Seabird–fisheries relationships in the northeast Atlantic and North Sea

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1. Abstract

Bioenergetics modelling indicated that seabirds consume 29% of pelagic fish production within a 45-km radius of one Shetland colony. Assuming this is typical, it implies that seabirds, predatory fish, and industrial fisheries are in direct competition. Overfishing of whitefish stocks in the North Sea began in the 1880s and, coupled with more recent reductions of herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) stocks, led to an increase in populations of small food-fish, particularly sandlance (*Ammodytes marinus*). Most seabird species have increased in numbers in Scotland since 1900, probably in response to the increased availability of food resulting from these ecosystem changes. Rates of increase have been higher in areas where sandlance have become most abundant. Seabirds breeding in Shetland feed mainly on sandlance and have increased many times faster than the populations of the same species on St. Kilda, an area where fishing pressures have been much lower and seabird diets are more varied. Large scavenging species in Shetland, particularly Herring Gulls (*Larus argentatus*), Skuas (*Catharacta skua*), and Northern Fulmars (*Fulmarus glacialis*), are dependent on refuse from whitefish boats. Current trends to reduce volumes of whitefish discarding and increase industrial fishing for sandlance are likely to reduce food availability to seabirds. Monitoring will be necessary to determine which aspects of life history are affected by this.

2. Résumé

La technique de modélisation bioénergétique révèle que les oiseaux de mer consomment 29 % de la production de poissons pélagiques dans un rayon de 45 km d'une colonie de l'île Shetland. En supposant que ce modèle soit typique, cela veut dire que les oiseaux de mer, les poissons prédateurs et la pêche commerciale sont en concurrence directe. La surexploitation des stocks de corégone dans la mer du Nord a commencé dans les années 1880 et, conjuguée aux réductions plus récentes des stocks de hareng (*Clupea harengus*) et de maquereau (*Scomber scombrus*), a donné lieu à un accroissement des populations de petits poissons-fourrages, en particulier celle du lançon (*Ammodytes marinus*). La plupart des espèces d'oiseaux de mer ont vu leur nombre augmenter en Écosse depuis 1900, probablement à cause d'une plus grande disponibilité de nourriture résultant de ces modifications d'écosystème. Les taux de prolifération ont été plus élevées dans les régions où le lançon est devenu plus abondant. Les oiseaux de mer qui nichent dans l'île Shetland se nourrissent principalement de lançons et se sont multipliés beaucoup plus rapidement que les populations de la même espèce vivant dans l'île St. Kilda, région où la pression de la pêche a été beaucoup plus faible et où le régime alimentaire des oiseaux de mer est plus varié. Les espèces de charognards de l'île Shetland, en particulier le Goéland argenté (*Larus argentatus*), le Grand Labbe (*Catharacta skua*) et le Fulmar boréal (*Fulmarus glacialis*) dépendent des rejets provenant des bateaux de pêche au corégone. Les tendances actuelles visant à réduire les volumes de rejets de corégone et à intensifier la pêche industrielle au lançon sont de nature à réduire la disponibilité de nourriture pour les oiseaux de mer. Il faudra exercer une certaine surveillance pour déterminer quelles étapes du cycle biologique des oiseaux sont touchées par ces changements.

3. Introduction

Increased competition between nations for fish catches in the northeast Atlantic has led to concern that top predators, such as seals and seabirds, remove large quantities of fish which would otherwise provide an economic profit for fishermen. Conversely, the increasingly intense exploitation of fish stocks may lead to changes in the marine ecosystem which adversely affect the seabird and seal populations we would wish to conserve.

The North Sea and the northeast Atlantic over the continental shelf provide one of the richest yields of fish in the world. Detailed data on catches, fishing effort, and stock size and composition have been collected for commercial fish species since the creation of the International Council for the Exploration of the Seas (ICES) in 1899. The long history of its exploitation is well recorded (Graham 1956, Hardy 1959, Lundbeck 1962, Hempel 1978*a*) and was the subject of a symposium on the causes of changes in fish stocks (Hempel 1978*b*). The structure and productivity of the North Sea marine ecosystem has also been investigated in considerable detail (Steele 1974).

The British Isles, and particularly Scotland, hold large breeding populations of seabirds. Changes in the sizes of these seabird populations have been documented for many species in many colonies and provide an opportunity to examine correlations between changes in seabird and fish populations over a long time period. In this paper I shall briefly review the evidence that seabirds are a major predator of pelagic fish and in competition with fisheries and predatory fish. I shall then outline the changes in fish stocks around Scotland since the end of the 19th century, and present data indicating the responses shown to these changes by breeding seabird populations. This will provide

the framework for some tentative predictions concerning the future influences of commercial fishery practices on seabird populations.

4. Fish consumption by seabirds

I have discussed the use of bioenergetics modelling in estimating the food consumption by seabirds (Furness, this volume). Application of this approach to one of the largest seabird communities in the British Isles (Furness 1981) suggested that the seabirds consume 29% of the annual pelagic fish production from the sea area within 45 km of the colony, on Foula, Shetland (Furness 1978). Similar values have been obtained in a number of different studies (e.g. Wiens and Scott 1975, Furness and Cooper 1982). Four species on Foula, Northern Fulmar (*Fulmarus glacialis*), Common Murre (*Uria aalge*), Shag (*Phalacrocorax aristotelis*), and Atlantic Puffin (*Fratercula arctica*) are responsible for 90% of the annual total energy requirements of the 18-species community, so the accuracy of calculations for these species determines the overall accuracy of the estimate for the community. Each of these species in Shetland feed their chicks almost exclusively on small pelagic fish, principally sandlance (*Ammodytes marinus*). However, diets of breeding and non-breeding seabirds may differ from each other, and from that fed to chicks (Furness and Hislop 1981). In particular, offal may make an important contribution to the requirements of adult, particularly non-breeding, Northern Fulmars so reducing their consumption of pelagic fish. This is not true for the other three species, though marine invertebrates may occur in the diet of non-breeding alcids. At present there are no quantitative data to indicate the importance of these two foods.

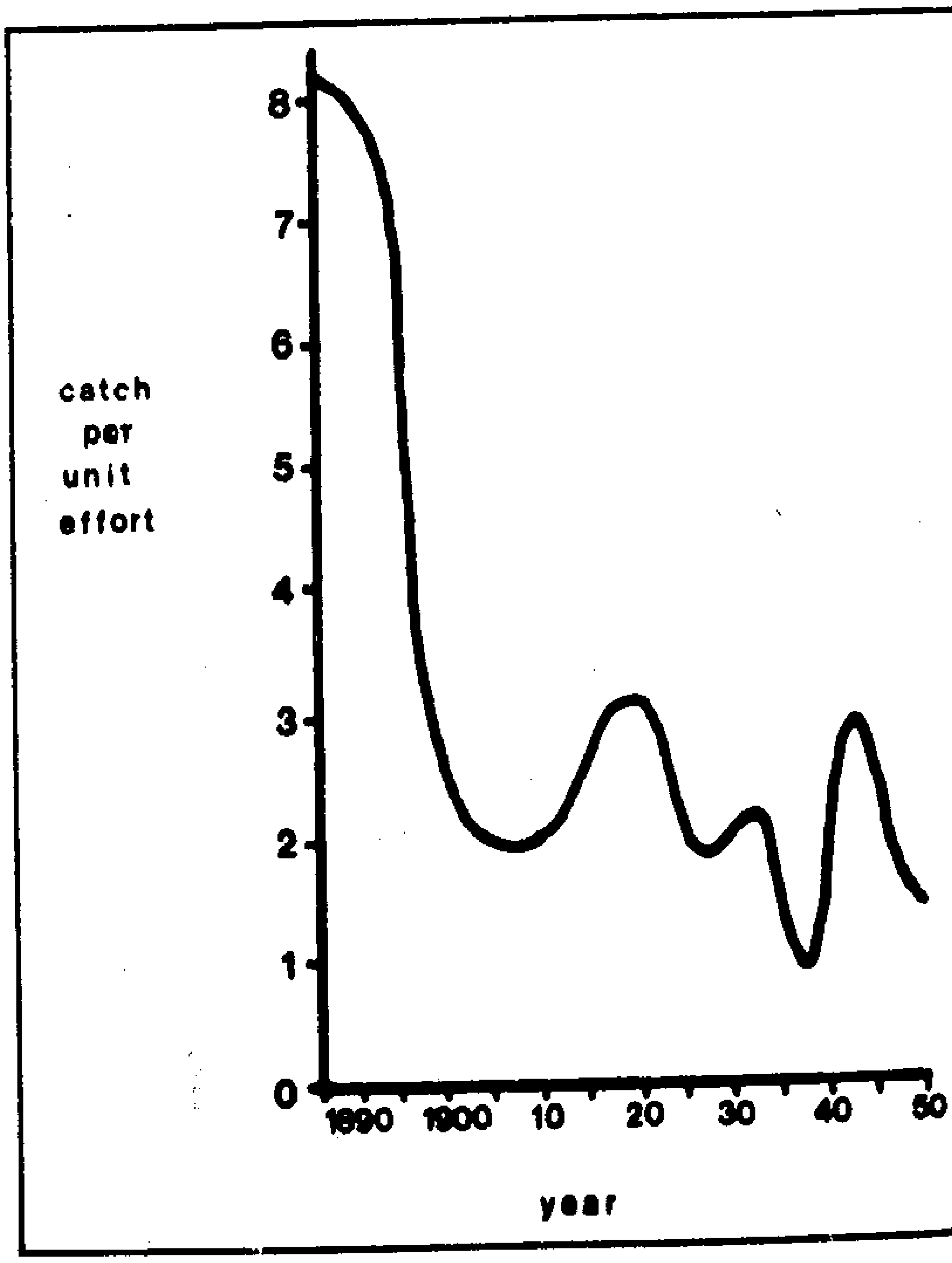
The second serious difficulty in relating population energy requirement to fish production stems from uncertainties in the range over which the seabirds forage. Transect counts near colonies show high concentrations of seabirds close to the colony and a low, patchy distribution at considerable distances, but it is unclear whether these are foraging breeders or immatures. However, they do indicate that in most situations around British colonies, Shags feed within a few kilometres of the colony, alcids travel a few hundreds of metres to a few tens of kilometres, and Northern Fulmars appear to spread themselves rather uniformly over at least 50 km from the colony. Dye-marking Northern Fulmars feeding chicks on Foula resulted in reports from fishermen who saw these individuals at sea. Most were reported from within 50 km; the few records from further afield could have been birds that deserted their nest as a direct result of being caught and dye-marked, since 20% of the birds marked were never seen at their nests again (Furness and Todd, in press). An index of the maximum foraging range can be obtained from the time spent away from the nest between chick feeds (Pearson 1968). These indicate that Atlantic Puffins, Common Murres, and Shags feed close to the colony, whereas Northern Fulmars depart for longer. Half the departures recorded at Foula by adult Northern Fulmars with chicks lasted for less than 6 h. If these birds flew in a straight line at 40 km/h they would have travelled no more than 120 km from the colony (Furness and Todd, in press). In practice, as feeding takes time, and flight is unlikely to be direct, their ranges were smaller than this. The main Shetland seabird communities are about 70 km apart, and placed at the corners of the archipelago. Birds travelling more than 35 km may enter the feeding zone of the adjacent colony, so to some extent will compensate for others travelling in the opposite direction. The estimate that all feeding occurs over a 45 km range from the colony seems a reasonable compromise given these uncertainties (see also Blake *et al.* 1980).

Steele (1974) indicated that, on average, 50% of pelagic fish production in the North Sea is taken by people. If the seabirds consume 29%, then 21% remains to be shared by marine mammals, and demersal and other predatory fish, indicating that the relationship between seabird consumption, pelagic fisheries, and predatory fish is tight, with little scope for an increase in one without a concomitant decrease in another.

5. Changes in fish stocks

The introduction of steam trawling and power winches between 1870 and 1900, together with the development of the otter trawl towards the end of the 19th century, greatly increased fishing power. Lundbeck (1959, 1960, 1962) showed that a severe reduction in whitefish biomass occurred almost immediately, particularly in the southern North Sea (Fig. 1) where stock biomass was reduced by 70% at the turn of the century. He attributed this to overfishing as a result of increased effort, and this interpretation is supported by the tendency for the stock to show temporary increases during the two world wars (1914–18 and 1939–45) when fishing effort was much reduced. Thus a major

Figure 1
Catch per unit effort of a standardized German trawler in the southern North Sea (Lundbeck 1962) showing effects of increased fishing on fish stock size: all whitefish species combined



reduction in whitefish stock biomass took place around 1890 to 1900, just when the exploitation of seabird populations by people was also tending to cease. The increase of many seabird populations dates from about 1900, suggesting that it could be a response to the reduced predation on "food-fish" by whitefish, making more food available to the seabirds. Protection of seabirds may have accelerated this process, but it seems likely that the increased food availability would have been necessary to allow most populations, except those reduced near to extinction, to increase.

Whitefish also responded to the improved food availability as a result of stock reduction. Haddock (*Melanogrammus aeglefinus*) growth rate increased (Jones and Hislop 1978) as did that of whiting (*Merlangius merlangus*) (Daan 1975). As a result of increased growth rates both species reached reproductive condition at an earlier age. Cod (*Gadus morhua*) showed no change in growth rate, but the age of maturity did decrease so that cod reached reproductive age at a smaller size (Daan 1978). All these changes may be ascribed to greater food availability per fish as a result of reduced competition.

Depletion of herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) stocks in the North Sea and northeast Atlantic had begun before 1950, but was greatly accelerated by the introduction of purse-seining. The adult biomass of North Sea herring remained around 2.5×10^6 t until 1965 when it was depleted in a few years to one-tenth of this. At the same time, the growth rate increased suddenly, and partly compensated for the reduction in stock (Burd 1978). When herring became unprofitable the purse-seine fishery turned to mackerel. The stock of 2×10^6 t before 1965 was reduced to about one-tenth of this in only 4 years of fishing (Hamre 1978). The fisheries for adult herring and mackerel before 1960 will have been directly beneficial to seabirds by reducing the average size of fish in the populations without greatly reducing stock biomass, so that a higher proportion of the stock will have been in the size range suitable for seabird consumption. After 1960 the reductions in stocks will not have been directly beneficial to seabirds, but as most species feed more on sandlance than on herring or mackerel there was probably an indirect beneficial effect.

Andersen and Ursin (1977) found that the reduction in stocks of herring and mackerel is likely to have led to increases in the populations of their ecological competitors: sandlance, sprats (*Sprattus sprattus*), and Norway pout (*Trisopterus esmarkii*). Evidence that such increases have taken place is not readily available as sandlance were of no commercial interest until recently; so stock sizes were, and still are, largely unknown. However, Sherman *et al.* (1981) have shown that there is good evidence for a large increase in sandlance stocks in the northeast and northwest Atlantic. Catch per unit effort of Norway pout by Scottish research vessels shows that the stock of this species has also greatly increased since the mid 1950s from a level which had previously been fairly constant (Richards *et al.* 1978).

Andersen and Ursin's model also predicted that whitefish stocks would increase as a result of decreased predation on their larvae by herring and mackerel. Such increases have occurred, and are very difficult to explain except in terms of such an ecosystem interaction (Hempel 1978*a*). As a corollary of their recovery the growth rates of whitefish have fallen again, which suggests that the superabundance of food generated by their stock depletion no longer exists (Hempel 1978*a*).

The reduction of herring and mackerel stocks will have been beneficial to seabirds in allowing an increase in their main food, sandlance, although the partial recovery of whitefish stocks will have increased predation on adult sandlance. A result of these ecosystem changes has been a rapid growth of industrial fishing for sandlance (and sprats and Norway pout) since its inception in the 1950s. In the 1970s total landings of industrial fisheries in the North Sea exceeded landings of whitefish, averaging over 2 million metric tons/year (Fig. 2). Sandlance catches are continuing to increase rapidly (Fig. 3), although little is known of the stock size or maximum sustainable yield for this species, so that fishing effort is likely to continue to be increased until the stock suffers fishery-induced reduction in size and yield.

Figure 2
Total landings of industrial fisheries in the North Sea (from Popp Madsen in Hempel 1978*a*)

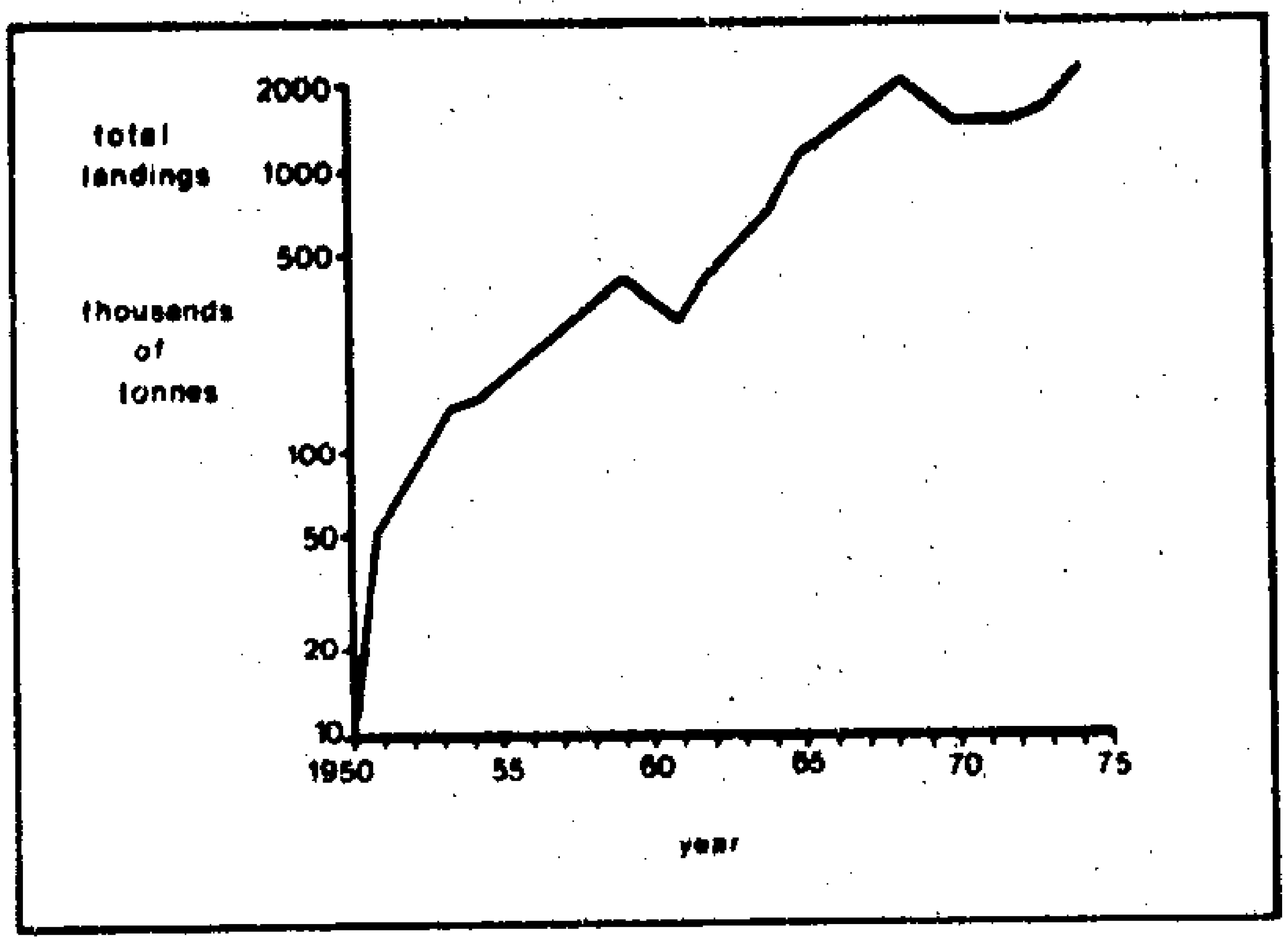
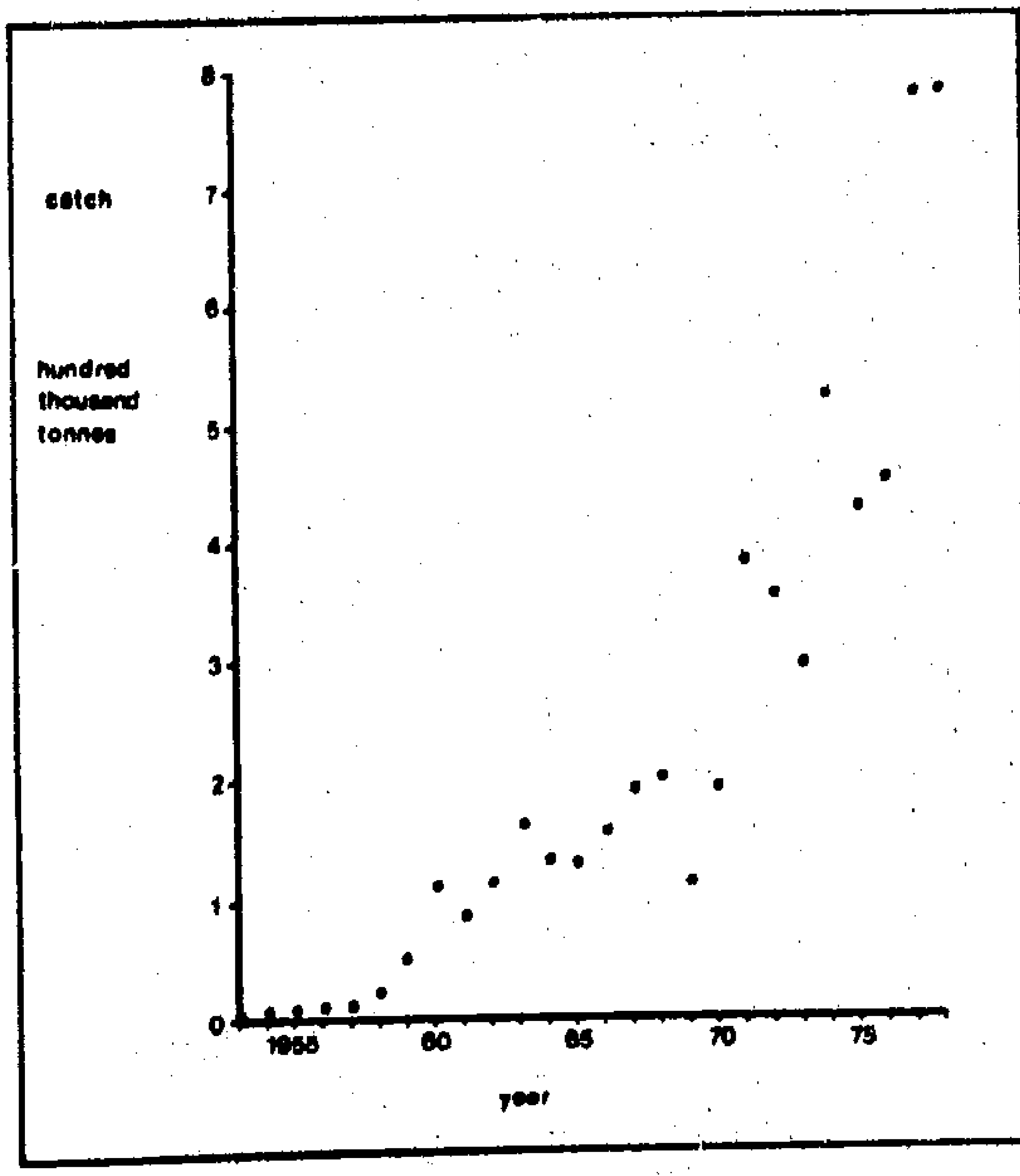


Figure 3
Annual catches of sandlance in the North Sea (from K. Warburton, pers. comm.)



The total annual landings of whitefish from the North Sea remained around 0.5 million metric tons from 1910 to 1960, then increased to slightly over 1 million metric tons after 1965, as a consequence of enhanced recruitment which may have been a response to decreased predation on whitefish larvae by the depleted herring and mackerel stocks (Hempel 1978*a*). Legal restrictions on the minimum sizes of fish that can be marketed, and fluctuations in market demand and catch quotas, result in a proportion of each catch being discarded, mainly dead, into the sea. This proportion has increased with the reduction in average fish size: now a higher proportion of the population is caught as soon as it is recruited into the fishable stock. Up to 30% of a whitefish catch in the North Sea may now be discarded at sea (Jermyn and Hall 1978). Discard fish, and offal, which is probably equal in weight to the amount of discards (Bailey and Hislop 1978), provide a source of food for Northern Fulmars, large gulls, Skuas (*Catharacta skua*), Northern Gannets (*Morus bassanus*), and Black-legged Kittiwakes (*Rissa tridactyla*). The yield of whitefish to commercial fisheries in the North Sea could be increased in the long term by increasing minimum net-mesh size, allowing smaller fish to escape and continue their growth until capture at a later date. Offal may be used to supplement industrial fish catches for reduction purposes, so that quantities thrown away may be reduced in future. Discarding undersized fish is also wasteful, though difficult to avoid with present fisheries management. Increased net-mesh size, or limited entry to fisheries through a licensing scheme have been suggested as conservation measures (Gulland 1982). These, or temporary closure of fisheries when quotas have been met, would further reduce food availability to seabirds.

6. Changes in seabird population sizes

Detailed surveys of breeding seabirds in Britain and Ireland have provided accurate information on the sizes and rates of increase of populations of many species. Most seabird populations in Scotland have been increasing for the last 80 years or so. Rates of increase have probably been highest in the gulls, stercorarids (Skua and Parasitic Jaeger *Stercorarius parasiticus*), and Northern Fulmar. For many species they have been highest in east Scotland and lowest in west Scotland (Table 1). These population changes are reviewed by Cramp *et al.* (1974), Harris (1976*a*, 1976*b*), Harris and Galbraith (1983), Harris and Murray (1978), and Furness (1982).

7. Regional differences in seabird diets and foraging

Seabirds can be classified into four major foraging guilds: zooplankton, trawler-waste, small pelagic fish, and

Table 1
Rates of change (percent per annum) of seabird population sizes at St. Kilda, Shetland, and east Britain. Data from Cramp *et al.* (1974), da Prato and da Prato (1980), Furness (1977, 1981), Harris (1976*a*, 1976*b*), Harris and Galbraith (1983), Harris and Murray (1978), Hawkey and Hickling (1981), Murray (1981), and Nelson (1978). Values quoted are average rates to nearest 1% over periods where the rate appears to have been constant

	West coast	Shetland			East coast		
Species	St. Kilda (57°48′N 8°35′W)	Foula (60°08′N 2°05′W)	Hermaness (60°52′N 0°54′W)	Noss (60°08′N 1°00′W)	Isle of May (56°10′N 2°32′W)	Berwickshire (55°55′N 2°10′W)	Farnes (55°38′N 1°36′W)
Northern Fulmar	1900–70 +1% 1970–80 0	1878–1976 +8%	1910–74 +6%	unknown	1930–81 +6% 1975–81 +15%	1957–78 +4%	1972–80 +4%
Northern Gannet	1900–70 +2% 1970–80 0	absent	1939–69 +2.6%	1939–69 +2.8%	absent	absent	absent
Shag	1930–80 0	unknown	1965–70 +7%	little change	1950–73 +16% (1973–76) −38% 1978–81 +24%	1957–78 0	1955–71 +2% 1971–74 +23% (1974–75) −65% 1975–80 +19%
Skua	1900–60 absent 1960–80 +18%	1900–76 +7% 1976–81 −2%	1900–76 +5% 1976–81 0	1910–32 +15% 1955–81 +1%	absent	absent	absent
Lesser Black-backed Gull	1930–80 0	very few	very few	1946–74 −8%	1930–72 +13% 1972–81 controlled	1957–78 0	1972–74 +13% 1974–80 controlled
Herring Gull	1930–80 −2%	very few	little change	1946–73 0 1973–80 −10%	1907–72 +13% 1972–81 controlled	1957–80 0	1972–74 +13% 1974–80 controlled
Great Black-backed Gull	1930–80 0	1900–80 +4%	very few	1946–73 +2%	absent	absent	absent
Black-legged Kittiwake	1930–70 0	1900–61 increased 1961–76 0 1976–80 −3%	1965–74 +2%	unknown	1921–52 0 1954–81 +6%	1957–78 +5%	1972–80 +4%
Arctic Tern	absent	1906–80 increased	very few	very few	absent	absent	1956–80 0
Common Murre	1960–80 +3%	increasing	1960–79 increasing	increasing	1974–81 +5%	1957–78 +4%	1972–80 +18%
Razorbill	unknown	unknown	1965–74 +4%	unknown	1969–81 +16%	1957–78 +5%	1957–72 0 1972–79 +13%
Atlantic Puffin	1940–50 increased 1970–80 0	increasing	increasing	increasing	1959–81 +22%	1957–78 0	1972–79 +3%

predation–scavenging. The sizes and composition of these guilds vary between areas (Table 2). In particular, at St. Kilda zooplankton feeding is most common, in Shetland most species are members of the small pelagic fish-feeding guild as sandlance is the staple diet of most seabirds in the area, and in east Scotland (specifically around colonies off the Fife and Lothian coast) zooplankton is of negligible importance during the breeding season but trawler-waste and small pelagic fish are both important (Table 2). Quantitative studies of seabird diets around Britain are rather few. I have examined the diets of Northern Fulmars, Herring Gulls (*Larus argentatus*), and Skuas at St. Kilda (west Scotland) and Foula (Shetland), and the diets of Herring Gulls around the islands off the Fife–Lothian coast (east Scotland). Harris and Hislop (1978) have described the diets of young Atlantic Puffins from these same colonies.

Northern Fulmars on St. Kilda feed largely on zooplankton (Table 3) and have derived little benefit from the small local fishing industry. In Shetland their diet consists chiefly of sandlance caught at surface shoals and lesser quantities of offal and plankton (Table 3).

Gulls are known to be catholic in their feeding. Although subject to a number of potential biases (Furness and Hislop 1981) analysis of regurgitated pellets of indigestible material indicates that Herring Gulls on St. Kilda feed largely by scavenging or predating seabird eggs and young, scavenging intertidally and, to a small extent by kleptoparasitism of Atlantic Puffins and scavenging at trawlers (Table 4). On Foula, most of their diet consists of whitefish from trawlers, with small amounts of other items. At the Fife–Lothian colonies the diet consists almost entirely of food from human activities: whitefish discards, Norway lobster (*Nephrops norvegicus*) remains from trawlers, urban refuse, and earthworms from ploughed fields and pastures (Table 4).

In the Faeroe Islands the Skua feeds by piracy and predation of seabirds, and on goose-barnacles, squid, berries, and insects (Furness 1979, Furness and Hislop 1981). In Shetland it feeds mainly on sandlance, taking discard whitefish when sandlance are not readily available. As a result it has a reliable and high quality food supply, giving high breeding success (Furness and Hislop 1981). The diet of the small number of pairs that recently colonized St. Kilda is based on predation of seabirds and scavenging dead birds, goose-barnacles, and intertidal invertebrates and contrasts with the dependence of the species in Shetland on sandlance and discards (Table 5).

Atlantic Puffins at the Isle of May, east Scotland, have a higher chick growth rate and fledging weight than those at St. Kilda. The chick diet at the Isle of May consists mainly of sprats, whereas that at St. Kilda varies between seasons, but usually includes a large component of juvenile whitefish, which are of low calorific value (Harris and Hislop 1978). In Shetland, Atlantic Puffin diet is intermediate in calorific value, comprising almost exclusively sandlance, and chick growth rate is also intermediate (Furness, unpubl.).

Table 2
Feeding guilds of seabirds in three areas of the northeast Atlantic and North Sea coasts of Scotland: St. Kilda (west coast), Shetland (north coast), and Forth Islands (east coast). Species are classed as primary members if this is their principal feeding method, secondary if it is important but one of several methods used regularly, and tertiary if this is a minor source of food. Species: NF = Northern Fulmar, SP = Storm-Petrel, LP = Leach's Storm-Petrel, MS = Manx Shearwater, SH = Shag, NG = Northern Gannet, HG = Herring Gull, GG = Great Black-backed Gull, LG = Lesser Black-backed Gull, BK = Black-legged Kittiwake, S = Skua, PJ = Parasitic Jaeger, AT = Arctic Tern, CM = Common Murre, RZ = Razorbill, AP = Atlantic Puffin, BG = Black Guillemot

		Feeding level		
Guild	**Area**	**Primary**	**Secondary**	**Tertiary**
Zooplankton	St. Kilda	NF,SP,LP,MS	BK	CM,RZ,AP
	Shetland	SP,LP,MS		NF
	Forth Islands			NF,BK
Trawler-waste	St. Kilda	HG	GG	NF,MS,NG,S,BK
	Shetland	HG,GG	NF,S	NG
	Forth Islands	NF,HG,GG,LG	NG,BK	
Small pelagic fish	St. Kilda	NG,SH,CM,RZ,AP	MS,BK,BG	NF,SP,LP
	Shetland	NF,NG,SH,BK,S,PJ,AT,CM,RZ,AP,BG	SP,LP,MS,HG,GG	
	Forth Islands	NG,SH,CM,RZ,AP	BK	NF
Predation on birds/mammals and scavenging at sea or on shore	St. Kilda	S,GG	HG	
	Shetland		S,GG	
	Forth Islands		GG	HG

Table 3
Diets of Northern Fulmars as indicated by presence (% occurrence) of ingested items in regurgitated samples from chicks and breeding adults collected between 1 June and 18 August 1978–81 (Furness, unpubl.)

	Foula, Shetland		St. Kilda, Hebrides	
Prey taxa	**No. samples**	**%**	**No. samples**	**%**
Sandlance	71	66	0	0
Sprats, herring	0	0	18	7
Fish offal	18	16	2	1
Polystyrene	2	2	30	13
Paper, plastic, metal	3	3	8	3
Benthic invertebrates* (presumed trawl discards)	0	0	12	5
Pelagic zooplankton†	15	13	168	71
Total items sampled	112	100	238	100

**Munida bamffica, Pagurus bernhardus, Nephrops norvegicus, Lucarcinus tuberculatus, Acanthephyra sp.*
†Meganyctiphanes norvegica, Gnathophausia zoea, Idotea metallica, Parapasiphaea sulcatifrons.

Table 4
Diets of Herring Gulls, expressed as % occurrence, as indicated by analysis of indigestible material in pellets (Furness, unpubl.)

	St. Kilda		Foula		Forth Islands	
Prey taxa	**No. pellets**	**%**	**No. pellets**	**%**	**No. pellets**	**%**
Sandlance	10	5	18	20	0	0
Sprats herring	10	5	0	0	2	1
Whitefish	14	6	124	50	255	52
Nephrops norvegicus	0	0	0	0	89	18
Mytilus edulis	18	8	22	9	21	4
Earthworms	0	0	0	0	36	7
Crabs	11	5	14	6	16	3
Other shellfish	9	4	6	2	9	2
Domestic refuse	2	1	4	2	60	12
Eggshells	58	27	7	3	0	0
Seabirds	86	39	21	9	0	0
Total	218	100	246	100	488	100

Table 5
Diet (expressed as % occurrence) of breeding adult Skuas on St. Kilda, Hebrides, and Foula, Shetland, based on analysis of pellets (Furness and Hislop 1981; Furness, unpubl. data)

	St. Kilda, Hebrides		Foula, Shetland			
	1980	1981	1975	1976	1980	1981
Prey taxa	%(N = 82)	%(N = 50)	%(N = 560)	%(N = 386)	%(N = 100)	%(N = 100)
Sandlance	0	0	42	80	51	62
Whitefish	11	4	54	16	42	31
Birds/mammals	61	76	3	2	6	4
Littoral and marine floating invertebrates*	28	20	1	2	1	3

*Goose-barnacles (*Lepas* sp.), horse mussels (*Mytilus edulis*), and other invertebrates.

8. Competitive relationships between seabird species

The extent of interspecific competition between alcids and other species feeding on small pelagic fish is unknown. There is a clear linear dominance hierarchy in the guild feeding on trawler waste. Northern Fulmars displace all other species, but select offal and rarely attempt to take entire discard fish. Skuas can displace all species except Northern Fulmars. Northern Gannets dominate Great Black-backed Gulls (*Larus marinus*). Herring Gulls displace Lesser Black-backed Gulls (*Larus fuscus*) but are subordinate to the larger Great Black-backed Gulls. Black-legged Kittiwakes rarely attempt to join these associations in Shetland as they are unable to compete with any of the bigger birds, but in east Scotland, where there are relatively fewer Northern Fulmars and Great Black-backed Gulls and no Skuas, Black-legged Kittiwakes are occasionally found feeding at trawlers. Furness and Hislop (1981) found that Skuas in Shetland consumed up to 57% of the whitefish discarded by the fishing industry, depending on the availability of sandlance. The hierarchical arrangement suggests that when sandlance are scarce and skuas take a disproportionate share of the available discards the species low on the list are likely to suffer severe food shortage. For this reason the interspecific relationships may play an important role in the responses of seabird populations to changing fish stocks or fisheries practices.

9. Discussion

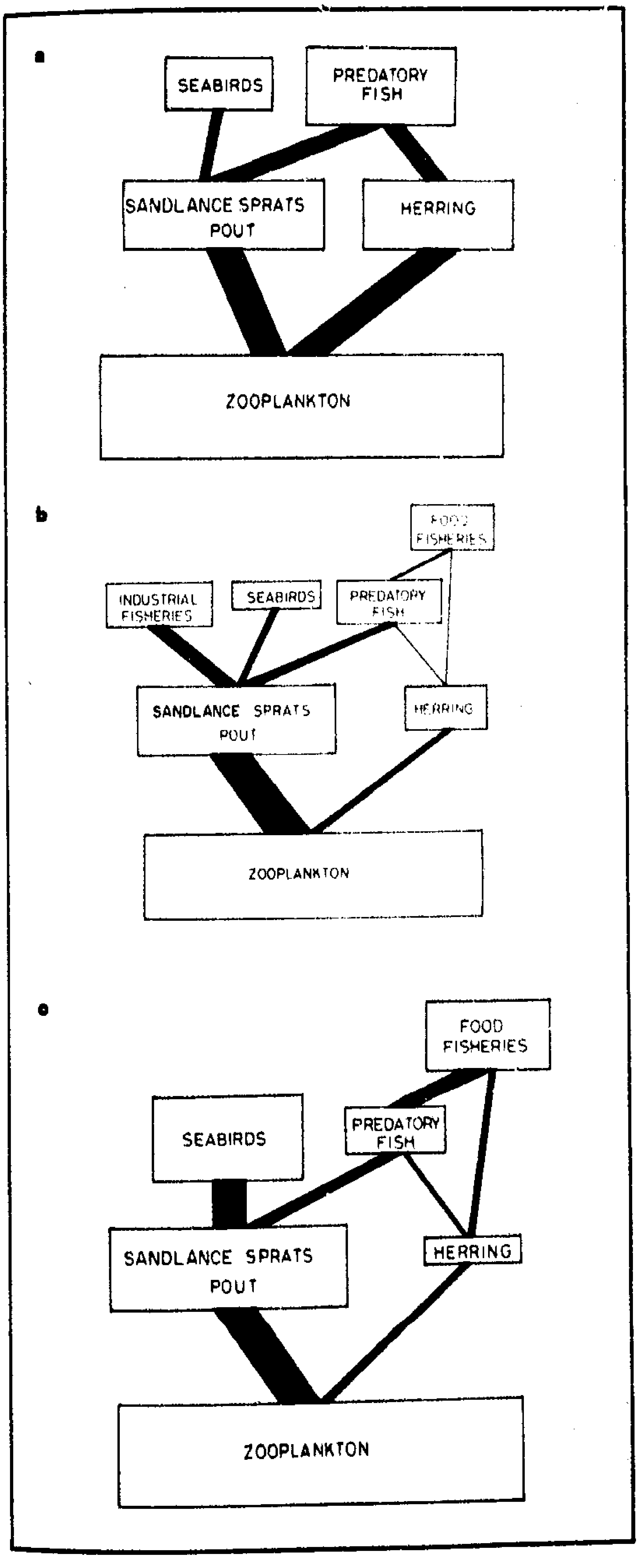
Seabirds have benefited from two quite distinct effects of North Sea fisheries. Firstly the provision of discards and offal has increased food available to scavenging species. Secondly, and of greater overall importance, ecosystem changes leading to expansion of sandlance stocks has increased food availability to almost all seabirds, as this fish is a major food for most seabirds in north and east Britain.

These changes can be summarized diagrammatically. Figure 4*a* shows the situation late in the 19th century. In Figure 4*b* the effects of reducing predatory fish and herring are indicated. Current, and likely future trends, to conserve whitefish and herring stocks and to increase industrial fishing on sandlance are seen as a threat to seabird populations (Fig. 4*c*).

Fishing intensity varies regionally. Off the west coast of Scotland whitefish catches have been rather small, and herring and mackerel stock depletion has only recently occurred. Comparisons of seabird diets in west, north, and east Scotland show that the seabirds on the east coast have altered their diets to take advantage of changes in food availability, whereas those on the west coast continue to utilize "traditional" prey. Rates of population growth mirror these dietary differences. On St. Kilda, the numbers of Northern Gannets, Common Murres, and Northern Fulmars have been increasing slowly; no change has been detected in recent years in numbers of Shags, Black-legged Kittiwakes, Lesser Black-backed Gulls, Great Black-backed Gulls, or Atlantic Puffins; and Herring Gull numbers have declined (Table 1). In Shetland, where sandlance stocks have increased and large quantities of whitefish discards and offal are available (Furness and Hislop 1981), increases have been measured in numbers of Northern Fulmars, Northern Gannets, Skuas, Black-legged Kittiwakes, Arctic Terns, Common Murres, and Atlantic Puffins. Herring Gulls and Lesser Black-backed Gulls have failed to show increases. East-coast colonies have shown a similar pattern to those in Shetland, except that gulls have also increased dramatically in this area, and rates of increase of several species have been higher than in Shetland, suggesting that changes in fish stocks have been most pronounced in this area, a conclusion supported by the fisheries data (Hempel 1978*a*, 1978*b*).

Northern Fulmars and Northern Gannets were subject to intense harvesting at St. Kilda up to shortly before the evacuation of the islands in 1931, yet their numbers have increased little since this chick mortality stopped. In other parts of Scotland both these species have shown rapid population increases. There appears to be no lack of potential but unused nesting space at St. Kilda. The failure of the St. Kilda populations to respond to relaxed predation is most easily explained by the populations being limited by food availability. This hypothesis is supported by the finding that the diet of Northern Fulmars at St. Kilda shows a negligible influence of fishery offal or increased availability of small pelagic fish, and so contrasts with the diets in the areas, such as Shetland, where the species is showing population increases. Unfortunately, little is known of Northern Gannet diets around Scotland. Atlantic Puffin numbers on St. Kilda are remaining approximately stable; numbers are increasing at eight other west-coast Scottish colonies, remaining constant at five and declining at two, whereas numbers in Shetland are increasing at eight colonies and stable at three. In east Britain all 10 colonies censused are increasing, at an average of 9% per annum (Harris 1976*a*; Harris and Galbraith 1983). Again, rates of population change reflect changes in food availability induced by commercial fisheries around Scotland.

Figure 4
A diagram of energy flow from zooplankton to top predators in the North Sea ecosystem: (*a*) late 19th century, (*b*) in the 1960s when herring stocks were depleted, (*c*) probable picture for the 1980s with increased industrial fishing, conservation of herring and whitefish stocks, and possibly a decline in seabird populations as a result. Sizes of rectangles and widths of flow lines are intended to be indicative of magnitude although only for comparisons between stages *a*, *b*, and *c*. Scavenging species associated with commercial food fisheries are ignored for simplicity



Herring Gulls are uncommon and declining at St. Kilda, numerous but not increasing at Shetland, and numerous and increasing at 13% per annum at east-coast Scottish colonies (Cramp *et al.* 1974). Again, the rate of increase is highest in the area where human influences (in this case, not just fishing) are greatest.

Shags have shown the same regional differences; Potts (1969) argued that the density of breeding Shags on the east coast of Scotland was so low early in this century that it could not have been food-limited in a density-dependent manner. However, the rapid increase of Shag numbers on the east coast of Scotland, contrasting with their stable numbers on the west coast, is also compatible with the hypothesis that numbers have responded in areas where fishing has allowed sandlance and sprat stocks to increase.

By 1900 the Skua had been reduced by human persecution close to extinction: less than 20 pairs remained in each of the two Scottish colonies and the Faeroe Islands. After 1900 numbers increased in response to protection measures introduced in both countries (Cramp *et al.* 1974); in the Faeroes numbers stopped increasing at a population of around 500 pairs (Gibbs and Mawby 1968; Bloch, pers. comm.). Numbers in Scotland increased at 7% per annum to over 6000 pairs in 1976 (Furness 1977). Many individuals colour-banded as chicks in Shetland have emigrated to found new colonies in the Hebrides and north Scotland. Rates of increase are highest in these newly formed colonies which depend on immigration to sustain them. Skuas in Shetland are highly dependent on discard whitefish and sandlance, whereas the smaller populations in the Faeroes feed by more "traditional" methods: kleptoparasitism and predation. As the Skuas at St. Kilda also feed by predation and scavenging dead birds, goose-barnacles, and intertidal invertebrates, I would predict that the Skua colony on St. Kilda is unlikely to increase to a size comparable to those in Shetland, and that any reduction of sandlance or discard availability to Skuas in Shetland is likely to result in severe predation rates on other seabirds as the Skuas turn to their more characteristic feeding methods.

10. Conclusions

1. Shetland seabirds probably consume about 29% of annual pelagic fish production within a 45-km radius of the colony, implying that they are in competition with predatory fish and industrial fisheries.

2. Increases of seabird populations can be attributed to increased availability of food resulting from provision of offal and discards, and from increased stocks of sandlance caused by ecosystem changes attributable to intense commercial fishing.

3. Increases of seabird populations have been greatest in areas where ecosystem changes have been most marked. Diets vary between regions and indicate the opportunistic utilization of these increased food resources.

4. Future increases in fisheries for sandlance are likely to result in reduced seabird populations.

5. Reductions in the quantities of fish discarded would affect species low on the feeding hierarchy most severely.

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