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Oil Pollution and Seabird Populations [and Discussion]

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Oil pollution and seabird populations

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Large numbers of seabirds may be killed from time to time by individual incidents of oil pollution, and throughout the year, especially in winter, dead seabirds, many of them oiled, are washed up on our shores. These dramatic events have given rise to a great deal of public concern about the effect of oil pollution on the wellbeing of seabird populations. It is important to consider this question from the point of view of population dynamics of seabirds so as to determine whether or not the observed mortality is substantial and additional in relation to the natural mortality. Such an approach requires detailed information on the distribution and numbers of seabirds at breeding colonies and at sea in their pre-breeding years, in association with their breeding activities and also in their 'wintering' areas. While the data from breeding colonies provide censuses of breeding birds in defined geographical areas, movements and dispersal of breeding birds result in great uncertainty about their distribution and abundance while at sea. Since many oil polluting incidents, and much of the chronic oil pollution, affect birds while they are at sea, it is very difficult to asess the size and the provenance of the populations of various species that are actually at risk.

Some evidence about the numbers of birds killed by oil and other causes can be obtained from both the beached bird survey, which are carried out monthly throughout the winter, and also from the recoveries of ringed birds. These sources of evidence give rather different results, but both are subject to difficulties of interpretation.

Most seabirds are long-lived, with low mean annual adult mortality rates, and many of them do not breed until they are several years old. An attempt is made to relate the numbers of birds found dead, and the numbers oiled to the numbers that might be expected to die according to the measured rates of annual mortality. Again there are very considerable problems in attempting to relate these two sets of information. However, it seems that in western European waters the numbers killed by oil pollution is in tens of thousands per winter on average, while the number expected to die naturally is in hundreds of thousands per year. It is not known whether or not oil-induced mortality is additional to natural mortality. It is also pointed out that current environmental circumstances seem favourable and that the present resilience of populations may not persist if conditions change.

Emphasis is placed on the very large numbers of pre-breeding birds and the need for information on the means by which they are recruited to breeding colonies.

Recent monitoring of the numbers of breeding seabirds throughout Britain shows that most populations are increasing.

Introduction

An enormous amount of information has been published on the effects of oil pollution on seabirds. Some of these effects are sublethal and affect physiology (Miller *et al.* 1978; Butler *et al.* 1979) and breeding success (Ainley *et al.* 1981; Szaro & Albers 1977; Coon *et al.* 1979), but most publications refer to the mortality of seabirds caused by oil spilt at sea. The subject has been extensively reviewed most recently by Bourne (1968, 1976) and R.S.P.B. (1979), so

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that it is not necessary here to provide data and references to demonstrate that large numbers of seabirds are killed each year in many parts of the world as a result of oil pollution. Large seabird kills, resulting from tanker accidents or strandings, such as the *Torrey Canyon*, the *Amoco Cadiz* or the *Esso Bernicia*, give rise to public outrage based on considerations of conservation and animal welfare. Less well known to the public but well known to ornithologists is the large number of dead or dying seabirds, contaminated with oil, that are washed up on our beaches each winter. These too give rise to grave concern among conservationists about the chronic oil pollution of the seas.

In this paper I shall not consider the sublethal effects that may impair the performance of seabirds and their breeding success: these must be substantially less significant in the context of population dynamics than the massive direct mortality that can be observed. I shall therefore try to look at this mortality in terms of the population variables, processes and dynamics of the species most at risk. I shall concentrate on the area around the British Isles but shall refer occasionally to other seabirds that may be similarly affected in other parts of the world.

Mortality due to oil pollution

The most conspicuous and most publicized mortality of seabirds is associated with major incidents when large tankers have accidents or when offshore oil production systems go wrong. The number of dead oiled birds picked up after the *Torrey Canyon* incident in 1967 was about 10000 (Smith 1968), 4572 were picked up after the *Amoco Cadiz* ran aground (Hope-Jones *et al.* 1978), 3704 after the *Esso Bernicia* (Heubeck 1979) and 2541 after the *Christos Bitas* (Stowe 1979). These are the numbers of dead bodies actually found and although with the *Esso Bernicia* this may be close to the total killed (Richardson *et al.* 1981), it is generally accepted that these are only a portion of the total killed. Experiments indicate that probably something between 10% and 60% of the dead birds may be recovered under particular conditions (Hope-Jones *et al.* 1970; Bibby & Lloyd 1977). It is therefore not surprising to hear Dr Conan (this symposium) indicate that the mortality due to the *Amoco Cadiz* incident was probably between 15000 and 20000, but such estimates can only be approximate.

However, the beached bird surveys carried out by the R.S.P.B. and the Seabird Group (Bourne & Bibby 1975) reveal that large numbers of seabirds are killed by oil throughout the winter, peaking in January–March. These surveys are carried out systematically from September to March when over 2000 km of beaches in the U.K. are patrolled by ornithologists who record the numbers of dead birds found and the percentage of them that is oiled; 3000 km of beaches in western Europe are similarly surveyed in February each year. The large number of dead birds picked up may be an index of the mortality that is occurring but certainly is not an absolute estimate of the numbers of birds dying. Even as an index, the data provided by beached bird surveys may be subject to error and their reliability has been challenged by Bourne (1976) and others. Dead birds on the surface of the sea are transported both by the surface water drift and by winds and, given particular weather systems, may be aggregated and fetch up on particular beaches. These patterns may vary from month to month and year to year and could be misleading in terms of the location of particular mortalities. Further problems arise relating to the cause of death, and it is admitted that a small proportion of oiled birds may be contaminated after death. In addition it is known (N.E.R.C. 1971) that seabird mortality may result from the synergistic effects of various stresses due to weather and pollution

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so that the proportion of dead birds that show some signs of oil contamination may not accurately reflect the mortality due directly or solely to oil pollution.

There are several estimates of the numbers of birds that might be killed in the North Sea or the northwest Atlantic by oil pollution. Mead & Baillie (1981) state that in the winter of 1980/1, one of the worst for seabird mortality due to oil, 60000 dead oiled seabirds were recorded on beaches in western Europe. This figure includes the very high mortality of 30000 birds picked up on the Skagerrak in early 1981. It is impossible to estimate the numbers of birds that actually died. R.S.P.B. (1979) gives data on the numbers of birds picked up on beaches and the proportion killed by chronic oil pollution or specific incidents, and gives values averaging about 5500 dead birds per annum from British beached bird surveys from 1971-79, of which 29% or 1600, are oiled. This would have to be multiplied by a factor of at least 2–10 to estimate the numbers actually dying from oil contamination. Much less well founded is the estimate that 150000–450000 birds, mostly auks, ducks and gulls, may be killed by oil in the North Sea and North Atlantic each year (Tanis & Mörzer-Bruyns 1968).

It is important to try to relate these large numbers of dead birds to the populations from which they come. There are a number of difficulties in doing this. Seabirds are known to be very mobile at sea and there are complex patterns of distribution of different components of populations, and different populations of the same species. Accordingly, birds killed in the North Sea in winter may be derived from populations breeding over a very wide area of Western Europe. Similarly birds killed in the western approaches or the eastern Atlantic will, depending upon the time of year, be derived from different geographical breeding populations of the various species. It is therefore very difficult to establish the actual numbers of seabirds present in different areas of the sea at different times of the year, and therefore to relate precisely the numbers of dead birds picked up on beaches to the numbers and provenance of the birds that are at risk locally at the time when the mortality occurs.

Characteristics of seabird species

Before attempting to relate mortality to the populations of the affected species we must consider some characteristics of the populations of the main groups of seabirds. I shall concentrate primarily on the auks (family Alcidae), petrels (Procellariidae) and gulls (Laridae) and shall mention also penguins (Speheniscidae) and sea ducks (Anatidae). Among these, auks are the most vulnerable to oil pollution in British waters, though considerable numbers of ducks and fewer of the more aerial petrels and gulls are also killed by oil (Bourne 1976). Some species of duck concentrate in large numbers in autumn moult flocks when they might be flightless, or in other areas in winter may be particuarly vulnerable (Milne & Campbell 1973). In the Southern Hemisphere some of the penguins that breed at lower latitudes are known to have suffered large mortality due to oil pollution (Frost *et al.* 1976; Jehl 1975). The most relevant population characteristics of these groups are the following.

(i) *Delayed maturity*

Most groups of seabirds do not breed until they are several years old (table 1). During the pre-breeding phase of their life their annual cycle and pattern of distribution may be very different from those of breeding adults. This is considered in more detail below.

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(ii) *Low breeding rate*

Most seabird groups are characterized by a very low breeding rate (table 1). Most extreme are the large albatrosses, the King Penguin *Aptenodytes patagonica*, and the tropical frigate birds *Fregata* spp. and Abbott's Booby *Sula abbotti*, which can rear a single chick only at 2 year intervals (Nelson 1971, 1976). Petrels lay only a single egg each year and are unable to replace it should it be lost even immediately after laying. The auks characteristically lay a single egg but are capable of replacing it and successfully rearing chicks from the replacement provided that

TABLE 1. AGE AT FIRST BREEDING, CLUTCH SIZE AND ADULT MEAN ANNUAL SURVIVAL IN CERTAIN SEABIRDS

	age at first breeding years	normal clutch size	mean annual survival rate of adults (%)	references
auks				
Guillemot	3–7	1	94	Birkhead & Hudson (1977)
Razorbill	4–5	1	91	Lloyd & Perrins (1977)
Puffin	4–5	1	95	Ashcroft (1979)
petrels and shearwaters				
Fulmar	9.2	1	97	Dunnet & Ollason (1978*a*), Ollason & Dunnet (1978)
Manx Shearwater	5–6	1	80–95	Perrins *et al.* 1973
gulls				
Herring Gull	5.25	2–6	91–96	Chabrzyk & Coulson (1976), Kadlec & Drury (1968)
Kittiwake	3–5	1–3	81–86	Coulson & Wooller (1976)
penguins				
Jackass	3–4	1–2	91.5	Siegfried & Crawford (1978), Frost *et al.* (1976)
Royal	7 (5–11)	1 (2)	> 86	Carrick (1972)
ducks				
Eider	2–3	4–5	93	S. R. Baillie (personal communication)
Common Scoter	2–3	7–9	77	Cramp & Simmons (1977)

relaying takes place early enough. Among the penguins there is a range of clutch size, with several species such as the Emperor Penguin (*Aptenodytes forsteri*) and the King Penguin laying only a single egg whereas some species of the genus *Eudyptes* lay a clutch of two with one egg smaller than the other, and other species such as *Pygoscelis antarctica* may have a clutch of two or three. The gulls in general have larger clutches and a greater capability of replacing lost clutches, and this applies also to the sea ducks, which have quite large clutch sizes on average, although smaller than those of freshwater ducks (Milne 1974; Bengston 1972).

(iii) *Long life*

Many seabirds enjoy extremely high mean annual survival rates as adults (table 1). While it is accepted for many birds with a low annual survival rate that a constant expectation of further life throughout their lives is normal (Lack 1954), this assumption is less easily made in the context of seabirds with a very small annual mortality rate. Thus for Fulmars, *Fulmarus glacialis*, the mean annual survival rate of adults of 97% leads to a constant expectation of further life, throughout adult life, of about 33 years. This implies that the mean duration of

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adult life for Fulmars is also 33 years. A further, and less acceptable, implication of this model is that starting with a cohort of 1000 adults the last bird would die after 228 years, for 10000 the equivalent age would be 302, and for 100000 birds, it would be 378. It does not seem likely that Fulmars could reach such great ages let alone have the same expectation of further life as young birds when they do. However, all the estimates of survival rates in table 1 are derived from the model, which assumes a constant survival rate throughout adult life. For short-term studies dealing with the survival from year to year of a marked sample representative of all age groups in the population the mean figure may be fairly accurate. However, in long-term studies, where new birds are marked each year and the survival of these birds is studied over the succeeding years it could be that the representativeness of the sample may be biased in favour of relatively younger adults. If, as seems plausible, the mortality rate does in fact increase with age in some way, the latter type of study could lead to an overestimate of survival rate. However, no evidence is yet forthcoming to show how the mortality rate varies with age in these long-lived seabirds, and the claim by Dunnet & Ollason (1978*a*) to have demonstrated it for Fulmars has not been sustained (Ollason & Dunnet, unpublished).

(iv) *Dispersal at sea*

Seabirds by definition spend much of their time at sea. All, however, must come ashore to breed, and many do so in large concentrations at favourable breeding sites. During the breeding season the adults use those areas of the sea that they can exploit from their breeding centres, but for the rest of the year or before they attain breeding age they may move over very considerable distances. The dispersal of seabirds at sea is perhaps the most difficult aspect of their ecology to study, and it is difficult to accumulate accurate quantitative and qualitative data (Bourne 1963; Brown 1980*a*, *b*). There are several aspects, which we may consider separately.

(*a*) *Distribution of pre-breeding and breeding components of seabird populations*

It is now well established for the Fulmar that birds in the first 2 or 3 years of their life may cross the Atlantic from Britain and extend north into the Arctic Ocean (Macdonald 1977). As they grow older, so the ringing recoveries indicate that birds do not move so far from their native or breeding areas and most of the recoveries of Fulmars ringed in Britain more than 4 years old are within a few hundred kilometres of the British Isles. Similarly, in Kittiwakes, *Rissa tridactyla* (Coulson 1966), Common Guillemots, *Uria aalge* (Mead 1974; Birkhead 1974), Razorbills, *Alca torda* (Lloyd 1974; North 1980) and Puffins, *Fratercula arctica* (Harris 1982), young birds generally move to more distant waters in their first winter than do the breeding adults and in some species they may remain there for a year or two.

Though these general patterns are known, there is little information about the patterns in which these age cohorts of the different breeding species are distributed at sea in the years before they become established breeders, or how mobile they are at sea during these years. This provides an interesting analogy with the pelagic larvae of many of the sessile benthic and intertidal marine organisms.

(*b*) *Seasonal aspects of dispersal of breeding birds*

(i) Some species, such as the Common Guillemot and Fulmar, remain near their breeding colonies throughout much of the year (Macdonald 1980; Taylor & Reid 1981). However, winter observations on Fulmars on the Aberdeenshire coast have shown that birds from other

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populations are present there too (Macdonald 1977). However, other species such as the Puffin and Razorbill largely leave the seas around their northern breeding areas and spend the winter farther south in the Bay of Biscay and elsewhere (Lloyd 1974; Mead 1974). Sea ducks, having completed their breeding, commonly aggregate in autumn in large moulting flocks, e.g. Eiders in Shetland (Kinnear 1976) and northeast Scotland (Milne 1965). In winter they gather in other concentrations elsewhere (Milne & Campbell 1973) before returning to their breeding areas in spring.

(ii) Not much is known about the foraging range of breeding seabirds from their breeding colonies. Some crude information on this has been derived by measuring the intervals between incubation stints, and between feeding visits to young birds, but these estimates make a large number of assumptions (Pearson 1968; Furness 1978). Ringing recoveries are usually not specifically helpful in this context but Fulmars known to be breeding adults in Orkney have been recovered either dead or alive during the months of the breeding season throughout the North Sea, up to 600 km from their nest (Dunnet & Ollason 1982). This indicates a very large foraging range for Fulmars, and it is undoubtedly much larger than that of other species of seabirds, such as the auks.

(*c*) *Mobility of seabirds at sea*

Much effort has been expended in attempts to measure the distribution and abundance of seabirds at sea (Bailey 1971; Bailey & Bourne 1972, Bourne 1980; Brown 1980*a*, *b*), and research is currently in progress by the Nature Conservancy Council (N.C.C. 1980). It is clear that species are not randomly distributed at sea but are frequently associated with oceanographic fronts, areas of upwelling and high productivity and are also much influenced by the weather, which affects the sea surface and thereby both the flying conditions for different species and the feeding conditions. It has not so far been possible to predict with any accuracy the patchiness and the distribution or the movements of seabirds while they are dispersed at sea, especially outside the breeding season.

(*d*) *Movements of seabirds between natal and breeding colonies*

Precise information on this subject is usually hard to obtain because most studies are concentrated at single seabird colonies where particular populations have been studied intensively. Searches at neighbouring or distant colonies for birds marked in these studies are usually not possible. However, Harris (1982) has shown that on the Isle of May, in the Firth of Forth, the Puffin population has increased at an average annual rate of 22% over the period 1951–80. Local production of young could result in an overall annual rate of increase of 7%. Clearly there has been a very substantial immigration of new breeders into the Isle of May. Of nestlings ringed on the Isle of May and subsequently found breeding at the age of 5 years, 75% were found breeding in their native colony while 25% were found breeding on the Farne Islands. By contrast, a very small proportion of those nestlings ringed on the Farnes that have subsequently been found breeding have settled on the Farne Islands themselves, which have a very large and stable Puffin population.

For the Fulmar we have estimated that only about 6% of those young birds that survive to be 9 years old (the mean age at first breeding) return to breed on Eynhallow. This is a situation where the Fulmar population in general is expanding and the population on Eynhallow is also increasing at a rate similar to the national rate (Dunnet & Ollason 1978*b*).

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Nelson (1978) and Wanless (1979) have shown that there is much interchange of young Gannets, *Sula bassana*, between the colonies on the west coast of Britain, but very little between the east coast colony on the Bass Rock and other colonies. Duncan (1978) has also shown in a programme of experimentally reducing the populations of Herring Gulls, *Larus argentatus*, on the Isle of May that a substantial number of immigrant birds have settled there from other colonies.

It is therefore clear that the amount of dispersal from native to other colonies is not a specific characteristic, but one that varies considerably in different circumstances. Further, the mechanism by which young birds, which may have spent several years at sea, eventually find and select a colony for breeding is substantially unknown. Nelson (1978) considers that social behaviour may well affect the establishment of new breeders. We know little of the dynamics of the 'reservoir' of potential breeders in terms of numbers, mobility of individual birds and distribution.

Table 2. Approximate estimates of the breeding and pre-breeding components of the populations of selected species of seabirds in Britain and Ireland, and the numbers dying per year, based on calculations and estimates of annual mortality rates

	breeding birds (thousands)	breeders dying annually† (thousands)	pre-breeding birds‡ (thousands)	pre-breeders dying annually‡ (thousands)	total dying annually (thousands)
Guillemot	1458§	87	552	164	251
Razorbill	300§	27	128	38	65
Puffin	1400§	70	599	175	345
Fulmar	312‖	9	335	86	96
totals	**3470**	**194**	**1614**	**463**	**757**

† From adult survival rates from table 1.
‡ Based on 30% fledging success, 50% mortality in first year, 16% annual mortality until breeding (Mead & Baillie 1981), and age at first breeding from table 1.
§ R.S.P.B. (1979). ‖ Cramp *et al.* (1974).

Size of populations at risk

'Operation Seafarer' was designed to locate all the coastal breeding colonies of British seabirds and to assess the numbers of birds in them (Cramp *et al.* 1974). There has been subsequent work summarized by the R.S.P.B. (1979) to update some of the estimates of breeding numbers, and it is known that almost all the species have been increasing in numbers over the last decade so that estimates now more than 10 years old will be underestimates. However, my purpose is to establish the orders of magnitude rather than precise estimates of numbers, and I have reproduced the appropriate figures for four of the commoner species from Cramp & Simmons (1977) and R.S.P.B. (1979) in table 2.

From what we know about the age of first breeding of these species, and using the assumptions made by Baillie & Mead (1982) that the mortality in the first year is 50% followed by an annual rate of 16% during years of immaturity, and also assuming that on average each pair will produce about 0.3 young each year, it is possible to make a rough estimate of the size of the pre-breeding components of these populations. These data are provided in table 2 and the total number of birds related to the breeding populations of Britain and Ireland can then be estimated. Of course, from the considerations given above, there are enormous problems in

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relating these numbers to any particular geographical area, and it is clear that the geographical area occupied will change greatly for different species and at different times of the year.

Other sets of estimates of the numbers of seabirds in the North Sea have been provided by Evans (1973) and Bourne (1980). In an attempt to determine the avian resources of the North Sea, Evans calculated the numbers of birds breeding around the North Sea, and arrived at a figure of 1 770 000 birds of the four species listed in table 2: about half the estimate for numbers breeding in Britain and Ireland. Bourne (1980) estimates 500 000 breeding large auks and petrels in the North Sea and Baltic, to which may be added a further 1 456 000 auks and 711 000 petrels to include Ireland, the Hebrides, Orkney and Shetland. Those estimates are all

TABLE 3. ESTIMATED NUMBERS OF SEADUCKS (THOUSANDS)

	alive in British waters‡	dying annually†	in winter, Britain and Ireland§	dying annually†	in winter, W. Europe§	dying annually†
Scaup	35	3.5	5–10	0.5–1	150	15
Eider	50	5.0	50–60	5–6	2000	200
Long-tailed Duck	15	1.5	15–20	1.5–2	500	50
Common Scoter	50	5.0	25–30	2.5–3	400	40
totals		**15.0**		**9.5–12**		**305**

† An overall mean annual mortality rate of 10% is used, based primarily on detailed data available for the Eider, perhaps the most seabird-like of the ducks in terms of population biology (Milne 1974, S. R. Baillie, personal communication), but the values for annual rates of these species by Cramp & Simmons (1977) vary between 23 and 52% so that numbers dying naturally may be 2–5 times as large as given here.
‡ N.E.R.C. (1977). § R.S.P.B. (1979).

consistent with a breeding population of these species of about 3 000 000 birds in Britain and Ireland. In addition there are large numbers of sea ducks in and around the North Sea during winter, and an estimate for the numbers in British waters has been provided by N.E.R.C. (1977); the numbers wintering in western Europe have been further estimated at approximately 3 500 000 (R.S.P.B. 1979) (table 3), with up to 1 500 000 in Danish waters (Joensen & Hansen 1977).

It is possible, from the information that we have on the 'normal' mortality rates experienced by these species, to estimate, again very approximately, the numbers of birds from these populations that may be expected to die each year (tables 2 and 3). These four species constitute about 70% of the breeding seabirds at risk to oil pollution in European waters in winter, and the other 30% will, on average, have higher natural mortality rates. Thus the numbers estimated to die as shown in tables 2 and 3 will be underestimated by at least 30%.

It can be seen from this very broad approach to the problem that hundreds of thousands of seabirds, indeed well over a million if all species are included, must die each year in western European waters from 'natural' causes and that the estimated annual mortality in these populations from oil pollution is of the order of tens of thousands. It is extremely difficult to compare these figures critically or to make any detailed assessment of them because we know little about the timing of these mortalities (though the oil-induced mortality is mainly in winter), the locations of the birds, the numbers actually dying or the causes of 'natural' mortality. A crucial question in comparing these values is whether or not the oil-induced mortality is additional to 'natural' mortality or whether there is a compensatory mechanism at work. At present we know nothing about this.

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Detecting change in breeding populations

Since the publication of the results of 'Operation Seafarer' (Cramp *et al.* 1974) the R.S.P.B. has undertaken a continuing monitoring programme of selected species and colonies around the U.K. (Stowe 1982). In addition a number of detailed monitoring programmes have been developed in relation to major new developments, and there is considerable coverage of seabird colonies in both Orkney and Shetland each year (Wanless *et al.* 1982; Richardson *et al.* 1981).

It is important to recognize that these monitoring activities refer generally to discrete breeding colonies or parts of them that may be assumed to be representative of regional or national populations. It is, however, extremely difficult to relate local and regional changes in breeding populations to the mortality of birds at sea as indicated by, for example, beached bird surveys or by major oiling incidents, since the last two are not in any sense colony-specific in most circumstances.

A great deal of work has been carried out on monitoring the numbers of seabirds in breeding colonies and a number of instruction booklets have been produced (Seabird Group (undated); Nettleship 1976; Birkhead & Nettleship 1980). There are also a considerable number of papers providing information on such matters as patterns of attendance of seabirds at their breeding colonies, both seasonally and throughout the day, and the effects of weather, tide and other factors on attendance (see, for example, Coulson & Horobin 1972; Lloyd 1973; Birkhead 1978; Macdonald 1980; Slater 1980). Work has also been done on the variability of results provided by different observers counting the same colonies (Dunnet 1977) and on the use of photography and direct counting (Harris 1976). There are additional problems in the selection of colonies, parts of colonies and specific patches within colonies that may be determined by their visibility and safe accessibility for the observer, but may not be representative of the population as a whole (Dunnet 1980). There is also a need to search for newly established colonies. These difficulties lead to considerable lack of precision in the estimates of the numbers present at any sample site or colony. There have been claims of accuracy for particular sampling procedures down to 5% (Lloyd 1975), but a more realistic figure especially for those species that do not build nests (e.g. Guillemot, Razorbill and Fulmar) may be between 10 and 30% (Wanless *et al.* 1982). In addition to these technical problems there is a considerable natural fluctuation in the numbers of birds at particular colonies even though longer-term trends may be apparent (see, for example, Dunnet *et al.* 1979).

However, despite these problems of precision, monitoring indicates that almost everywhere seabird populations are on the increase in Britain and Ireland (Stowe 1982; Wanless *et al.* 1982; Heubeck 1981), though there are some locations where some species show declines. For example, towards the edge of their breedings ranges on the coast of Brittany populations of auks, subject to chronic and sporadic massive pollution, are still declining (Bourne 1976) and in Shetland some colonies of Kittiwakes have been shown to decline while others have increased (Heubeck 1981).

Recruitment to the breeding population

Earlier in this paper I have distinguished between the pre-breeding and breeding components of populations of seabirds. We recognize that the sizes of seabird populations are generally determined from estimates of the numbers of birds breeding at particular colonies and changes

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in these populations from year to year will be brought about by some combination of adult mortality and the recruitment of new birds to the breeding population. In general, since populations of seabirds in this part of the world have been increasing over recent years, recruitment exceeds mortality. It is well established that young birds settling to breed in particular colonies may not have been born there, and it has also been demonstrated that the proportions of new breeders that establish themselves in their native colonies vary considerably within species from one colony to another, and between species. There has been some speculation about the mechanism of recruitment that involves both the mobility and dispersal of birds in their pre-breeding phase, and also the factors that determine the colony in which the recruit eventually settles. It has been suggested that the last problem may involve social factors, since seabird breeding colonies are highly organized socially. The resilience of seabird populations after unusual mortalities may thus depend greatly on the wellbeing of the pre-breeding component of these populations, and on the mechanisms by which young birds are eventually recruited to particular breeding colonies.

We have been studying Fulmar populations on the island of Eynhallow in Orkney since 1950, and for each year we have information on the number of breeding pairs on the island, the annual survival rate of breeding adults and an approximate index of the number of new recruits coming into the population (Dunnet *et al.* 1979; Ollason & Dunnet, unpublished). In considering the observed population changes in this species over 30 years we have tried to assess the relative importance of variations in the survival rate of the breeding adults and the recruitment of new birds. A preliminary simulation model showing the relation between population change, survival and recruitment, which was constrained to have a minimum recruitment value of zero (that is that no birds that once bred on the island ever go and breed elsewhere) produced a pattern of population change that had substantially less variability than the observed. It is, for example, impossible to account for observed drops of up to 35% in the number of breeding birds in consecutive years given a very low annual mortality rate, averaging 3% and varying between 0 and 12%, in terms of mortality alone, even with zero recruitment. Accordingly we have had to consider the possibility of allowing recruitment to be 'negative', that is to accept that in some years or some circumstances birds, presumably those that have recently bred for the first time in the colony, may not breed at all, or may depart and go elsewhere. Making allowance for this possibility a model can simulate very much more accurately both the changes in population size and the range of variation in population size over the relevant period (22 years) for which acceptable data are available. The lack of correlation between the change in the numbers of breeding adults and the adult survival rate over the appropriate year interval, and the very strong correlation between changes in the numbers of adults and the crude indices of recruitment (Ollason & Dunnet, unpublished), indicate the very great importance of recruitment to fluctuations in the size of the Fulmar population on Eynhallow. Predictions from the model are that with the highest observed rate of recruitment the population will increase at a rate of 44% per annum even if adult mortality is maintained at its maximum observed level (0.1176), while even with minimum observed mortality rate (0.0025) the population will decline at an annual rate of 34% and reach the last pair in 13 years, if recruitment rate is held at its lowest observed value of −0.332 (Ollason & Dunnet, unpublished).

This relates very strongly to the analogous situations described earlier in this symposium in relation to sessile marine organisms and fish stocks. It does emphasize our lack of knowledge of the processes involved in recruitment and the need for further information in order to achieve

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a proper understanding of it. I suggest that a way forward might be to embark upon the use of transmitters and satellite tracking in both the general area of trying to understand something about the mobility of birds during their pre-breeding lives, and also, in more intensive studies, the mobility of potential recruits and the pattern of their activities in relation to possible colonies in which they may become established.

Conclusion

I have attempted in the broadest terms to relate the mortality of seabirds due to oil pollution to the expected 'natural' mortality of these populations. There have been very substantial difficulties in achieving this. While seabirds are present at their breeding colonies they can be identified as localized populations, but for much of the year breeding adults are widely dispersed at sea, presumably intermingling with other populations of the same species and with part of the large pre-breeding components of these populations. In species with long-delayed maturity, immature birds in their earliest years may have dispersal patterns at sea quite different from those of the breeding birds, and details of their distribution and mobility are largely unknown. Estimates of population size of seabirds are derived almost entirely from numbers present at breeding colonies, and estimates of 'natural' mortality rates are derived from intensive studies concerned with the return of breeding adults to the colonies in which they have become established. Estimates of survival rates of pre-breeding birds are based on a number of difficult assumptions. Direct information about dead birds comes from those washed up on beaches, some of which may have been ringed and some of which may be studied in detail by using biometric and other biological techniques. It is, however, usually impossible to relate these corpses to any particular breeding colony, and it is also difficult to be sure about the place where death occurred or its cause. However, the conclusion seems inescapable that the numbers of birds killed by oil are relatively small in relation to the total expected annual mortality from these seabird populations. What is not known is whether this mortality is additional to the normal mortality or is compensated for.

The information, again not very precise, that comes from the monitoring of breeding seabird colonies indicates that in general the populations of all species are increasing. There are some local areas where decreases occur, particularly in southwest England and the Brittany coast, which is the edge of the breeding range of Guillemots and Razorbills. It is also clear that some colonies may be decreasing, while most are not. There are considerable problems in interpreting these data because of the natural fluctuations taking place from year to year at breeding colonies and because of technical difficulties in sampling and assessing the number of breeding birds present. However, monitoring at breeding colonies shows no general trend of decrease in any seabird species at present; indeed the trend of increase is widespread.

It is important to see these data in the context of a situation in which seabirds seem to be experiencing a particularly favourable general environment (Cramp *et al.* 1974). Several species have been increasing for decades: Fulmar (Fisher 1966), Kittiwake (Coulson 1974) and Gannet (Nelson 1978). This may be due to a reduction in the exploitation of seabird resources by man (Fisher & Lockley 1954; Cott 1953), to the effects of commercial fisheries which, apart from making offal available at the sea surface (Fisher & Lockley 1954), could conceivably have led to a greater availability of small fish and other organisms near the surface for seabirds, or to changes in climate (Salomonsen 1965). It has also been shown experimentally that several

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species with small clutches are able to rear double-sized broods successfully, e.g. Gannet (Nelson 1964) and Great Skua (Furness & Hislop 1981), suggesting that food is plentiful. It must be recognized that should these generally favourable features of the environment change, for example by an increase in commercial fisheries for industrial purposes (cf. Schaefer 1970; Crawford & Shelton 1978), populations may not be in such a buoyant state, and that mortalities of the magnitude that we have demonstrated to be due to oil pollution may become much more significant in terms of population dynamics.

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Discussion

D. J. Crisp, F.R.S. (*Marine Science Laboratories, Menai Bridge, U.K.*). Fishing practice and oil spills have in common the danger of destroying a significant part of a biological resource. Fishery biologists have recognized that it is important to be able to relate fishing mortality to the particular stock of breeding individuals, rather than to species as a whole. Therefore they need to find the size and limits of each stock comprising the whole population. To this end, genetic markers (blood groups, isozymes and other polymorphic components) have been used fairly extensively to identify panmictic subpopulations. Perhaps these techniques should be applied equally to ornithological conservation problems. Once the breeding groups have been recognized, numbers of moribund birds could be referred to their origin, whether or not any of them were ringed, since every individual carries its own set of genetic tags.

G. M. Dunnet. Some preliminary work has been done in relation to the use of genetic markers such as isozymes in the context of seabird populations, but nothing that I am aware of has yet been published. This is undoubtedly an area worth investigating.

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G. Conan (*C.O.B.–C.N.E.X.O., Brest, France*). It has been stated in the press that many of the seabirds oiled and killed after the *Amoco Cadiz* spill were in fact migrating birds with nesting colonies along the British Isles. Is it known to what extent the *Amoco Cadiz* spill will have a long-term impact on some local nesting colonies in Great Britain?

G. M. Dunnet. I should be very surprised if it were possible to detect any long-term changes in local seabird colonies in Great Britain that could be attributed to the mortality associated with the *Amoco Cadiz* oil spill.

W. R. P. Bourne (*Zoology Department, Aberdeen University, U.K.*). It was postulated by Joseph Grinnell as long ago as 1920 (*Condor* **22**, 101–110) that the high survival but low productivity rates of seabirds could render them vulnerable to new unstabilizing factors such as increased disturbance of the breeding-places by man or oil pollution of the sea. When there were severe losses of auks in western Britain, due to first the *Torrey Canyon* disaster and then the Irish Sea birdkill in the late 1960s, the Seabird Group and the Royal Society for the Protection of Birds started sample breeding censuses to verify this, with results summarized in the evidence presented by the R.S.P.B. to the Royal Commission on Environmental Pollution (R.S.P.B., *Marine oil pollution and birds*, 1979) which has escaped much comment. It was found that after the Irish Sea birdkill the birds returned late the following spring and many did not breed, but then the situation returned to normal. Much the same thing also occurred when there were massive losses of birds due to oil pollution at Flamborough Head, Yorkshire, early in 1977, so that it appears that the bird populations are not as vulnerable as we thought.

The population dynamics of seabirds have been discussed by N. P. Ashmole (*Ibis* **103**, 458–473), who concluded that their low reproductive rate is an adaptation for overcrowding and competition for food where they are compelled to concentrate at a limited number of possible breeding sites. It follows that if their numbers there are reduced this density-dependent limiting factor will cease to operate and their productivity is likely to improve until it comes into operation again. In fact, observations summarized by C. M. Perrins (*Ibis* **120**, 128–129) imply that the first response to losses from the breeding population is for young birds at sea to return to the colonies to breed earlier. The Seabird Group–R.S.P.B. beached bird surveys (summarized in the Eighth Report of the Royal Commission on Environmental Pollution) suggest that this is then followed by an improved survival of the young birds at sea, which tend to form the majority of those washed up dead on beaches, in subsequent winters.

Thus, for example, after heavy mortality due to a series of hard winters, among other factors, in the late 1960s, there was an improved rate of survival during milder winters in the mid-1970s until the population had built up again, and further hard winters started to cause more mortality recently, culminating in a massive wreck of birds all down the west coast of Europe last winter. While many of the birds appear to have died as a result of oil pollution, the general pattern of the mortality agrees more closely with natural processes, notably prolonged gales, likely to bring the birds into vulnerable situations in southerly inshore waters, than with that of oil pollution itself, which one would expect to be more uniformly distributed through the year. It follows that while (as observed by the Royal Commission) there are ample grounds to object to oil pollution because it kills the birds cruelly, in the long term it is only reinforcing the effects of natural processes usually operating on a much larger scale, to which they are specifically adapted to respond.

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