's). Hoffman *et al.* (1981) grouped the Alaskan and Washington seabird flocks into three types on the basis of flock size and longevity and the nature of the food source (Table 2). We found that, in most cases, the boundaries of small flocks were obvious. In case of some larger flocks, covering a large area, the smaller units were usually recognised by the field worker, while the larger assembly was not recorded. Using Hoffman's classifications, we believe that Type I MSFA's will seldom have been overlooked during our fieldwork. Larger and longer-lasting flocks formed over prey that apparently do not act as cohesive units (Type II and III) could often only be recognised with hind-sight, and certainly not for all data, because these require hydrographical observations on the spot. Type II MSFA's, besides those immediately recognised in the field, were searched for in the database by lifting high num-

Table 3. The role of seabirds (or marine mammals) in multi-species feeding associations, using terms, categories and classifications proposed by others.

term proposed	description	remarks	source
catalysts	species whose feeding behaviour is highly visible to others	catalysts usually initiate feeding flocks by indicating feeding opportunities to other birds; initiators in the definition of Bayer (1983)	Hoffman *et al.* 1981
divers	species that employ pursuit diving and pursuit plunging		Hoffman *et al.* 1981
kleptoparasites	species that join flocks to steal prey from other birds	joiners in the definition of Bayer (1983)	Hoffman *et al.* 1981
surpressors	species whose presence decreases the availability of prey to other group members	joiners in the definition of Bayer (1983)	Hoffman *et al.* 1981
initiators	the first two birds forming a flock		Bayer 1983
joiners	all birds that join a flock after the initiators	scroungers in the definition of Barnard & Sibly 1981; Beauchamp & Giraldeau 1996	Bayer 1983
producers	seabirds actively searching for food (1983)	initiators in the definition of Bayer e.g. Barnard & Sibly 1981;	Beauchamp & Giraldeau 1996
scroungers	birds exploiting patches discovered by producers	joiners in the definition of Bayer (1983)	e.g. Barnard & Sibly 1981; Beauchamp & Giraldeau 1996
beaters	seabirds or marine mammals disturbing prey that subsequently becomes available for other predators		e.g. Evans 1987; Källander 1998

bers (100+) of seabirds in consecutive series of counts and examining the (foraging) behaviour of the birds and marine mammals recorded.

Seabirds were often seen accompanying cetaceans and marine mammals were observed joining feeding frenzies of seabirds. Pierotti (1988a) suggested five types of associations between seabirds and marine mammals (Table 2). We have ignored type A, the simplest form and involving birds and mammals that occur in close proximity to one another, but do not seem to interact. We have never seen attempts of marine mammals to actually try to catch and kill any seabirds during any of our surveys in the North Sea (Type E). We have classified all our observations using the remaining categories, as to types B (prey sharing), C (profiting) or D (scavenging).

The role of (sea-)birds in MSFA's has led to

several classifications (Table 3). In a system proposed by Hoffman *et al.* (1981), *'catalysts'* are those species whose feeding behaviour is highly visible to others. Catalysts usually initiated feeding flocks and other flocking species used catalysts as indicators of feeding opportunities. Seabirds labelled as *'divers'* include those species that employ pursuit diving and pursuit plunging in prey captures. A third category was *'kleptoparasites'*, species that join flocks to steal prey from other birds. The last group was *'suppressors'*, species whose presence decreases the availability of prey to other group members. Bayer (1983) distinguished flock *'initiators'* and *'joiners'*. Flock initiators were the first two birds in a flock, joiners were all the other birds that came in later. Whether or not to search for food is a frequency dependent problem for social foragers and this has been modelled as a 'producer-scrounger' (PS) game (Barnard & Sibly 1981, Beauchamp & Giraldeau 1997). In a PS system, individuals either search for food patches (*producers*) or exploit patches discovered by others (*scroungers*). To avoid introducing new definitions again, we try and apply the terms listed in Table 3 where appropriate.

MSFA's were formed around fishing vessels (scavenging seabirds), in association with cetaceans (Type B or C assemblages) and around sources of more natural prey (fish, plankton, carrion). For the smaller (type I) MSFA's, species richness (the number of species in these flocks), and heterogeneity (or diversity; evenness of the relative abundance's of the species observed) were examined and compared between these three categories. Species richness was calculated using the Jack-knife Estimate ($\hat{S}$; Krebs 1989):

$$(\hat{S}) = s + (\frac{n-1}{n})^k$$

where s is the observed total number of species in n MSFA's sampled, and k is the number of unique species (occurring in a single MSFA). The variance of this estimate is given by:

$$\mathrm{var}(\hat{S}) = \left[(\frac{n-1}{n}) \sum_{j=1}^{s} (j^2 f_j) - \frac{k^2}{n}\right]$$

where f_j is the number of MSFA's containing j unique species, so that the 95% confidence interval can be presented for each estimate. As a non-parametric measure of diversity we used the Simpson's Index (D) of heterogeneity:

$$D = \Sigma p_i^2$$

where p_i is the proportion of species I in the community (Krebs 1989).

RESULTS

Seabird community and generalised distribution patterns

The offshore seabird community off the British east coast consists of approximately 34 species of seabirds (Table 4). Further top-predators in the area that were recorded during our surveys were 10 species of marine mammals (8 cetaceans, 2 pinnipeds; Table 4). Among the seabirds, all types of feeding behaviour listed in Table 1 were frequently represented in at least two species. Pursuit plunging, only known from shearwaters, which are rather scarce in these waters, was the rarest type of foraging behaviour observed. Surface feeding seabirds occurred scattered over the study area and this type of foraging was the most prominent form at greater distances from the coast (Fig 2A). Deep plunging (Northern Gannets) and pursuit plunging seabirds (shearwaters), probably exploiting prey down to a depth of 20-30 m, occurred in low densities overall, with slightly higher concentrations east and south-east of the gannetry of Bass Rock (Fig 2C). Shallow plunging seabirds, feeding on prey at a maximum of perhaps 2m, and deep pursuit diving seabirds, which could probably reach the bottom during feeding in most of if not in all our study area, occurred highly concentrated in a band off Orkney, in the Moray Firth, off the Scottish east coast,

Table 4. Relative abundance (%) of seabirds (n= 265 326 individuals) and marine mammals (n= 1737 herds) recorded during ship-based surveys off the British east coast, 1987-98, the common feeding method of each seabird and its occurrence (%) in Type I multi-species feeding associations (MSFAs) engaged in 'natural feeding' (n= 42,915 seabirds, 71 cetacean herds), around cetaceans (n= 1837 seabirds, 178 cetacean herds), and in association with fishing vessels (n= 45,505 seabirds, 5 cetacean herds). An * indicates species that deploy scavenging at fishing vessels frequently next to their more 'natural' feeding strategy.

Group		spec.	common feeding method	relative abundance	nat.feed	MSFAs cetaceans	trawlers
divers	*Gavia spp.*	3	pursuit diving	0.0			
Black-browed Albatross	*Thalassarche melanophrys*	1	surface seizing	0.0	0.0		
Northern Fulmar	*Fulmarus glacialis*	1	surface seizing*	29.0	4.1	5.9	62.5
Sooty Shearwater	*Puffinus griseus*	1	pursuit plunging	0.1	0.1	0.7	0.0
Manx Shearwater	*P. puffinus*	1	pursuit plunging	0.1	0.2		
Storm Petrel	*Hydrobates pelagicus*	1	dipping	0.3	0.4	0.8	0.1
Leach's Petrel	*Oceanodroma leucorhoa*	1	dipping	0.0	0.0		
Northern Gannet	*Morus bassanus*	1	deep plunging*	7.8	2.9	50.9	6.8
Cormorant	*Phalacrocorax carbo*	1	pursuit diving	0.0			
Shag	*Stictocarbo aristotelis*	1	pursuit diving	0.0	0.0		
phalaropes	*Phalaropus spp.*	2	surface seizing	0.0			
Pomarine Skua	*Stercorarius pomarinus*	1	aerial pursuit	0.0	0.1		0.0
Arctic Skua	*S. parasiticus*	1	aerial pursuit	0.2	0.2		0.0
Long-tailed Skua	*S. longicaudus*	1	aerial pursuit	0.0	0.1		
Great Skua	*S. skua*	1	aerial pursuit	0.6	0.3	0.7	0.4
Little Gull	*Larus minutus*	1	dipping	0.2	0.9	1.1	
Black-headed Gull	*L. ridibundus*	1	dipping	0.1	0.0	0.1	0.0
Common Gull	*L. canus*	1	dipping	0.1	0.0	0.1	0.1
Lesser Bl.-backed Gull	*L. graellsii*	1	surface seizing*	0.5	0.3		1.2
Herring Gull	*L. argentatus*	1	surface seizing*	1.2	1.7	1.4	3.4
Great Bl.-backed Gull	*L. marinus*	1	surface seizing*	3.2	0.7	3.3	12.1
other Larus gulls	*Larus spp.*	2	dipping/surf. s.	0.0			
Black-legged Kittiwake	*Rissa tridactyla*	1	shallow plunging*	16.9	41.0	33.0	13.2
Sandwich Tern	*Sterna sandvicensis*	1	shallow plunging	0.0	0.0		
Arctic Tern	*S. paradisaea*	1	shallow plunging	0.2	0.1	0.3	
Common Tern	*S. hirundo*	1	shallow plunging	0.1	0.0		0.0
other terns	*Sterna/Chlidonias spp.*	2	shallow pl./dipping	0.0	0.0		
Common Guillemot	*Uria aalge*	1	pursuit diving	32.1	36.1	1.9	0.1
Razorbill	*Alca torda*	1	pursuit diving	3.8	8.0	0.1	
Atlantic Puffin	*Fratercula arctica*	1	pursuit diving	3.6	2.8		
other auks	*Alle/Cepphus*	2	pursuit diving	0.0			
Number of species:				(34)	(25)	(14)	(15)
Fin Whale	*Balaenoptera physalus*	1		0	1		
Minke Whale	*Bal. acutorostrata*	1		16	14	9	
Bottle-nosed Dolphin	*Tursiops truncatus*	1		0			
Common Dolphin	*Delphinus delphis*	1		0		1	
White-beaked Dolphin	*Lagenorhynchus albirostris*	1		21	21	35	20
White-sided Dolphin	*Lag. acutus*	1		2	6	6	
Risso's Dolphin	*Grampus griseus*	1		0			
Harbour Porpoise	*Phocoena phocoena*	1		54	49	48	40
Grey Seal	*Halichoerus grypus*	1		5	8	1	40
Harbour Seal	*Phoca vitulina*	1		1		1	0
Number of species:		10		(10)	(6)	(7)	(4)

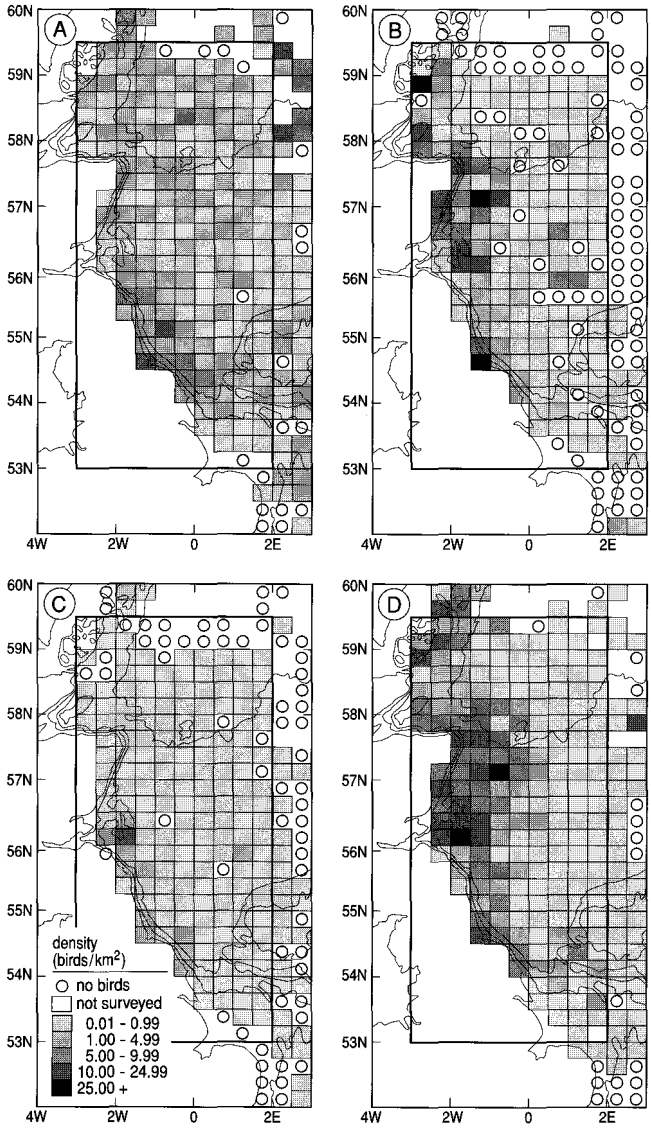

Fig. 2. Distribution of (A) surface feeding seabirds (e.g. Northern Fulmar, Great Black-backed Gull), (B) shallow plunge diving seabirds (e.g. Black-legged Kittiwake, Arctic Tern), (C) deep plunge diving or pursuit plunging seabirds (e.g. Sooty Shearwater, Northern Gannet), and (D) deep pursuit diving seabirds (e.g. Cormorant, Common Guillemot) off the British east coast, Jul-Sep 1987-98. Seabirds associated with fishing vessels were excluded from the analysis.

over Wee Bankie (shallow banks off the Firth of Forth) and locally off the English east coast (Fig. 2B, 2D).

Deep pursuit diving seabirds dominated the scene, both numerically (39%) as in terms of biomass (35%), closely followed by surface feeding seabirds (35% and 32% respectively). Shallow plunging seabirds, albeit quite important numerically (18%), formed only 7% of the seabird biomass in this area. The reverse was true for deep plunging seabirds (mainly the 'heavy' Northern Gannets), which formed only 8% of the total numbers of seabirds recorded, but 25% of the total biomass.

The overall distribution patterns observed in this part of the North Sea can be summarised as follows (Fig. 3). A broad band with high densities of seabirds and with a great variety of species (shearwaters, gannets, cormorants, gulls, terns and auks) along the coast. Within this area, colony

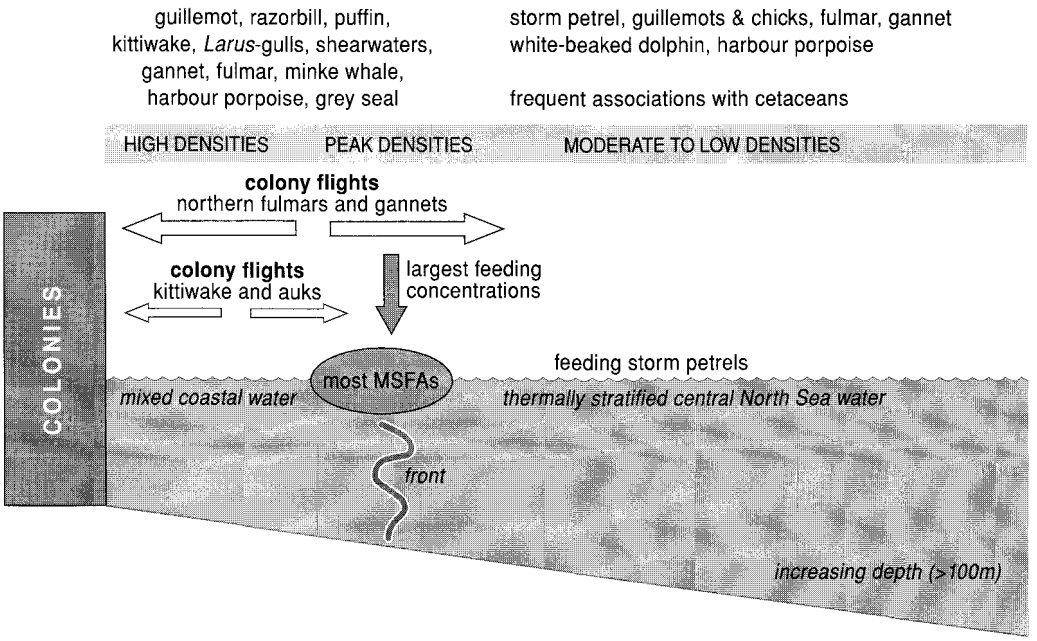

Fig. 3. Schematic representation of the seabird community off the British east coast, late summer (see text).

flights (movements to and from the breeding stations) were common. Next to this coastal zone, less obvious in places and at times (tidal cycle?), was a rather narrow strip with very high densities of seabirds (sometimes over 1000 km^{-2}), with proportionally many individuals either feeding or searching. The seabird community in this zone was dominated by shallow plunge feeding seabirds (mainly Black-legged Kittiwakes *Rissa tridactyla*) and deep pursuit diving species (mainly Common Guillemot and Razorbill). This band coincided with the hydrographical frontal zone between thermally mixed coastal waters, characterised by a relative low surface temperature (Pingree & Griffiths 1978), and stratified offshore waters, with higher surface temperatures, a cold bottom layer and a thermocline usually at 30-40 m depth. Further offshore, overall seabird densities were rather low and Northern Fulmars and Storm Petrels dominated the community. Northern Gannets roamed this offshore area in substantial numbers (but low densities), and 'father-chick' combinations of Common Guillemots occurred widespread and in large numbers. Colony flights of auks, gulls and terns were not seen at the offshore side of the front. Pursuit diving seabirds and shallow plunge divers were virtually confined to the nearshore and frontal zones, with impressive concentrations and mass feedings at or around the front. Surface feeders and deep plungers such as Northern Gannets were more widespread and for these the front was apparently of limited importance.

Multi-species feeding associations (Type I)

Multi-species flocks of seabirds of the smallest type were observed in association with fishing vessels (n= 162), with cetaceans (n= 150) and as self-sustained ('natural') assemblages (n= 1777). MSFA's around fishing vessels were comparatively large, and Northern Fulmars, Black-legged Kittiwakes, Northern Gannets, Great Black-backed Gulls *Larus marinus* and Great Skuas *Stercorarius skua* were particularly numerous (Table 4). Species richness in MSFA's around fishing vessels was estimated at $\hat{S}$= 16.0 ± 1.96 (Jack-knife

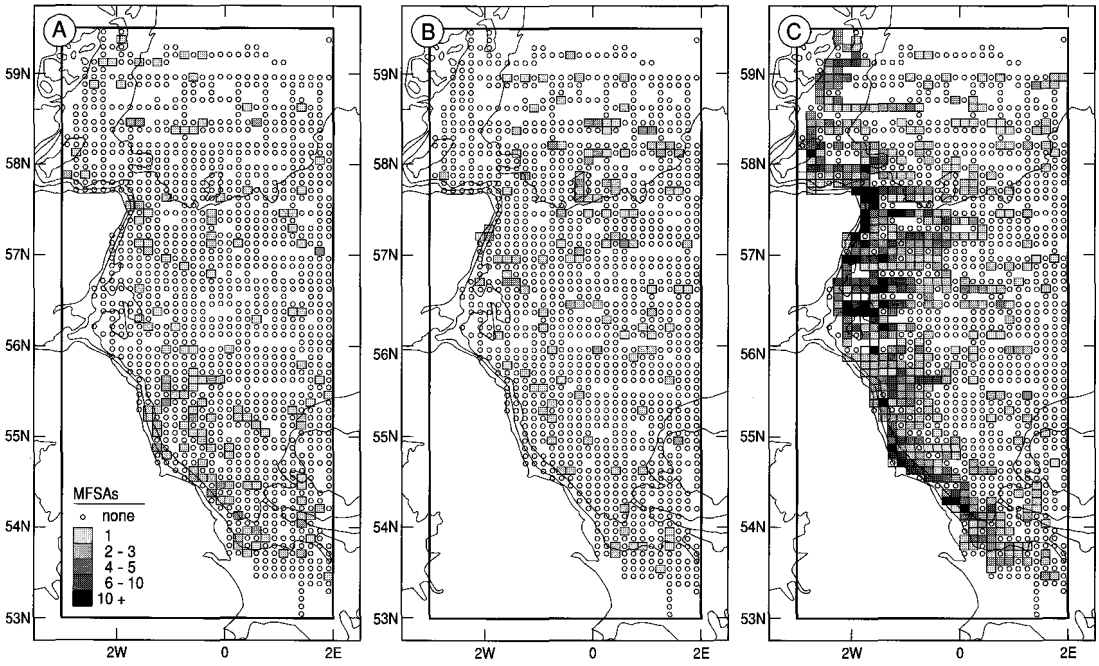

Fig. 4. Occurrence of multi-species feeding associations (number of flocks per 10' longitude x 5' latitude square) around fishing vessels (A), around cetaceans (B) and under 'natural' conditions (C), July-September, 1987-98.

estimate and 95% confidence interval; see methods), the heterogeneity was rather low (Simpson's Index D= 0.57). The spatial distribution of these flocks (Fig. 4A) closely followed the distribution of commercial fishing vessels working the area, which were particularly numerous off the English east coast.

MSFA's around cetaceans were those where the whales attracted birds (Type C and D; Table 2; Pierotti 1988a), not flocks where whales and birds were simply attracted to the same resource. On four occasions (seabirds in association with Minke Whales), there might have been an attraction to a common resource rather than any interaction between birds and mammals (Type B), but in the absence of firm evidence these flocks were included here. Harbour Porpoises *Phocoena phocoena* and White-beaked Dolphins *Lagenorhynchus albirostris*, the commonest hosts of these associations occurred both offshore and inshore in appreciable numbers. Most seabirds in association with cetaceans were Northern Gannets and these occurred widespread over the study area, but particularly over offshore waters that were thermally stratified (Fig. 4B). Species richness ($\hat{S}$= 15.0 ± 5.56 species) was similar, but more variable than that in MSFA's around fishing vessels, the heterogeneity (or diversity) was moderate (D= 0.63).

Common Guillemots, Razorbills, and Black-legged Kittiwakes were most frequently encountered in the 'natural' assemblages, the distribution of which (Fig. 4C) was very similar to the overall distribution of shallow plunge divers and pursuit diving seabirds (Fig 2B, 2D). Of these MSFA's, 1761 flocks should be categorised as Type I assemblages, 16 as Type II flocks (see below). Type I MSFA's contained a minimum of two and a maximum of eight species of seabirds and up to 673 individuals. Species richness was considerably higher than the former to types ($\hat{S}$= 26.0 ± 10.2 species), and so was the heterogeneity (D=

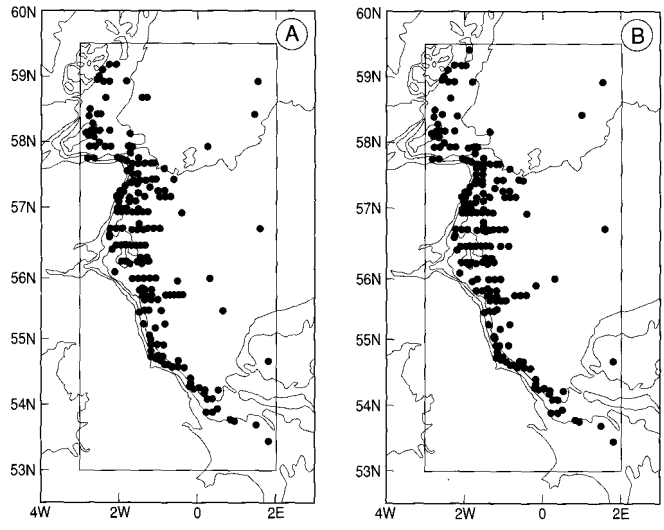

Fig. 5. Multi-species feeding associations including foraging Black-legged Kittiwakes (A) and including foraging Common Guillemots and/or Razorbills (B), July-September, 1987-98.

0.71). Seabirds in many of these 'natural' assemblages were not seen to forage or feed when (shortly) encountered at sea during the ship-based surveys. The distribution of MSFA's of this type with actively feeding or searching Black-legged Kittiwakes (Fig. 5A) or with actively feeding large auks (Razorbills or Common Guillemots; Fig. 5B) was strikingly similar, underlining the frequent co-occurrence of both groups in these flocks. Cetaceans most commonly observed in association with these flocks (Type B associations; Pierotti 1988a) were Harbour Porpoise (35 records, 112 individuals), White-beaked Dolphins (15, 47), and Minke Whales (8, 20; but see above).

Multi-species feeding associations (Type II)

During fieldwork, 16 'natural' MSFA's (not associated with fishing vessels or cetaceans) were recognised as Type II assemblages. These flocks were larger and often contained a number of Type I flocks scattered over some small area, plus a large number of mono-specific feeding flocks. Type II MSFA's, as recognised in the field, contained a minimum of 2 and a maximum of 10 species, a minimum of 40 and a maximum of 2071 individuals. With hindsight, while combining 10-minute counts with particularly high densities of birds, a total of 50 Type II MSFA's were identified and 8 of the MSFA's recognised in the field were 'embedded' in these larger assemblages of seabirds. Thirteen of these flocks were found to contain over 1000 seabirds (Table 4), and 11 of these assemblages had also attracted some marine mammals (mainly cetaceans; Type B association). On four of the occasions listed in Table 4, sandeel was definitely the attraction for the feeding seabirds and in most these groups, a vast number of birds was actually recorded as 'foraging' or 'feeding'. It is not difficult to see that Black-legged Kittiwakes and Guillemots dominated the scene in most cases, and one of the more spectacular MSFA's were nearly 13 000 seabirds (including 4200 Kittiwakes and 7900 Guillemots), of 12 species, of which 97% were actually recorded as foraging. This flock was found well offshore of Aberdeen on 19 August 1994, and was located somewhere between thermally mixed and stratified water, but the precise location of the front was not assessed that day.

The actual flock-size is underestimated by these figures, because the observations were restricted to a 300 m strip-transect with additional information from a 180° scan ahead of the ship (maximum range perhaps 1000 m). Densities of Black-legged Kittiwakes and larger auks (Guillemots

Table 5. Presence of common seabirds in MSFAs around fishing vessels, MSFAs of seabirds associated with cetaceans and in type I 'natural' (feeding) assemblages. Shown are the most numerous species, the frequency of occurrence in all MSFAs of each type (freq., %) and the mean number present in MSFAs.

	Freq.	%	mean
MSFAs around trawlers (n= 162)			
Fulmarus glacialis	126	77.8	226
Rissa tridactyla	103	63.6	58
Morus bassanus	95	58.6	33
Larus marinus	66	40.7	83
Stercorarius skua	52	32.1	3
Larus fuscus	32	19.8	17
MSFAs around cetaceans (n= 150)			
Morus bassanus	128	85.3	7
Rissa tridactyla	22	14.7	28
Fulmarus glacialis	11	7.3	10
'natural' MSFAs (n= 1761)			
Uria aalge	1334	75.8	8
Alca torda	837	47.5	4
Rissa tridactyla	767	43.6	20
Fratercula arctica	286	16.2	4
Fulmarus glacialis	262	14.9	6
Morus bassanus	219	12.4	5

and Razorbills) ranged between 6 to 1716 km^{-2} (mean density 179 km^{-2}) in 50 type II MSFA's identified with hindsight. From these figures it may be estimated that these assemblages can easily number several 10 000s of seabirds.

Multi-species feeding associations (Type III)

Strictly according to Hoffman's classification, we were unable to recognise any Type III MSFA's. The frontal zone between mixed coastal and stratified central North Sea water would generally hold very large numbers of seabirds (including multiple Type I and Type II MSFA's). This zone, which was particularly strong and obvious between 58°N and 56°N during most of our offshore surveys, could in fact qualify for a Type III MSFA ('very large flocks formed where local water-mass discontinuities involved downwelling, concentrating zooplankton and small fish', Hoffman *et al.* 1981), for it was apparently a rather predictable, albeit rather distant feeding area for birds breeding on the Scottish and English northeast coasts.

Principal prey in type I MSFA's

Feeding frenzies around fishing vessels were obviously scavenging seabirds exploiting discards and offal that were produced as part of the fishing process. Our distant observations did not permit us to examine the principal prey in any detail, but we expect that offal and small discarded roundfish were the key attractions for seabirds visiting these commercial fishing vessels (*cf.* Camphuysen *et al.* 1995a).

Of seabirds feeding in association with cetaceans, we could not often establish the prey type. Two type D associations with Minke Whales were probably seabirds feeding on the excrements of the whale (Sooty Shearwater, Northern Fulmar, and Great Skua). The common type, Northern Gannets or Black-legged Kittiwakes in type C associations with Harbour Porpoises and (White-beaked) dolphins, were probably cetaceans chasing fish towards the surface. In many cases, seabirds were simply following small herds of swimming cetaceans (head-down or circling). Most of the active feeding of seabirds (shallow or deep plunge dives) occurred when the cetaceans were apparently herding fish. We could not see any prey with certainty, except for the occasional clupeoid fish leaping out the water.

At least 73 'natural' MSFA's were seabirds exploiting tight balls of sandeels near the surface, three further flocks were feeding on fish balls near the surface which could not be identified. The very characteristic behaviour of the Black-legged Kittiwakes feeding in association with auks (see below) suggested that near-surface (small) fish schools were the main resource exploited in these MSFA's and the typical drive of most multi-species feeding frenzies. Sandeels were identified as prey within

Table 6. The largest of 50 Type II MSFAs recorded between July and September 1987-98 off the English and Scottish east coast. Shown are the numbers of Northern Fulmars, Northern Gannets, Kittiwakes, Guillemots, Razorbills, Puffins, Minke Whales, Harbour Porpoises, the presense of one (*) or more (**) visible sandeel balls as prey, the number of animals recorded, the percentage of feeding seabirds, the number of bird species and the number of species of marine mammals (mainly cetaceans).

#	Fulmar	Gannet	Kittiwake	Guillemot	Razorbill	Puffin	Minke Whale	Porpoise	sandeels	totals	% feeding	species of birds	species of cetaceans
35	240	26	4238	7906	181	357	1	7		12971	97	12	2
9	20	503	531	4211	1145	1694	28	93		8256	36	12	2
36	5	13	728	1731		2	1	3		2488	90	10	2
22	819	7	4	1404	1	6	1	3		2252	12	9	2
24	7	37	942	544	1	4				1906	64	14	0
38	27	1	997	645	67	12	2	76	**	1876	70	11	5
27	2	29	1620	94	33					1832	0	11	0
8	5	87	384	892	219	35		1		1631	37	9	3
42	10	10	929	571	17	3	3	12	**	1560	35	7	2
18	33	6	41	944	310		1			1398	74	10	1
13			242	748	224		14	6		1236	27	5	2
44	1	24	542	409	57	49	8	23	**	1134	49	8	3
10	4	2	284	553	53	158		20	*	1118	64	12	2

MSFA's on another 18 occasions (Black-legged Kittiwake, Common Guillemot, Razorbill and Atlantic Puffin), clupeoid fish were recorded once under these conditions (Razorbill). Other jointly exploited resources in MSFA's were 'large fish' (Northern Fulmar, Black-legged Kittiwake), small unidentified particles (presumably zooplankton; Northern Fulmar, Black-legged Kittiwake), and seal, whale, and bird carcasses (Northern Fulmar, Great Skua, Great Black-backed Gull).

MSFA formation and the role of different species

We will further ignore the details of MSFA's around fishing vessels, for the assemblages around fishing vessels, including dominance hierarchies among the attendants, have been amply described elsewhere on the basis of more adequate data (Hudson & Furness 1989; Camphuysen 1995; Camphuysen *et al.* 1995a; Garthe & Hüppop 1998). Of the two 'natural' MSFA's (attracted by cetaceans or comprising a number of seabird species), we describe the formation and the specific role of birds and cetaceans attracted only of the forms most commonly observed.

In most of the type I MSFA's and in all type II MSFA's comprising multiple smaller seabird flocks, a small group of auks, either Common Guillemots, Razorbills, Atlantic Puffins or a mixture of these was found. While being uncertain with respect to the Atlantic Puffins, it was very obvious that both the diving and reappearing of Common Guillemots and Razorbills was normally highly synchronised. Such small flocks of auks, most of which comprised a single species, occurred scattered over a fast area off the Scottish and English east coast, but not normally beyond the frontal zone (or over strongly stratified water; Fig. 2d). Since the auks usually triggered MSFA formation, but apparently did not play an active role in the actual development (small flocks of auks were abundant, only those detected by more aerial seabirds developed into typical MSFA's), we would describe the auks generally as 'initiators' and 'producers' rather than 'catalysts' (see also Ostrand 1999).

Over these same waters, there is a constant

Table 7. Participation of seabirds in mono- and multi-species feeding flocks attracted to 'natural' prey.

	mono-sp.	multi-sp.	all flocks	% multi-sp.	feeding method
Great Skua	4	46	50	92	aerial pursuit
Herring Gull	3	32	35	91	surface seizing
shearwaters	3	31	34	91	pursuit plunging
smaller skuas	10	57	67	85	aerial pursuit
Lesser Black-backed Gull	2	9	11	82	surface seizing
Little Gull	9	30	39	77	dipping
Common Gull	1	3	4	75	dipping
Razorbill	83	239	322	74	pursuit diving
Great Black-backed Gull	10	18	28	64	surface seizing
Kittiwake	200	332	532	62	shallow plunging
Guillemot	402	404	806	50	pursuit diving
Black-headed Gull	1	1	2	50	dipping
Northern Gannet	217	109	326	33	deep plunging
Puffin	168	66	234	28	pursuit diving
Northern Fulmar	186	66	252	26	surface seizing
terns	54	15	69	22	shallow plunging
cormorants	4	1	5	20	pursuit diving
storm-petrels	135	10	145	7	dipping

stream of searching, more aerial species such as Northern Fulmars, Northern Gannets, Black-legged Kittiwakes, terns, *Larus*-gulls (particularly near the coast), shearwaters, storm-petrels and skuas. Very many MSFA's would suddenly develop after a Black-legged Kittiwake or, less frequently, another of those searching birds showed interest in a flock of auks. A change of course and hovering of this bird over the diving auks would immediately attract other seabirds, and a MSFA was soon formed. We would categorise those birds as the actual 'catalysts' of MSFA's off the Scottish and English coast and conclude that the abundant Black-legged Kittiwake is the most important species in this respect. More species would draw in, dependent on the area where the MSFA was formed, with large gulls and skuas normally arriving rather late (both groups often operated as kleptoparasites in these flocks). The arrival of substantial numbers of large gulls (most notably Herring Gulls) was a sure sign that the MSFA would soon fall apart (suppressors). On all occasions where over 5 Herring Gulls joined a MSFA with Kittiwakes over a sandeel ball, the larger species would simply land in the middle of the feeding frenzy, on top of the fish, blocking off both the view and feeding opportunities of the smaller seabirds. A whole spectrum of seabirds can therefore be categorised as 'joiners', 'scroungers' (all aerial species), or 'suppressors' (particularly large gulls such as Herring and Great Black-backed Gull) (Giraldeau & Beauchamp 1999). We have occasionally observed Guillemots and Razorbills flying into such MSFA's.

When type I MSFA's broke-up, the Black-legged Kittiwakes, Little Gulls, Northern Gannets and Northern Fulmars normally dispersed and resumed a wide-ranging search pattern. Species such as Herring Gull, Great Black-backed Gull and Great Skua usually sat on the water at the old flock site until a new MSFA began to form within sight. These observations underline that the former four species are normally the catalysts in this system, while the latter were joiners. Kleptoparasitism was a feeding strategy that was more typical for the latter group, although Black-legged Kittiwakes and Northern Gannets were occasionally seen to sneak away fish picked up by others.

The importance of MSFA's for seabirds

Some species of seabirds foraging off the British east coast showed little or no tendency to join multi-species feeding flocks, while others were nearly always observed feeding in the middle of a multi-species feeding frenzy (Table 7). Storm-petrels were normally feeding alone, away from other birds, and a low tendency to join MSFA's was also found with cormorants, terns, Northern Fulmars and Puffins (<30% of feeding flocks were MSFA's). On the other extreme, skuas, Herring Gulls, Lesser Black-backed Gulls and shearwaters were clearly aiming for these assemblages (>80% of feeding flocks in MSFA's).

DISCUSSION

On the basis of our observations, we have described the seabird community in our study area in very broad terms and with respect to feeding methods (Figs. 3-5). In the west, with a large population of seabirds breeding on mainland cliffs and small nearshore islands, the nearshore waters have the highest diversity in species of seabirds and cetaceans and feeding and foraging seabirds are abundant. Colony flights (foraging seabirds flying away from or towards the breeding sites) are common in a band of approximately 100 km along the coast. MSFA's are particularly common and relatively large in a narrow zone which was

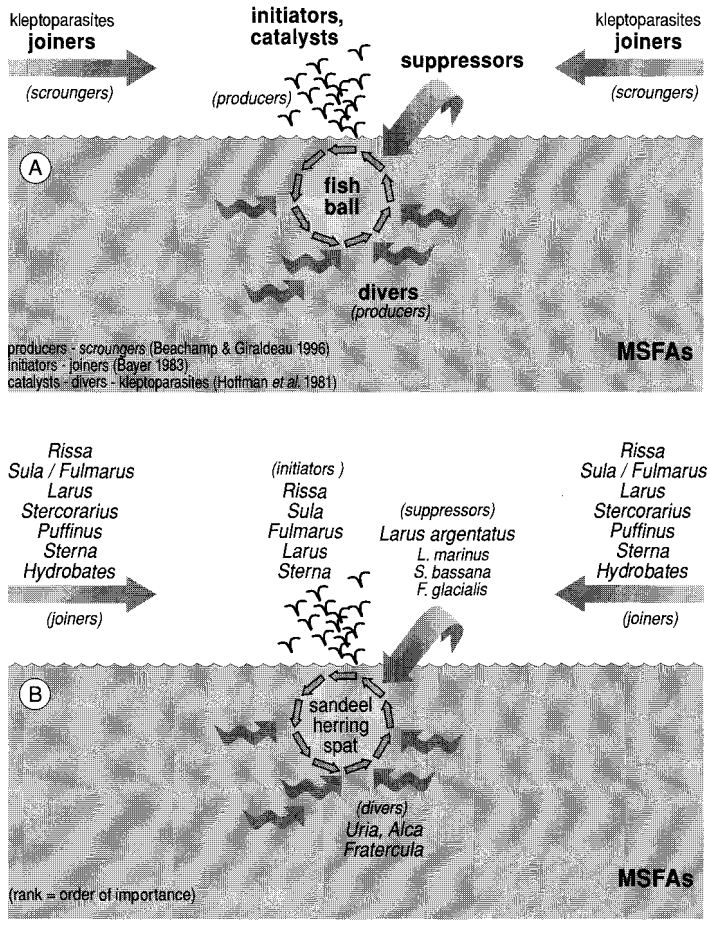

Fig. 6. Schematic representation of the commonest type of multi-species feeding associations observed off the British east coast (A) and indications of the specific role of participants (B).

often characterised as coincident with a hydrographical front between coastal mixed and thermally stratified offshore waters. Cetaceans occurred on either side of the front, but associations between seabirds and cetaceans were more common over offshore waters. Northern Fulmars and Northern Gannets commonly crossed the front on their feeding excursions. For those species the front appeared to be a feature of rather limited significance. MSFA's over 'natural' prey were attracting a greater diversity of species than those formed around fishing vessels and attracted by cetaceans. This difference is simply caused by the fact that only specialists joined MSFA's around fishing vessels (surface feeding scavengers and kleptoparasites) or were attracted by cetaceans (mainly aerial plunge diving seabirds). The MSFA's over natural prey included the complete variety of feeding techniques and, hence, virtually all seabirds working these waters.

The auks and Kittiwakes formed massive concentrations around the front, but were comparatively scarce further out to sea. The typical situation over near-front waters off the Scottish east coast and at the frontal zone was the rapid and frequent development and subsequent break-down of relatively small MSFA's. Normally, up to ten of these small 'natural' MSFA's, either still 'active' or just stopped were within view, indicating that searching time between feeding frenzies was very short. The sandeel balls observed in MSFA's were all rather small (a few meters in diameter at most). On the importance of the front itself as a generator of prey availability can so far only be speculated.

The final break-down of flocks, as far as could be observed from a moving ship, was usually caused by the auks ceasing to drive prey to the surface. Before MSFA's fell apart, there was a constant entering and leaving of seabirds from and to the flock, suggesting intense competition or at least interference. Although the presence of predatory fish cannot be excluded, the observations suggest that pursuit diving species in the local seabird community were successfully generating near-surface fish schools (fish balls), offering themselves and other species rich feeding opportunities (Fig. 6). The establishment of MSFA's in relatively deep water may explain why seabirds of very different entity, and including surface feeding species or shallow plunge divers, can exploit demersal fish such as sandeels as staple food. It is tempting to speculate that the presence of feeding auks is crucial for Kittiwakes to feed so far away from their colonies over very deep water, on prey that would normally be out of reach. It could well be that auks set the limits of the foraging range of Kittiwakes.

Tendency to join MSFA's

Some species of seabirds foraging off the British east coast showed little or no tendency to join multi-species feeding flocks, while others were nearly always observed feeding in the middle of a multi-species feeding frenzy (Table 7). On the lower end of the spectrum, we find planktivorous species (petrels and Northern Fulmar), but also pursuit diving species like cormorants and Puffins, and birds that normally search their own prey and that are capable of catching individual fish by plunge diving (terns and Northern Gannet). On the upper end, the skuas and larger gulls are either notorious kleptoparasites, or were frequently acting as scroungers and even suppressors. Misplaced in this list seems the Great Black-backed Gull, the behaviour of which was normally rather similar as that of Great Skuas and/or Herring Gulls, and of which we would expect a great tendency to join feeding frenzies.

The function of MSFA's (1): food-finding hypothesis

The cues for seabirds and marine mammals to locate and exploit prey patches in an at first sight relatively homogeneous environment are only partly understood. Olfactory cues as used by some procellariforms may steer individual foraging decisions. Prominent phenomena on the sea surface or for instance the clarity or rather the turbidity of certain bodies of seawater may guide more visually orientated species. The signalling function of certain plumage characteristics (Simmons 1972) and the immediate response of individual

birds (Hoffman *et al.* 1981) and perhaps marine mammals (Pierotti 1998a) to foraging activities of others, either conspecifics or other species, indicates that foraging efficiency may be increased by simply following others. The food-finding hypothesis is therefore the first to be addressed when examining MSFA formation in more detail. Hoffman *et al.* (1981) noted that seabirds involved in feeding flocks search individually for patchy resources and MSFA's are formed only after these sources are located. We are not certain that prey searching is indeed at the individual level, but our observations confirm that the searching phase is usually on a mono-specific basis. The regular type I MSFA participants responded to circling or plunge diving Black-legged Kittiwakes in much the same way as described by Hoffman *et al.* (1981): they seemed able to distinguish searching Black-legged Kittiwakes from successfully feeding individuals.

The function of MSFA's (2): feeding opportunities

One of the most important biological factors promoting the formation of dense concentrations of prey near the sea surface is the action of marine predators such as tuna (Au & Pitman 1986; Safina & Burger 1988), seals (Rijder 1957; Pierotti 1988b), and cetaceans (Evans 1982; Enticott 1986; Camphuysen *et al.* 1995b). Pursuit diving seabirds appear quite capable of herding prey and their activities under water may drive schools of fish to the surface (Grover & Olla 1983). Hunt *et al.* (1988) described the feeding possibilities for Black-legged Kittiwakes, picking up injured and disorientated shrimps coming up from 30 m deep schools of Euphausiids as a result of the feeding activities of deep pursuit-diving Common Guillemots. Within these MSFA's, Common Guillemots were evenly dispersed on the water, with individuals constantly diving and reappearing. Contrary to these observations, in our study the diving and reappearing of Common Guillemots and Razorbills was highly synchronised. The same has been observed with fish-herding Rhinoceros Auklets *Cerorhinca monocerata* by Grover & Olla (1983), and the synchronisation of the underwater attack by auks is probably a highly effective means of concentrating prey such as sandeels. Hoffman *et al.* (1981) observed alcids diving, apparently beneath and around fish balls, and suggested that this activity may have concentrated the school of fish or prolonged its contact with the surface. In our study area, Black-legged Kittiwakes were constantly looking for small flocks of feeding auks, and set off most MSFA's that were formed over pursuit diving seabirds. It was quite unusual to see auk recruits flying in with plunge-diving gulls. A very high proportion of feeding Kittiwakes had joined (or formed) MSFA's over synchronised diving auks, indicating the vital importance of the presence of foraging auks for these birds. We interpret the synchronised diving of auks as indications of social feeding (co-operatively herding fish towards the surface), not as a means to dilute the chances of being attacked by an aggressive kleptoparasite. Guillemots and Razorbills normally swallow their prey while submersed and very few (aerial) seabirds are seen to attack auks in an attempt to steal prey. Yet, the associations of a few gulls with a small flock of auks in the North Sea, also common in other seasons, has usually been described in terms of host/kleptoparasite relationships (Scott 1972; Dathe 1981).

Advertising the presence of food: flock initiators

The commonest MSFA's described in this paper often included several species that feed differently and sometimes in a complementary manner. This differentiation in feeding methods increased the 'effective food supply' in each patch (Sealy 1973, Hoffman *et al.* 1981). Although Black-legged Kittiwakes, as catalysts, were very important in the formation of mixed-species feeding flocks, their benefits as flock initiators are not completely understood. The consumption of a common resource by several species, or just by more individuals, implies niche overlap and suggests that a state of competition among the foraging birds may exist (Sealy 1973). While it is evident that flock-initiating Black-legged Kittiwakes

help other species to find places where food is available, it is highly unlikely that any benefit accrues to the Black-legged Kittiwakes that discover the food source. Bayer (1983) concluded that this behaviour is reciprocal altruistic, because signal recipients for one flock could signal new feeding sites to previous signallers at a future time. However, flock initiators in some carefully studied flocks along the Alaskan coast had significantly greater proportions of successful dives and plunges than did joiners (Bayer 1983). It can be predicted that early departures should occur more often when the competition intensity in the patch increases (Beauchamp & Giraldeau 1996). Finally, 'advertising' the presence of available prey may lead to the arrival of suppressors whose presence simply cut-off the flock initiators from the prey they had discovered. The PS system predicts that initiators (producers) would abandon their food discoveries more rapidly once scroungers arrive when (1) expected searching time is short, (2) more scroungers arrive, and (3) patches are small.

Scroungers and suppressors

From our observations in 'natural' type I MSFA's it was quite obvious that some species searched and initiated (e.g. Black-legged Kittiwakes and Northern Gannets), while others, such as Herring Gulls, Great Black-backed Gulls, shearwaters and skuas were more passive and joined later. Kleptoparasites were more common among the latter group. Herring Gulls were typical suppressors in MSFA's over sandeel balls near Aberdeen, by simply joining late, landing on the fish ball and blocking both view and feeding opportunities for Black-legged Kittiwakes that had started the frenzy.

There are some interesting parallels to be drawn from these 'natural' MSFA's and feeding associations at commercial fishing vessels (Camphuysen 1995; Camphuysen *et al.* 1995a). At trawlers, Black-legged Kittiwakes and small *Larus*-gulls were usually the birds that arrived first, that worked very near the ship and tried to pick up smaller morsels which could be instantly swallowed. Particularly the larger gulls and Great Skuas are birds that usually keep some distance at first, arrive later, and simply get what they wanted either by picking up from the surface, or by taking it from a nearby (smaller) seabird which had been incapable of swallowing in time or which is forced to regurgitate. We hypothesise that Black-legged Kittiwakes in 'natural' MSFA's cannot afford to arrive late, when competition is more intense and while scroungers are arriving on the scene. These smaller birds must take advantage of the very first stages of MSFA development, when the feeding success rates are still comparatively high (Bayer 1983). In other words, the Black-legged Kittiwakes *have* to search, while larger and more powerful species can afford to let others search and detect food resources and simply join in and take their share.

Commensalism

The most common form of MSFA observed of the British east coast were small flocks of Kittiwakes foraging an feeding around a small flock of Guillemots and/or Razorbills. These associations were clearly short-lived, and whenever there was time to watch the feeding birds, it was clear that the auks had synchronised their diving and surfacing, while the Kittiwakes were mainly active when the auks were submerged. We never observed any irritation from the auks (illustrated by avoidance behaviour) when the associated flock only comprised some Kittiwakes and we suggest that commensalism is the mechanism used by these gulls to open up a vast resource of prey that would otherwise be largely unavailable for them. Nearshore MSFA's were often ruined by larger gulls streaming in, and the auks would soon drift away, head-up, just before the MSFA would become inactive. Our observations strongly suggest that these flocks of auks drive fish towards the surface and that while doing so, the auks are fuelling the engine of these common Type I MSFA's (cf. Grover & Olla 1983). As soon as the auks fail to drive and produce the fish, all more aerial participants in the MSFA have to give up feeding. These flocks and this type of behaviour was so common, that we believe that this mechanism is

underestimated as a driving force in the distribution of foraging seabirds at sea and in the analysis of offshore seabird communities.

The typical 'natural' MSFA is illustrated in Fig. 6A. Apparently, a near-surface fish ball is formed, driven by diving seabirds ('divers' following Hoffman *et al.* 1981, 'producers' using the PS game terminology, Barnard & Sibly 1981). The fish ball and the activity of these diving seabirds is detected by an aerial, foraging seabird (catalyst or flock initiator) and sudden shift in behaviour attracts other seabirds (joiners and/or suppressors). The feeding success and intake rates of the initiators and joiners will probably be negatively correlated with the numbers streaming in these flocks, and eventually the flock will fall apart. From our rather distant observations, we could fill in the role of species that are 'typical' players in these MSFA's off the British east coast (Fig 6B) and we suggest that more detailed studies, preferably from stationary platforms, will focus on this feature so that both the mechanism and the interspecific relationships of foraging seabirds in the North Sea will become better understood.

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SAMENVATTING

Sinds het begin van de jaren zeventig hebben onderzoekers in alle landen rondom de Noordzee bijgedragen aan de inventarisatie van vogelvoorkomens op zee. Deze informatie werd tot dusverre vrijwel uitsluitend gebruikt om de 'kwetsbaarheid' van gebieden voor bijvoorbeeld olievervuiling onderling te kunnen vergelijken. Deze tellingen hebben veel inzicht verschaft in de verspreiding en de seizoenspatronen van zeevogels op zee, maar tot dusverre werd verrassend weinig aandacht besteed aan het foerageergedrag van vogels op zee. Tot nu toe werd verondersteld dat de geregistreerde dichtheden vogels op zee (n km^{-2}) automatisch een afspiegeling zouden geven van de ligging van foerageergebieden.

In dit artikel wordt een overzicht gegeven van de verspreiding van foeragerende zeevogels in de nazomer voor de Britse oostkust en vooral van de vele groepen foeragerende vogels, al dan niet samen voorkomend met zeezoogdieren. Hiertoe werden verschillende typen foerageergedrag onderscheiden en behalve de aantallen vogels werd voor dit onderzoek ook precies bijgehouden waaruit hun activiteiten bestonden. In totaal werden 34 soorten zeevogels, 2 soorten zeehonden en 8 soorten walvisachtigen gezien. Groepen foeragerende zeevogels bestonden dikwijls uit verscheidene soorten (multi-species feeding associations: MSFA's). Dergelijke groepen werden niet alleen gevonden rond vissersschepen, maar ontstonden ook omdat de vogels werden aangetrokken door walvisachtigen, of rondom natuurlijke voedselbronnen (vooral scholen vis. De laatste categorie van MSFA's kende de grootste soortenrijkdom. Het meest voorkomend waren kleine groepjes zeevogels, duikend naar een concentratie zandspiering of haringachtige vis dicht onder de oppervlakte, die na korte tijd weer uiteenvielen. Drieteenmeeuwen *Rissa tridactyla* speelden een belangrijke rol bij het ontstaan van deze groepjes, die steevast werden gevormd na de ontdekking door deze meeuwen van een kleine groep synchroon duikende alkachtigen (vooral Zeekoeten *Uria aalge* of Alken *Alca torda*). Het opvallende gedrag van Drieteenmeeuwen maakte dat allereerst soortgenoten, maar vervolgens ook allerlei andere zeevogels toestroomden. Er waren duidelijke aanwijzingen dat de alkachtigen vis naar de oppervlakte dreven, waardoor er vis beschikbaar kwam die onder gewone omstandigheden buiten het bereik van de ondiep duikende meeuwen zou zijn gebleven. De specifieke rol van elk van de waargenomen zeevogels wordt beschreven aan de hand van toevallige waarnemingen vanaf het passerende schip. Het bleek dat een kleine groep Drieteenmeeuwen niet snel tot 'verontrusting' leidde bij de visopdrijvende alkachtigen. Zodra grotere zeevogels zich echter in de strijd mengden, viel de groep meestal snel uiteen. Dit uiteenvallen werd steevast voorafgegaan door het uit de groep wegdrijven van alkachtigen. De kop werd hierbij karakteristiek hoog opgeheven, terwijl de alkachtigen zich in verschillende richtingen verspreidden. Hieruit bleek eens te meer de rol van deze vogels bij het ontstaan en instandhouden van dergelijke foerageermogelijkheden.

Veelvuldig werden zeevogels gezien die aangetrok-

ken werden door (vooral) Bruinvissen *Phocoena phocoena* en Witsnuitdolfijnen *Lagenorhynchus albirostris*. Dergelijke zeezoogdieren leken, feitelijk net zoals de eerder beschreven alkachtigen, vis op zodanige manier op te drijven dat zeevogels zoals de Jan van Gent *Morus bassanus* en Drieteenmeeuw daarvan konden profiteren.

De betekenis van dergelijke MSFA's is groot, zoals wel blijkt uit de 'bereidheid' van vogels om zich in dergelijke groepen te concentreren. Het 'minst' aangetrokken werden stormvogeltjes, aalscholvers en Noordse Stormvogels *Fulmarus glacialis*, terwijl foeragerende jagers, Zilvermeeuwen *Larus argentatus* en Kleine Mantelmeeuwen *L. graellsii* vrijwel uitsluitend in groepen met verscheidene vogelsoorten werden aangetroffen. Dergelijke groepen kunnen van grote betekenis zijn bij het opsporen van prooien, omdat ze al van grote afstand zichtbaar zijn. Een andere functie, wellicht nog veel belangrijker, is dat in een dergelijke groep voedsel binnen bereik komt dat anders te diep in het water zit of wellicht onvoldoende geconcentreerd voorkomt. Deze voordelen moeten dan opwegen tegen het onvermijdelijke nadeel van interspecifieke concurrentie. Er werden opvallende verschillen gezien in de bereidheid om dergelijke voedselbronnen op te sporen. Van Drieteenmeeuwen werd na het uiteenvallen van zo'n groep steeds gezien dat de vogels uiteengingen en erna verder gingen zoeken, terwijl grote meeuwen meestal op zee bleven zitten en pas weer in actie kwamen als ergens in de omgeving weer zo'n groep ontstond.

Voor een voldoende begrip van de verspreiding van zeevogels op zee en van de onderlinge verbanden tussen zeevogels is een gedetailleerde studie van de interacties tussen verschillende soorten zeevogels buitengewoon belangrijk. Het is duidelijk dat het afzonderlijk beschouwen van verschillende soorten niet tot een compleet beeld kan leiden.

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