

Cyclones and pelagic seabird movements

Sven Blomqvist¹ and Mats Peterz²

¹Askö Laboratory, Institute of Marine Ecology, University of Stockholm, S-106 91 Stockholm, Sweden

²Snickargatan 18, S-754 37 Uppsala, Sweden

ABSTRACT: Records of Fulmar *Fulmarus glacialis*, Sooty Shearwater *Puffinus griseus*, Gannet *Sula bassana* and Kittiwake *Rissa tridactyla*, off Kullen in south Sweden, in the decade 1970 to 1979 have been analyzed with respect to meteorological conditions. A causal model describing the occurrence of flap-gliding pelagic seabirds off Kullen is proposed, based upon evidence of (1) close association of these birds with eastward travelling deeper cyclones; (2) restrictions of bird movements due to certain wind directions and velocities; (3) absence of documented cyclonic centre passages south of Latitude 58° N at Longitude 10° E in connection with observations of birds; (4) earlier flight behaviour studies. A clockwise movement of birds in the Kattegat is ascribed to the interaction of (a) prevailing wind conditions in cyclones, (b) inertia of wave topography, (c) the birds' flight technique. The apparent conformity between the successive clockwise coastal pattern of movement of flap-gliding pelagic seabirds in the Kattegat and the North Sea is considered.

INTRODUCTION

Remarkably little is currently known about the mechanisms which cause regional and more ephemeral movements of pelagic seabirds in coastal areas in association with gale conditions. The development of theory in this field of marine ecology is of crucial importance when discussing population dynamics and distribution patterns in fundamental terms as well as in more applied problems, e.g. environmental effects of offshore activity and oil pollution. This paper presents and summarizes conclusions of a 10 yr study concerning the strong association between the occurrence of certain pelagic seabirds off Kullen, in south Sweden, and gale conditions. It became evident at the end of the 1960s that in this area during certain weather conditions, movements of these birds were a recurrent phenomenon (Hall, 1971). During non-gale conditions pelagic seabirds are normally not seen from land. Seabird records from Kullen during the 1970s have been summarized by Jönsson and Peterz (1976), Peterz (1978) and Peterz et al. (1982).

Southward movements of pelagic seabirds along the Skagerrak and Kattegat coast of Sweden were originally reported by Unger (1965) and Hall (1971). The latter suggested that the birds make a clockwise movement in this area. Pettersson and Unger (1972) proposed that this is a combined effect of (1) the birds' movements perpendicular to the wind direction, along

the wave troughs, and (2) the influence of the clockwise wind shift in connection with passing cyclones. Originally this attractive theory was based on very sporadic observations.

In this paper we develop the theory in the light of more extensive meteorological data and observations of pelagic seabirds off Kullen during the 1970s. Our expanded model is mainly supported by (1) relations between seabird observations and prevailing wind conditions; (2) detailed studies of the flight behaviour of the birds; (3) knowledge of general sea-surface dynamics. We also consider the apparent similarity between the successive clockwise coastal pattern of movement of pelagic seabirds in the Kattegat and the North Sea.

MATERIALS AND METHODS

All observations dealt with in this paper were carried out at Kullen (56° 18' N lat. / 12° 27' E long.). This is the westernmost point of a NW projecting headland, Kullaberg, in the province of Scania in south Sweden (Fig. 1). With its bold topography, with cliffs rising about 70 m above sea level, it provides a particularly suitable place for surveying seabird movements (Jönsson and Peterz, 1976).

The field observations consist of daily minimum numbers of recorded seabirds during the decade 1970 to 1979. Until 1976, the data were collected less sys-

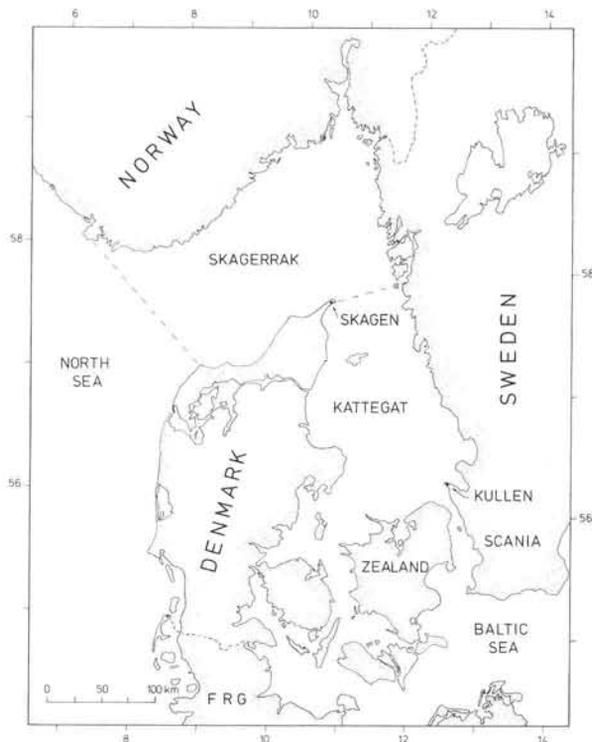


Fig. 1. Observation site Kullen, south Sweden, and other geographical locations mentioned in text

tematically, whereas during the autumns 1977 to 1979 the observations were organized on a regular daily basis (Peterz et al., 1982).

The study comprises the occurrences and movements of 4 of the most frequent pelagic seabirds in the area. Days when the numbers of birds did not exceed those assumed to represent a local fraction of Kattegat birds have been excluded. The species studied, and the chosen minimum number of birds considered during a day were: Fulmar *Fulmarus glacialis* L. (5), Sooty Shearwater *Puffinus griseus* Gmelin (3), Gannet *Sula bassana* L. (5) and Kittiwake *Rissa tridactyla* L. (500). Of these 4 species, the Kittiwake is the only one which breeds in the Kattegat, with an estimated breeding population of 100 to 200 pairs (Oldén, 1980).

Deep depressions, mainly from SW-NW, commonly cross southern Scandinavia, especially in autumn and early winter. In order to obtain an estimate of the track of the cyclones which brought pelagic seabirds to the area off Kullen, the latitudinal positions of the cyclonic centres were plotted at Longitudes 10° W, 0° and 10° E. Information of the positions at 0700 local time (G.M.T. + 1 h), was obtained from synoptic daily weather bulletins of the Swedish Meteorological and Hydrological Institute. Wind observations for every third hour were obtained from the local weather observatory at Kullen.

The normally low numbers of pelagic seabirds in the Kattegat, a marginal sea fairly easy to survey, were

advantageous for our study. The structure of our field data – which is such that the seabirds were either 'present' or 'absent' – has made it easier to discern movement patterns and their relation to meteorological factors.

RESULTS

General occurrence of seabirds off Kullen

Of the 4 pelagic seabird species studied; Fulmar, Sooty Shearwater, Gannet and Kittiwake; about 90 % of the individuals seen through the years were recorded during the period 15 September to 30 November. The annual occurrence of each species is illustrated in Fig. 2. Appearance of the birds off Kullen is closely associated with eastward travelling

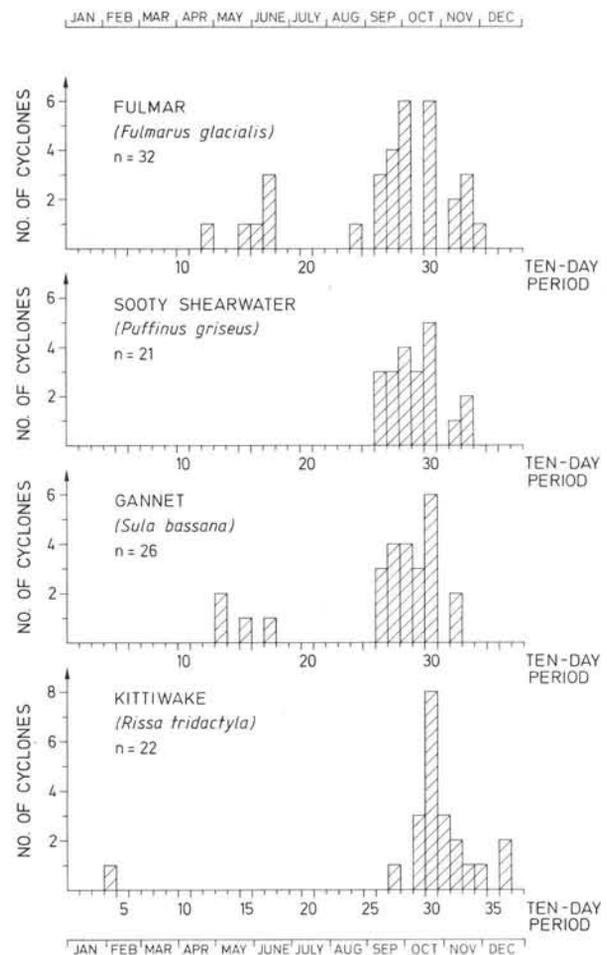


Fig. 2. Seasonal occurrence of cyclones from 1970 to 1979, expressed as number of cyclones per 10 d period bringing the 4 seabird species Fulmar *Fulmarus glacialis*, Sooty Shearwater *Puffinus griseus*, Gannet *Sula bassana* and Kittiwake *Rissa tridactyla* respectively, off Kullen in numbers exceeding those assumed to represent local levels

cyclones from the Atlantic Ocean and with strong westerly winds (Jönsson and Peterz, 1976; Peterz, 1978). When the wind speed falls below 10 m s^{-1} the seabirds cease to appear in any appreciable numbers (Table 1).

Cyclones

In the years 1970 to 1979 a total of 53 cyclones brought numbers of pelagic seabirds in excess of those assumed to represent local levels. Six of these cyclones were excluded from our analysis due to difficulties in identifying an accurate track. The 4 bird species were brought in by the remaining 47 cyclones as follows: Fulmar – 30 cyclones, Sooty Shearwater – 20 cyclones, Gannet – 23 cyclones and Kittiwake – 20 cyclones. The same cyclone, thus often brought more than one species.

All of the identified cyclone centre tracks which brought in seabirds in numbers exceeding the assumed local levels are plotted in Fig. 3. It can be seen that all of these cyclonic centres passed north of Latitude 58°N at Longitude 10°E .

Comparative pattern of occurrence

Correlations were calculated between number of individuals of the different species occurring during cyclone transits in October, i.e. the month when all 4 species occurred simultaneously (Fig. 2). No significant correlations were obtained except between Fulmar and Sooty Shearwater (Spearman rank correlation, see Zar, 1974; $r_s = 0.73$, $df = 12$, $p < 0.01$).

A priori it is reasonable to believe that the interspecific variation in the occurrence of seabirds off Kullen may be partly due to differences in the geographical origin of the cyclones. Therefore, the antecedent positions of cyclone centers, at Longitude 10°W , 0° and 10°E , were compared by single-factor analysis

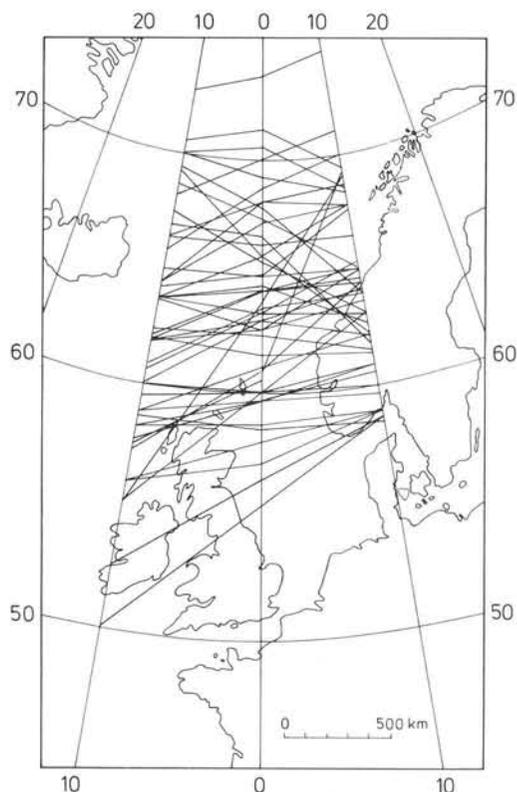


Fig. 3. Identified track of cyclonic centres which brought one or more of the 4 seabird species studied off Kullen in quantities exceeding those assumed to represent local levels

of variance (ANOVA) (see Zar, 1974). However, no statistically significant interspecific difference between mean positions was found when all 47 contributing depression transits were analyzed (highest $F = 0.27$, $df = 3 : 89$, $p > 0.5$). In order to clarify whether this was only a bias due to dependent data, i.e. whether the same cyclone often brought more than 1 species, the 10 cyclones bringing the highest number of birds of each species were also compared by single-factor ANOVA, but no significant difference was found (highest $F = 1.28$, $df = 3 : 36$, $p > 0.5$).

Table 1. Total number of hours of observation from 1970 to 1979 for days when the 4 pelagic seabird species studied were recorded off Kullen. Hours of observation are described in terms of wind direction and wind speed. Only days when the number of individuals of one or more species were greater than those assumed to represent local levels are included

Wind speed (m s^{-1})	Wind direction								Total (h)	Percent (%)
	SSW	SW	WSW	W	WNW	NW	NNW	N		
25–29	0.5	4.5	4.0	5.0					14.0	2.9
20–24		22.3	38.2	47.0	16.9				124.4	26.1
15–19		23.7	37.6	77.6	19.6	7.3	2.2	0.2	168.2	35.2
10–14	0.5	6.7	30.9	46.7	33.3	21.5	7.2	8.0	154.8	32.4
0–9		3.3		2.1	2.5	2.7	4.8	0.5	15.9	3.3
Total (h)	1.0	60.5	110.7	178.4	72.3	31.5	14.2	8.7	477.3	100
Percent (%)	0.2	12.7	23.2	37.4	15.1	6.6	3.0	1.8	100	

These statistical analyses imply that there is no easily perceived qualitative interspecific difference in the occurrence of the 4 species with respect to the preceding track of the cyclones. Neither was any quantitative covariance pattern distinguished between these pelagic seabird species off Kullen, except between Fulmar and Sooty Shearwater.

The relation between intraspecific differences in the recorded numbers of the pelagic seabirds studied off Kullen and the antecedent geographical position of the cyclone centres at Longitude 10°W, 0° and 10°E was analysed by Kolmogorov-Smirnov's 2-sample test (see Daniel, 1978). The cyclones were ranked according to the number of birds which they brought, and divided into two groups with respect to the median. For each species, the distribution of the positions of the cyclones from the group bringing the highest numbers of birds was compared with the distribution of the remaining cyclones. No statistically significant differences were discerned ($p > 0.05$).

Timing of movements

The occurrence of greater numbers of these 4 seabird species is closely associated with passing cyclones. This is reflected by the timing of the bird movements off Kullen during the day in relation to the geographical position of the cyclonic centres in the morning (0700 local time), shown in Fig. 4. This indicates that westerly cyclone centres (average position 65°12'N

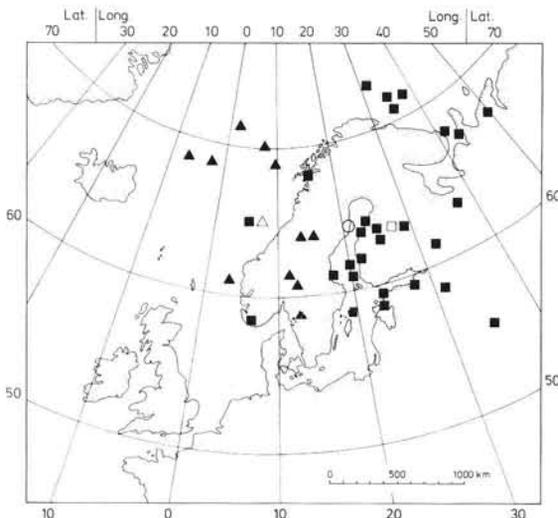


Fig. 4. Position of cyclonic centres, at 0700 local time (G.M.T. + 1 h), which resulted in a culmination of bird movements during morning (■) or afternoon (▲) off Kullen. Only cyclones which brought one or more of the pelagic seabird species studied in quantities exceeding those assumed to represent local levels are included. Open symbols □ and △ denote the calculated average position. The symbol ○ indicates the common centre of gravity

lat. / 7°18' E long. $n = 11$) usually give rise to the heaviest bird movements after noon, whereas easterly cyclone centres (67°42' N lat. / 27°18' E long. $n = 27$) result in maxima in the morning (only observation periods covering whole days are included here). The distribution of the positions of cyclonic centres bringing morning and afternoon maxima were compared using a Mardia-Watson-Wheeler-test (Batschelet, 1978) and were found not to be coincident ($R^2 = \chi^2 = 78.96$, $df = 2$, $p < 0.0005$).

Flight direction in relation to wind

The majority of the pelagic seabirds observed off Kullen head approximately SW (Table 2). The birds are mainly observed when winds are from a narrow sector ranging from SW to WNW (Table 1), i.e. when there is a head wind component. These wind directions are found south of the occlusion of cyclones, behind the cold front. Movements of seabirds in the rear of cold fronts have previously been observed and emphasized by Elkins and Williams (1972) and Oliver and Davenport (1972). The few northbound moving seabirds observed off Kullen (Table 2) are mainly recorded when winds are approximately NW-N, i.e. also heading into the wind.

Further scrutiny shows that there are interspecific disparities between bird species associated with the SW-WNW wind sector (Table 3). The Fulmar and Sooty Shearwater differ partially from the overall bird distribution (Chi-square test, see Zar, 1974; $\chi^2 = 47.83$, $df = 5$, $p < 0.001$ and $\chi^2 = 25.69$, $df = 5$, $p < 0.001$, respectively). Fulmars are observed with more northerly winds whereas Sooty Shearwaters are mostly recorded when winds are from a narrow WSW-W sector. Interspecific differences in flight technique and flight velocity may explain these discrepancies.

DISCUSSION

Unlike birds which utilize terrestrial habitats, pelagic seabirds at sea do not have any sheltered refuges. To avoid temporarily unfavourable weather

Table 2. Numbers of 4 pelagic seabird species off Kullen from 1970 to 1979 given in terms of main flight direction. Only days when numbers of individuals of each species exceeded those assumed to represent local levels are included

Species	SW	N	% moving N
Fulmar <i>Fulmarus glacialis</i>	1251	32	2.6
Sooty Shearwater <i>Puffinus griseus</i>	244	16	6.6
Gannet <i>Sula bassana</i>	1327	58	4.4
Kittiwake <i>Rissa tridactyla</i>	36639	1663	4.5

Table 3. Distribution of hours of observation and individual numbers of 4 pelagic seabird species flying south-west off Kullen in 1970–1979. Only days when numbers of individuals of each species exceeded those assumed to represent local levels are included. Absolute numbers are designated 'n'

Species		Wind direction								n
		SSW	SW	WSW	W	WNW	NW	NNW	N	
Fulmar <i>Fulmarus glacialis</i>	Hours of observation (%)	0.0	2.2	11.1	45.8	23.8	11.9	3.5	1.7	181
	Number of birds (%)	0.0	1.0	4.2	71.7	16.2	4.8	1.5	0.7	1224
Sooty Shearwater <i>Puffinus griseus</i>	Hours of observation (%)	0.0	1.9	25.1	55.2	13.4	4.4	0.0	0.0	108
	Number of birds (%)	0.0	1.2	20.7	64.9	11.1	2.1	0.0	0.0	242
Gannet <i>Sula bassana</i>	Hours of observation (%)	0.3	12.7	24.3	39.0	13.0	5.2	3.3	2.2	181
	Number of birds (%)	0.2	18.3	28.2	37.4	9.9	3.3	2.1	0.5	1314
Kittiwake <i>Rissa tridactyla</i>	Hours of observation (%)	0.0	12.4	18.2	37.1	16.9	9.2	6.2	0.0	148
	Number of birds (%)	0.0	9.5	18.4	43.0	11.8	13.7	3.6	0.0	36 639

they have to escape. Movements of seabirds in front of gathering cyclones have been observed by Manikowski (1971) from fishing boats in the North and Labrador seas. In Europe, coastal movements of pelagic seabirds have mostly been recorded in connection with onshore winds.

Flight technique. It has long been postulated that a variety of aerial seabirds may exploit wind velocity gradients and wave topography by so-called dynamic soaring (Idrac, 1925; Jameson, 1959; Ramel, 1954; Pennycuick, 1960; Berger and Gødhe, 1965; Berger and Berger, 1968; Klauswitz, 1971; Nelson, 1978). Theoretical models of dynamic soaring are given by Cone (1964) and Wood (1973). Pennycuick (1972, 1975, 1982) and Wilson (1975) have also discussed a static soaring method (slope lift/slope soaring), called sweeping flight by Wilson, which can be used in combination with or as an alternative to dynamic soaring. Sweeping flight relies on rising air currents directly related to the waves, whereas dynamic soaring depends on the vertical gradient in wind velocity, caused by wind shear, over the sea surface. Smaller pelagic seabirds in particular, are also prone to fly in the troughs to leeward of wave crests in strong winds (Pettersson and Unger, 1972; Lockley, 1974; Jansen, 1981).

Detailed direct observations of Fulmar, Sooty Shearwater, Gannet and Kittiwake (Peterz and Rønnertz, 1980) prove that these 4 species are flap-gliders (*sensu* Pennycuick, 1982) and display types of dynamic soaring and/or sweeping flight when passing off Kullen in strong winds (Fig. 5). The main heading of the birds is along the wave train alignment, and they fly long distances in the wave troughs (see also Jansen, 1981). However, when compensating insufficiently for wave propagation the birds obtain an apparent track with an angle of more than 90° to the wind direction (Fig. 6).

Flight direction. At first glance, it might be expected that pelagic seabirds flying in the wave troughs in

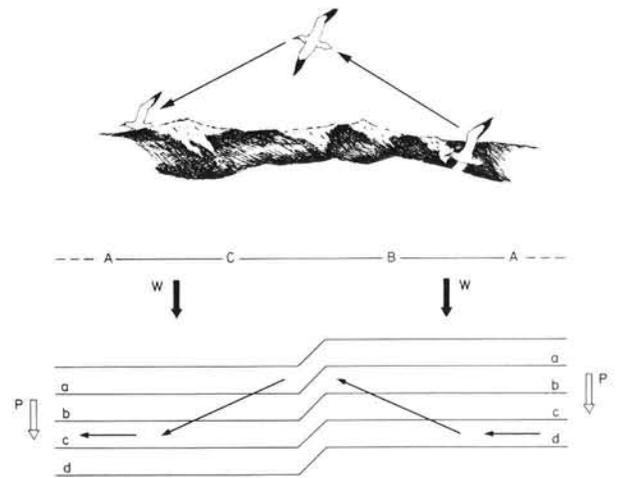


Fig. 5. Flight cycle maintained by flap-gliding (soaring) pelagic seabirds in strong winds, illustrated here by a Gannet. Upper picture shows bird's flight seen from side, with the wind blowing towards the observer. Lower part is a corresponding schematic outline of this flight pattern in relation to perpendicular wind direction W (filled arrows) and wave propagation P (open arrows). A: Flight in wave trough d between 2 wave crests; B: bird climbs against the wind; C: by gliding downwind bird descends back into wave trough c , thereby completing the cycle

strong winds would be equally distributed in opposite main flight directions. However, the inertia of the water mass (e.g. Phillips, 1977; Dietrich et al., 1980) causes a delayed orientation of the wave train alignment (a combined effect of swells and seas) to the wind which gradually veers clockwise during the passage of cyclones (see observations by Schumacher, 1950). Hence, in order to reduce their energy expenditure, the birds may be expected to fly at an obtuse angle (α) away from the prevalent wind direction, so as to benefit from a tail wind component (Fig. 6).

Therefore, when a cyclone is approaching, a majority of the pelagic seabirds would be likely to head in certain main directions relative to the approaching

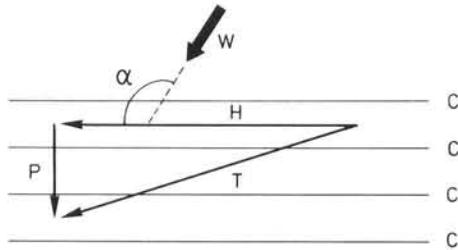


Fig. 6. Vectors for lower part of Fig. 5, showing result of insufficient track compensation in relation to wave propagation and direction of bird's flight in relation to the veering wind and the delayed orientation of wave alignment. C: wave crest; H: heading; P: wave propagation; T: tracking; W: wind direction; α : obtuse angle between wind direction and bird's heading

cyclone centre. In the Northern Hemisphere, birds in front of eastward travelling cyclones would tend to head eastwards in winds with a southerly component; southwards in winds with a westerly component; and west- to northward in winds with north and northeast components. This pattern of movement would also enable the birds to avoid flying into the cyclone centers and reduce time spent in weather conditions unfavourable for foraging.

Coastal movements. Special conditions occur offshore. Pelagic seabirds encounter the terrestrial environment as an obstacle. When seabirds that are flying along the wave train alignment in strong wind encounter the coastline and do not reverse their main flight direction, they must fly along the coast into the wind (Fig. 7). Observations showing that this type of

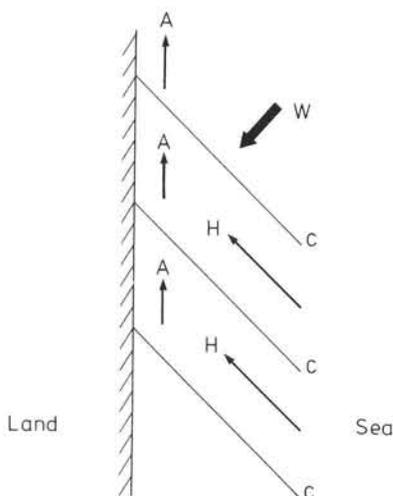


Fig. 7. Schematic outline illustrating the apparent track along the coastline of flap-gliding pelagic seabirds encountering land. In this simplified case the wave front alignment is perpendicular to the wind direction. A: apparent track; C: wave crest; H: bird heading in the wave trough; W: wind direction

movement predominates can be found in works by Jönsson and Peterz (1976), Ree (1977), Bourne (1981, 1982), Jansen (1981) and Oldén (1982). Seabirds that hesitate and then reverse their main flight direction to move away from the coastline, will not normally be observed from land. However, reversal of their flight direction exposes the birds to the risk of flying into the cyclone (see under 'Flight direction'). It should therefore normally be preferable for the birds to fly along the coast in winds with a head wind component.

Seabird movements in the Skagerrak and the Kattegat. Occurrence and movements of flap-gliding pelagic seabirds in the Skagerrak and the Kattegat can be explained on the basis of earlier studies and our field data from Kullen. In the Northern Hemisphere, an eastward travelling cyclone has south winds on its eastern side. If the cyclone is deep enough, the wind force will exceed a critical value, enabling the seabirds to exploit the wind velocity gradient, up-currents and the wave topography by means of dynamic soaring and/or sweeping flight (Fig. 5). During this initial stage the birds will fly westward or eastward. In the former case, they will not reach the Skagerrak and the Kattegat, but these are probably in the minority (see under 'Flight direction').

Birds which have reached the eastern part of Skagerrak when the wind veers SW by the passage of the cyclone, would be heading south along the NNW-SSE running Swedish coastline. Thus, when the wind continues to veer WSW-W conditions become optimal for the passage of birds off Kullen (Table 1). The transit of a cyclone further to the east, and the subsequent change of wind direction to approximately NW, brings pelagic seabirds onto the northern coast of the Danish island of Zealand (Oldén, 1980, 1981, 1982). Normally the wind speed then drops. Seabirds are next observed during NW-N winds, at the northernmost point of Denmark, Skagen, coming from the south and heading back to the Skagerrak and North Sea (Braae, 1977; Oldén, 1980, 1981, 1982). This latter northerly directed movement will sometimes result in birds hitting northern parts of the Swedish Kattegat coast, but this would occur mainly in connection with on-shore winds (WNW-NW) (Unger, 1965; Oldén, 1982). Very few pelagic seabirds continue into the Baltic Sea.

If the centre of the cyclone has a track far to the south, i.e. if the centre is lower than approximately 58°N when it crosses Longitude 10°E (Fig. 3), the depression will not cause the requisite south and subsequent west winds over the Skagerrak to bring birds into the Kattegat but will instead give rise to an east wind which will take birds out to the North Sea. Locally propitious west winds may then still occur at Kullen, but pelagic seabirds are not recorded in appreciable numbers. This supports the assumption

that normally there are only small numbers of pelagic seabirds in the Kattegat.

Movements in the North Sea. Successive clockwise movements of pelagic seabirds in the Kattegat during the passage of deep depressions appear to reflect wider movements. Southbound movements also seem to predominate along the westward facing coast of continental Europe and Scandinavia, as on the Swedish west coast. This has been reported from Norway (Ree, 1977), Denmark (Meltofte and Overlund, 1974; Noer and Sørensen, 1974 give scant details but south seems to dominate), the Netherlands (Jansen, 1981) and from France (Oliver, 1971; Oliver and Davenport, 1972). On the other side of the North Sea the coastal movements of seabirds are mostly northbound and are observed some time after the transit of depressions, as the wind veers north. This occurs along the English east coast (Phillips, 1963; Bourne, 1976) and the Scottish east and north coasts (Elkins and Williams, 1970, 1972; Bourne, 1976, 1982), as is the case along the Danish Kattegat coast and off Skagen. Thus there is an analogous trend (Fig. 8) of successive clockwise move-

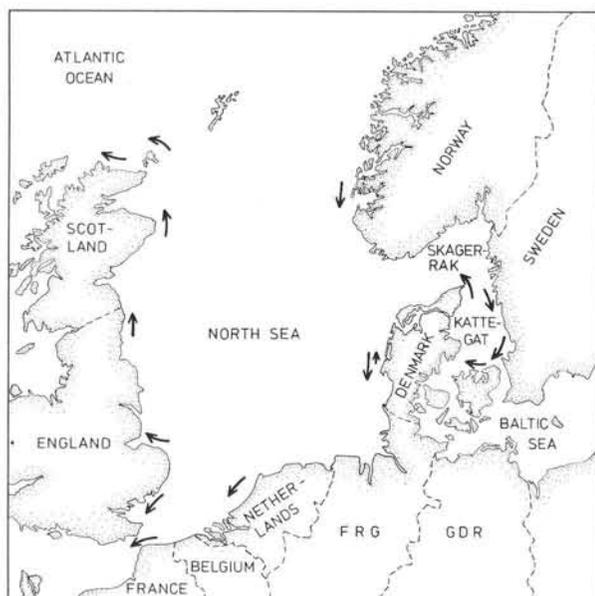


Fig. 8. Main pattern of movement of pelagic seabirds in the Kattegat-Skagerrak seas and the North Sea in association with the deeper cyclones travelling east. Arrows denote the observed main flight directions (references in the text)

ments which seem to be a major feature of seabird flight patterns in both the Kattegat and the North Sea as deep cyclones pass eastward. These clockwise movements may enable the birds to accomplish a return flight to their foraging areas shortly after each cyclone passes. This flight model may also help to explain some of the more ephemeral year-to-year vari-

ations in pelagic seabird numbers offshore (e.g. Wallace and Bourne, 1981).

Epilogue. At present there has been no internationally published attempt to provide a unified theoretical and mechanistic explanation for regional and more ephemeral movement patterns of pelagic seabirds in coastal areas in association with gale conditions. To study this topic in all its aspects would require extraordinary facilities. For example, it is very difficult to observe pelagic seabirds at sea during gale and storm conditions (although it might be possible to do so from some offshore oil-drilling platforms). Our contribution can be regarded as a first-order approach. It is based on 10 yr of observations, detailed flight-behaviour studies and extensive meteorological data. Our conclusion concerning the conformity between successive clockwise coastal movement patterns in the Kattegat-Skagerrak seas and the North Sea may be wrong. However, we find it suggestive, and it may be of heuristic value and worth attending to in this respect.

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