THE PELAGIC ECOLOGY OF SEABIRDS*

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ABSTRACT

Recent developments in the study of the pelagic ecology of seabirds are described, with particular emphasis on work off eastern Canada and in the eastern Canadian Arctic. Quantitative mapping can be used to provide insights into factors controlling seabird distributions. The distributions of Cory's Shearwater (*Puffinus diomedea*) and the Greater Shearwater (*P. gravis*) in the northwest and southwest Atlantic are compared; the very different summer and winter pelagic habitats of Wilson's Storm-Petrel (*Oceanites oceanicus*) are described. It is suggested that the distributions of the Northern Fulmar (*Fulmarus glacialis*) and the cold-water zooplankton fauna off Newfoundland may be controlled by a common factor. Dovekie (*Alle alle*) winter distributions are related to an area of vertical turbulence on the western slope of the Grand Banks, and summer distributions to high-latitude areas where there is an early "biological spring." On a finer scale, the feeding areas of Thick-billed Murres (*Uria lomvia*) from a colony in Hudson Strait are described; birds were flying at least 75 km to feed.

The problems of making detailed correlations between seabird distributions and oceanographic factors are discussed. The use made by Greater Shearwaters and Red Phalaropes (*Phalaropus fulicarius*) of tide rips in the Bay of Fundy is described, and the results of interdisciplinary work relating these birds to physical and biological oceanographic factors are summarized.

The possibilities of using quantitative seabird data to define, compare, and contrast pelagic seabird communities, and to link these with zooplankton communities, are discussed.

Most work on seabird ecology has been done on breeding birds, and a great deal is now known about breeding success, feeding ecology, population dynamics, and so on, during the breeding season. Yet seabirds spend the greater part of every year away at sea, and we know very little about their distributions, let alone their ecology, at such seasons. The reason pelagic studies have lagged so far behind is basically a logistic one. It is only with the recent boom in oceanographic research that ornithologists have been able to get to sea often enough to collect the basic information on seabird distributions necessary for an understanding of the birds' pelagic ecology, and the same boom has produced the framework of oceanographic knowledge which they need in interpreting these distributions. Even so, although work on the pelagic ecology of seabirds has expanded greatly within the last 15 years, the subject is still only at the stage that studies of terrestrial ecology reached 50 years ago.

This paper examines, in a fairly speculative way, the preliminary results of these investigations. It is based primarily on the work which the Canadian Wildlife Service has been doing in eastern Canadian waters since 1969 (Brown, Nettleship *et al.*, 1975; Brown, 1977). Most of this has been done from oceanographic vessels, though we have recently developed an aerial census technique—a system which allows wider, more frequent and more detailed coverage than is usually possible from ships (Johnson *et al.*, 1976; Nettleship and Gaston, 1978). The quantitative base for our shipboard observation is the number of birds seen during a standardized 10-minute watch, and is modelled on the Smithsonian Institution's POBSP survey

(King, 1974). We now have reasonably good map coverage all year for the waters off Atlantic Canada, but there is still much to be done in the eastern Arctic.

The quantitative mapping of distributions is of course only the first step toward an understanding of the birds' pelagic ecology. Even so, the maps can provide insights into the factors which may influence those distributions.

1. Cory's Shearwater (*Puffinus diomedea*) and the Greater Shearwater (*P. gravis*) are two large shearwaters which are non-breeding visitors to eastern North American waters during the summer. The maps show that their distributions have virtually no overlap: Cory's is a bird of the warm slope water at the edge of the Gulf Stream, while the Greater occurs in the cooler waters to the north (Brown, 1977: maps 2 and 3). This segregation of two similarly sized, closely related species is what one would have predicted from Lack's (1971) competitive exclusion principle, although differences in foraging technique make one wonder about the extent to which the two could actually be competing for food (Brown *et al.*, 1978). Their preferred habitats, as indicated by surface water temperatures, seem very similar in both the North and South Atlantic (Brown, Cooke *et al.*, 1975; Brown, Nettleship *et al.*, 1975). This may seem obvious, but in fact it is not true of all trans-equatorially migrating seabirds. By contrast, Wilson's Storm-Petrel (*Oceanites oceanicus*) breeds in the Antarctic and Subantarctic but "winters" in the northwest Atlantic at the warmer edge of the Boreal Zone. The reasons for this striking seasonal discrepancy are not yet known.

2. Off the Atlantic coast of Canada, Northern Fulmars (*Fulmarus glacialis*) are commonest in waters influenced by the cold Labrador Current. The southern edge of their pelagic range retreats some 500 miles northward between May and September (Brown, Nettleship *et al.*, 1975); this withdrawal coincides with a withdrawal of cold-water zooplankton species (Vladimirskaya, 1965). Further investigation might well show that birds and zooplankton are in some sense part of the same marine community, and that both are reacting to the same seasonal changes in pelagic habitat.

3. Dovekies (*Alle alle*) are common off eastern Canada in winter, yet they are by no means uniformly distributed. Fig. 1 shows the situation on the southern Grand Bank early in 1971. Unlike murres (*Uria* spp.), which were fairly evenly distributed over the Bank and both western and eastern slopes, the Dovekies were concentrated over the western slope. In this area the bottom rises abruptly from 2000 m to 100 m, and this immense cliff stands squarely across the path of the Gulf Stream. It seems likely that the vertical turbulence as the current flows up and over it brings food up into the surface layers and into the Dovekie's reach, much as tide rips do in the Bay of Fundy (see below).

4. In some cases the distribution of colonies can give some clues on pelagic factors important in the birds' ecology. Dovekies breed in the high Arctic from northwest Greenland east to Severnaya Zemlya (Dement'ev and Gladkov, 1968; Fisher and Lockley, 1954; Norderhaug *et al.*, 1977; Salomonsen, 1950). The largest colonies tend to be the most northerly, and comparison with an ice atlas (*e.g.* Anon., 1958) shows that these are either in waters close to pack-ice which
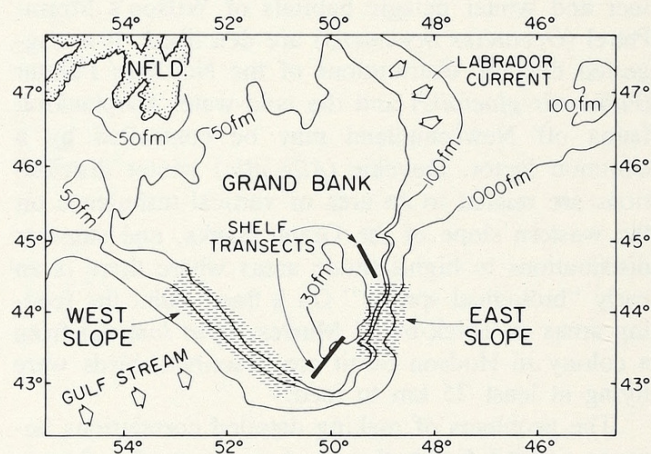
DISTRIBUTIONS OF DOVEKIES *ALLE ALLE* AND MURRES *URIA* SP. ON THE SOUTHERN GRAND BANK 27 FEB - 8 MAR 1971

	WEST SLOPE	SHELF TRANSECTS	EAST SLOPE
NO.10 MIN. WATCHES	13	11	28
AVERAGE NUMBER OF BIRDS / 10 MINUTES			
DOVEKIES	34.76	0.27	3.04
P	<0.001		
		<0.001	
MURRES	2.38	5.27	9.89
P		<0.05	

P - SIGNIFICANCE LEVEL OF DIFFERENCES BETWEEN PAIRS OF AVERAGES, USING THE MANN-WHITNEY U-TEST
ONLY SIGNIFICANT DIFFERENCES ARE SHOWN

Figure 1. Dovekie (*Alle alle*) and murre (*Uria* sp.) distributions on the southern Grand Bank.

never freeze (northern Baffin Bay, west Spitsbergen), or in areas which freeze but are more or less clear of ice by the last half of July, when the chicks hatch. This is an early break-up period for those high latitudes. It implies that the "biological spring," in which zooplankton biomass suddenly increases tenfold, will also be early; it occurs in July on the ice-free Greenland side of Davis Strait, but as late as September on the ice-bound Canadian side (Pavshtiks, 1968). So it seems that the timing of hatching and the siting of the colonies are linked to the presence of an abundant food supply early in the short high-Arctic summer. The fact that daylight is continuous at these latitudes would allow thorough exploitation of that food supply, and the birds do indeed appear to forage throughout the 24 hours (e.g. Brown, 1976).

These are all rather general points. However, really detailed, fine-grain mapping can yield a great deal of information, especially if one notes behavior as well as numbers. Flight direction and the percentage of birds sitting on the water (and therefore potential feeders) can be very useful in locating important feeding areas and in estimating the foraging range of breeding birds. Fig. 2 gives an example: it shows the average numbers of Thick-billed Murres (Uria lomvia) seen at various points on a transect past the very large colony at Digges Island/Cape Wolstenholme, in Hudson Strait, along with directions of flight and proportions of sitting birds. On the days of the transect most of the birds were evidently foraging west or northwest of the colony. The largest numbers, and the highest percentage of sitting birds, were just north of Mansel Island; the temperature and salinity differences in that area suggest that the birds were attracted to a boundary between water types, where food may be concentrated (e.g. Pingree et al., 1974). The flight directions clearly indicate that these were birds from the Digges colony. One may doubt whether they could have been flying 75 km out to Mansel Island to collect food for the chicks which must have been on the colony at that time (see Tuck, 1961). But it is not out of the question; murres carrying fish—presumably for chicks—have been seen returning to Prince Leopold Island, Lancaster Sound, from distances as great as 60 km (Nettleship and Gas-

ton, 1978: Fig. 16). The fact that murres can forage at such ranges shows the need for a re-examination of the geographical scope of environmental impact surveys, for example, and Cody's (1973) hypotheses on the structure of alcid species communities.

The next stage in trying to understand something about the pelagic ecology of seabirds is to try to make some direct links between the distributions of the birds and of oceanographic factors, but in more specific ways than in the scenarios outlined above. At the physical oceanographic level this is fairly simple, if not very informative. Water types can be defined by their temperature/salinity ratios (e.g. Pickard, 1971), much as terrestrial habitats can be defined, for example, by the acidity of the soil. Brown, Cooke et al. (1975) have linked the distributions of certain seabirds to those of water types in the Chilean fjords, and Pocklington (1979) has done the same for much of the Indian Ocean. This does not necessarily mean that the birds are responding to temperature or salinity as such, but that they are part of a biological community which can be defined by these parameters. The actual link is presumably some prey organism. Unfortunately, attempting links at the biological oceanographic level is much more difficult. To begin with, it requires an interdisciplinary approach. But oceanographers are still reluctant to think of seabirds as legitimate subjects for research, so the initiative has to come either from an ornithologist, who usually lacks the necessary background, or from an ornithologically-minded oceanographer, who usually lacks the time. Moreover it is usually impractical to collect birds for their stomach contents from a large oceanographic ship, or to collect fish and plankton precisely where the birds are feeding. Collections of both kinds can easily be made from a small boat (e.g. Bédard, 1969; Hartley and Fisher, 1936), but this usually limits one to inshore areas, and thus to coastal species, or to pelagic species in the breeding season only.

Canadian Wildlife Service work in the Bay of Fundy shows what one can expect to come out of such an interdisciplinary approach (Brown, in prep.). In late August large flocks of "wintering" Greater Shearwaters and post-
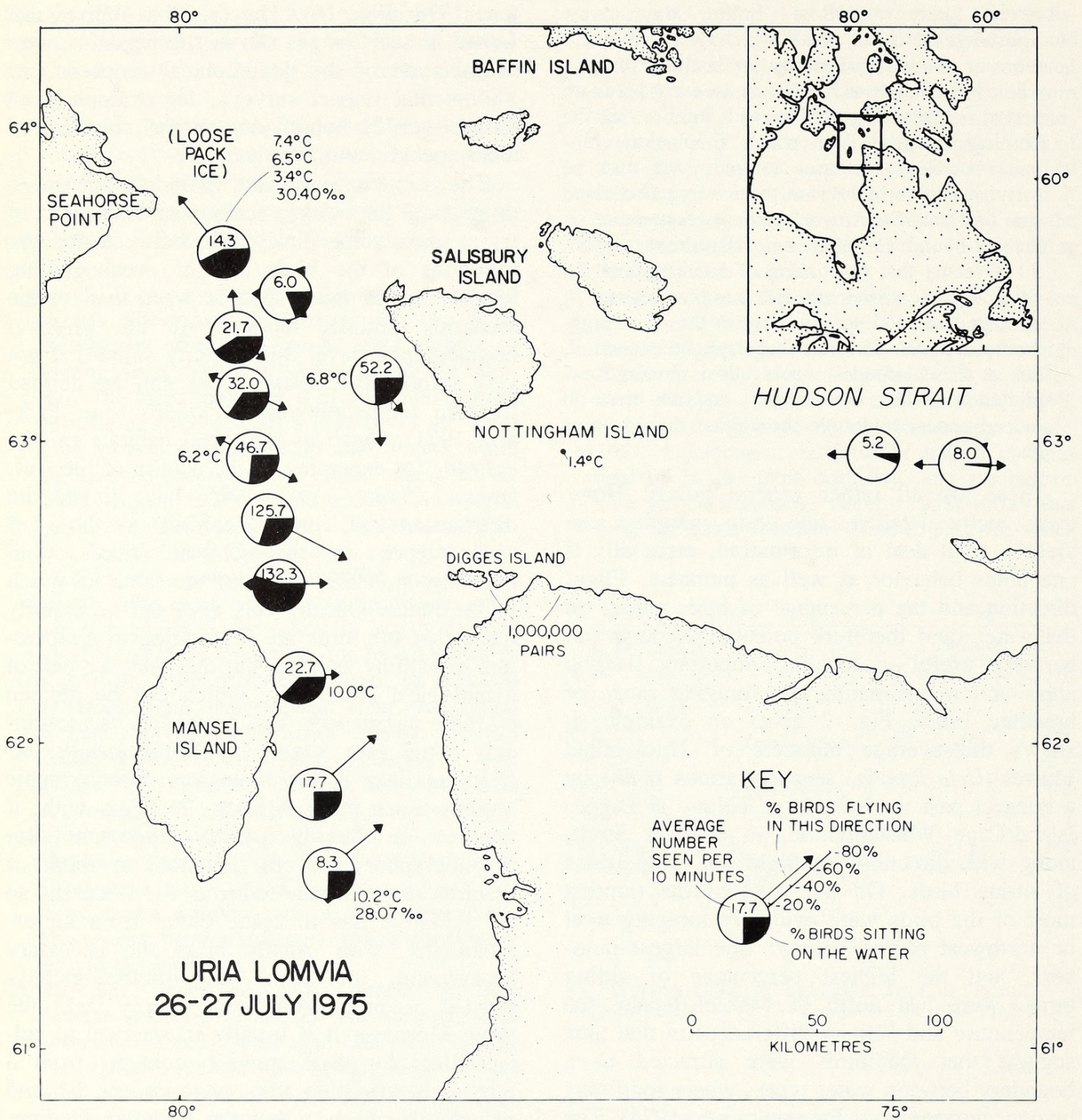
Figure 2. Distributions of Thick-billed Murres (*Uria lomvia*) in western Hudson Strait, as observed from a ship. The two easternmost symbols refer to observations made on 26 July; the remainder were made next day. The observations immediately west of Nottingham Island were made at first light; birds were already returning to the colony, and may have been feeding at night. Averages are based on at least three 10-minute watches. Temperatures (°C) and salinities (‰) refer to surface water.

breeding Red Phalaropes (*Phalaropus fulicarius*) assemble 5-10 km off Brier Island, Nova Scotia. The birds are attracted to an area of turbulence caused when strong tidal streams run up against steep underwater ledges which reach almost to the surface. This creates a "tidal pump" which brings cool bottom water and abundant copepods up to the surface. Both

drift downstream until the cool water sinks beneath the warmer surface water offshore, leaving the copepods trapped at the edge of the convergence line. Red Phalaropes feed on the copepods in the two areas where these are most abundant—immediately over the "pump" and in the convergence line. Both areas are easily identified by the presence of "streaks" of calm water at the surface. The birds rarely feed away from the "streaks," and it is interesting that they feed in similar areas out at sea where food may be locally concentrated: at the offshore oceanic front off Senegal, for example, and in Langmuir circulation cells off Peru (Brown, 1979 and unpublished; see also Pollard, 1977). Meanwhile swarms of the euphausiid *Meganyctiphanes norvegica* also appear at the surface, apparently following the copepods and feeding on them. These are fed on in turn by the shearwaters and by Great Black-backed and Herring Gulls (*Larus marinus* and *L. argentatus*, baleen whales, Mackerel (*Scomber scombrus*), Herring (*Clupea harengus*) and Short-finned Squid (*Illex illecebrosus*); on occasion, the birds also take the fish and squid. In short, the "tidal pump" and the copepods are the physical and biological bases of a short food chain supporting a marine community of which the seabirds are an integral part. A comparable "pump"-copepod-euphausiid system exists across the Bay in Head Harbour Passage, New Brunswick, but the community it supports shows two intriguing differences from Brier Island—for as yet unexplained reasons Bonaparte's Gulls (*Larus philadelphia*) replace the shearwaters, and there are Northern Phalaropes (*Phalaropus lobatus*) instead of Red. The investigation is continuing.

Quantitative information on seabirds at sea can be used for more than just the preparation of distribution maps. One can use it to define objectively groups of species which regularly occur together, just as Fager (1957) and Fager and McGowan (1963) have done for zooplankton communities. If one applies Fager's "index of affinity" to the seabird species which occur together in 10-minute watches, it appears that, for example, the offshore summer seabird community in Baffin Bay includes only four

species: Northern Fulmar, Black-legged Kittiwake (*Rissa tridactyla*), Thick-billed Murre, and Dovekie. These are, respectively, a larger and a smaller surface feeder and a fish- and a plankton-eating diver. Such a segregation is to be expected on the basis of Lack's (1971) principle of competitive exclusion of species with similar diets; it is also clear that Arctic marine habitats are as species-poor in birds as are those on land. It would be worth using this technique to define other seabird communities in order to compare and contrast them; how, for instance, does the Baffin Bay community compare with the equivalent seabird community in the Antarctic? One might also gain some insights into possible key food species by calculating "affinities" for a combined species pool which included both the plankton collected in surface tows and the seabirds seen during those tows. I have in fact begun to do this, but the results so far are inconclusive.

Finally, quantitative information will eventually provide estimates of seabird biomass, and it will be particularly useful to be able to take non-breeding migrants into account, and also periods outside the breeding season. I do not think we yet know enough about the correction factors needed to convert the existing data into any *absolute* estimate of population size and hence of biomass of birds at sea. But we can make rough *relative* estimates of biomass simply by multiplying the average numbers of each species seen per 10-minute watch by its weight, and use these to compare seabird communities in different areas. For example, the relative biomass of seabirds in the Senegal upwelling is only about 6 kg/10 minutes, against more than 100 kg for the Benguela Current, the comparable upwelling in the South Atlantic (data calculated from Brown, 1979; Jehl, 1973; Summerhayes *et al.*, 1974). At first sight the difference is not too surprising, since off Senegal the tertiary productivity of the fish on which most seabirds feed is at most 15% of the figure for Benguela (Cushing, 1971). But this cannot be the whole explanation. Productivity at the southern, least productive end of the Peru upwelling is similar to that off Senegal, yet that area supports a relative seabird

biomass of at least 24 kg/10 minutes. For some reason, seabirds are not using the Senegal upwelling to full capacity.

Why not? The answers will require a "whole ocean" approach—an appreciation not just of the immediate situation off Senegal, but of all the potential food resources available to seabirds over the whole of the North and South Atlantic. Obviously we do not yet know this. But one of the factors must be the lack of suitable nest sites in the Senegal area; alone of the four major eastern boundary upwellings, it has no significant population base of breeding birds. Timing is another factor; the Senegal upwelling occurs in the first three months of the year, and this is probably too late to be of much use to wintering northern hemisphere seabirds. The availability of richer feeding areas in the Benguela Current and on the Patagonian Shelf and off eastern North America perhaps explains why southern hemisphere seabirds do not use it. There must be many other possibilities. But I quote this speculative scenario as an example of some of the questions we will ask, and answers we will receive, as the study of the pelagic ecology of seabirds develops further. Comparisons of biomass between seabird communities are outlined, with particular reference to an apparent under-exploitation of the Senegal upwelling by seabirds.

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COMMENTS

Bourne: I should like to congratulate Dick Brown on what he has been doing. He has clearly found a very useful situation in the Bay of Fundy. I meant to mention these situations where you have an estuary with a considerable tidal fall and a rich productivity offshore. Stuff gets swept into the estuary with the tide and made available. We have this in northeast Scotland in the Ythan Estuary which supports a large tern colony. The terns feed largely on shoaling fish which get swept in and out of the estuary with the tide so that they are made available to the birds.

You were mentioning West Africa. I think there are enormously rich seabird colonies on the Banc d'Arguin in Mauritania which is immediately inshore from this area of upwelling. I would suspect that a lot of the biological material produced offshore in the upwelling is swept in over the shallow banks surrounding it to become available to the bird colonies there.

Brown: Yes, I agree, but I should also say that a better example would be Southwest Africa or Peru. The Banc d'Arguin colonies are minuscule. You have few birds off Senegal simply because there is no breeding base—just a few small rocks where the birds breed, some rather shifting sand banks subject to hyena predation, and this is about it. So the Senegal area, as you say, has potential richness but has to depend on migrant birds who have other more attractive places to breed.