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The summer distribution of *Procellariiformes* in the central North Atlantic Ocean

By Henrik Skov, Jan Durinck, Finn Danielsen & Dorete Bloch

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The summer distribution of *Procellariiformes* was studied in the central North Atlantic Ocean. Bird observations collected during gross scale surveys (50–500 km distances between transects, in total 9000 km line transect) in 1987 and 1989 were correlated between species and with physical oceanographical data. Seven species of petrels were common, and their distributions indicated a clumped pattern over the ocean. The majority of the concentrations was found close to edges of the continental shelves and over oceanic ridges along the flanks of the Gulf Stream. With the exception of Fulmar *Fulmarus glacialis*, cold sea surface temperatures affected the distribution of most species negatively. Distance from land affected the distribution of North Atlantic breeding species differently. Leach's Storm-petrel *Oceanodroma leucorhoa* was concentrated in waters within 100 km of the main colony on St Kilda. British Storm-petrel *Hydrobates pelagicus* were found within 400 km of land, while Manx Shearwater *Puffinus puffinus* and Fulmar occurred at distances of more than 1000 km from nearest colonies, though Manx Shearwaters were common only within 600 km of land. Fulmar and British Storm-petrel recorded away from colonies (more than 200 km) seemed to form groups of birds in areas with different oceanographical characteristics than the birds of the two species recorded in near-colony areas. The oceanographical characteristics of areas with concentrations of Manx Shearwater and Leach's Storm-petrel were rather similar. The distributions of Great *Puffinus gravis*, Sooty *Puffinus griseus* and Cory's Shearwater *Calonectris diomedea* overlapped little with those of the other species, the majority of these species being recorded in southern areas of the Mid Atlantic Ridge (Charlie Gibbs Fracture Zone), which were out of the range of local species. Although correlated in this area, we show that these three visitors to the area occupied slightly different oceanic habitats.

Key words: Petrel distribution, oceanic habitat, fronts, North Atlantic Ocean, Mid Atlantic Ridge, principal component analysis.

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I. Introduction

Studies of seabird distribution and abundance in the North Atlantic Ocean have focused on shelf areas such as the North Sea and the Scotian Sea. Studies in the deeper oceanic zones indicate that the bird fauna beyond the continental shelves is dominated by *Procellariiformes* (Brown 1986, Danielsen *et al.* 1990, Jespersen 1929, Rankin & Duffey 1948, Webb *et al.* 1990 and Wynne-Edwards 1935).

We studied the gross scale distribution of *Procellariiformes* over the deep North Atlantic in July and August 1987 and 1989, outside the wellstudied areas near Britain, Ireland and the Faroes, and gained insight into the reasons underlying these distributions by comparing patterns of distributions between species and patterns of the physical environment.

2. Methods

Study area

The study area was within a rectangle of about 850,000 km² in the North Atlantic bounded by 65° N and 50° N, and 10° W and 45° W.

Most of the area lies within the boreal marine zone (Salomonsen 1965), which has surface water temperatures between 10° and 19°C in late summer, and is strongly influenced by the Gulf Stream (Krauss 1955). The northern-most part of the area lies within the low arctic zone having summer surface temperatures between 8° and 10°C. A gradual decrease in surface temperatures from 17°C in the south to 9°C in the north was recorded both in 1987 and 1989 (Fig. 3). The most turbulent regions are found along the flanks of the Gulf Stream, where coarse-scale meanders and eddies are common. In several areas, notably the Iceland-Faroe Ridge, the Reykjanes Ridge and the Charlie Gibbs Fracture Zone, large changes in surface temperature occurred over short distances, indicating frontal zones. On some occasions enclosures of colder water of limited horizontal dimensions were crossed.

The bathymetry of the area is dominated by the Mid Atlantic Ridge System in the west, and by the large plateaus to the east, with depths less than 1000 meters (Fig. 3). Major areas of the ridge system are the Reykjanes Ridge and further south the Charlie Gibbs Fracture Zone. A number of seamounts occur along the eastern border of the Reykjanes Ridge. To the east the Rockall Plateau and the Iceland-Faroe Ridge form a continuous rise above 2000 meters with shallow banks like the Hatton Bank, Rockall Bank, George Bligh Bank, Rosemary Bank, Outer Bailey Bank, and Bill Bailey's Bank. Only one large seamount exists in the eastern part, the Anton Dohrn, northwest of Scotland. The 1000 m continental slopes are found relatively close to Greenland, Iceland and west Britain, whereas a large area off Ireland including the Porcupine Bank is above 1000 meters. The upper continental shelves south of Iceland and west of Britain and Ireland lie within the study area, but have not been included in the analyses, as extensive knowledge about the distribution of Petrels in these areas is already available. Despite the extensive ridge systems, seamounts and banks, half of the study area is made up of the Irminger and Iceland Basins with depths exceeding 2000 m.

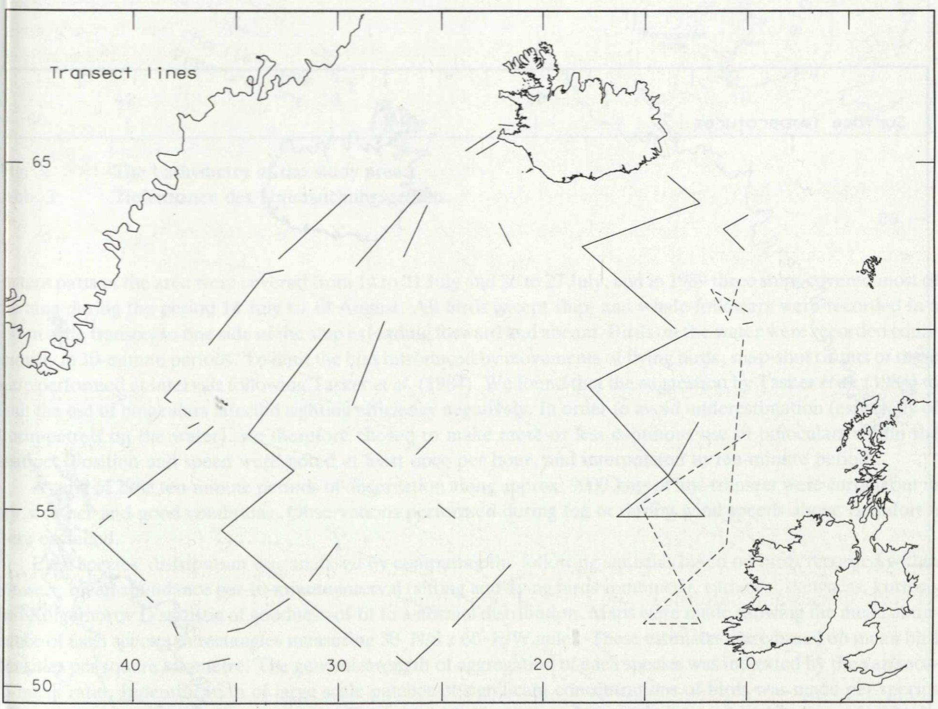


Fig. 1: The line transects used during the 1987 surveys (dotted lines) and 1989 surveys (solid lines).
Abb. 1: Die verwendeten Transekt-Strecken, für 1987 gestrichelt, für 1989 ausgezogen.

Selection of species

Seven species of *Procellariiformes* were observed commonly: Fulmar *Fulmarus glacialis*, Cory's Shearwater *Calonectris diomedea*, Great Shearwater *Puffinus gravis*, Sooty Shearwater *Puffinus griseus*, Manx Shearwater *Puffinus puffinus*, British Storm-petrel *Hydrobates pelagicus* and Leach's Storm-petrel *Oceanodroma leucorhoa*. Less than 10 Little Shearwater *Puffinus assimilis* and Soft-plumaged Petrel *Pterodroma mollis* were observed; these two species are not considered further in this analysis. Five of the species studied breed in the North Atlantic, although Cory's Shearwater south of the range of this study, and the period of surveys covered their chick-rearing period. The Great and Sooty Shearwater breed in the southern hemisphere, and both spend a large proportion of their non-breeding season in the North Atlantic. The principal breeding colonies of Great Shearwater are Gough Island and Tristan da Cunha, while the only known colonies of Sooty Shearwater in the Atlantic are found on the Falkland Islands and Tierra del Fuego (Croxall *et al.* 1984). Some of the Sooty Shearwaters wintering in the North Atlantic may originate from the much larger Pacific population (Danielsen *et al.* 1990).

Data sampling and analyses of bird distribution

The survey platform was the IWC North Atlantic Whale Sighting Survey (NASS), which was carried out along four v-formed tracks covering the entire span of the central North Atlantic with distances of 50–500 km between tracks. Bird observations were carried out by 1–2 observers from the top deck of four different ships at a height of about 10 m above sea level. All four ships measured about 40 m in length and had an average cruising speed of 8.5 knots/h. The transects along which continuous observation was carried out are depicted in Fig. 1. In 1987 the

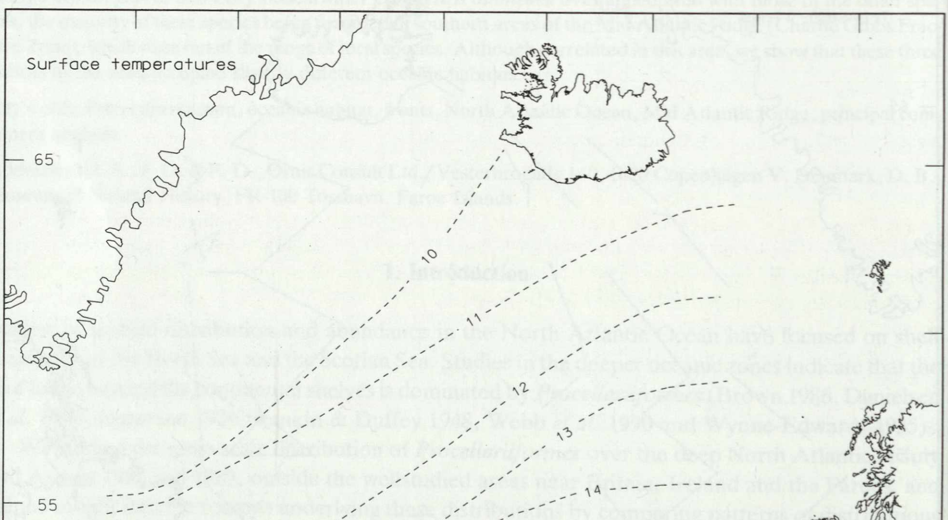


Fig. 2: The distribution of surface temperatures during the 1989 survey. Isohalines marking zones of generally different surface temperatures by whole centigrades celsius.

Abb. 2: Die Verteilung von Oberflächentemperaturen während der Untersuchung 1989. Die Isolinien markieren Zonen mit verschiedenen Oberflächentemperaturen in vollen Grad Celsius.

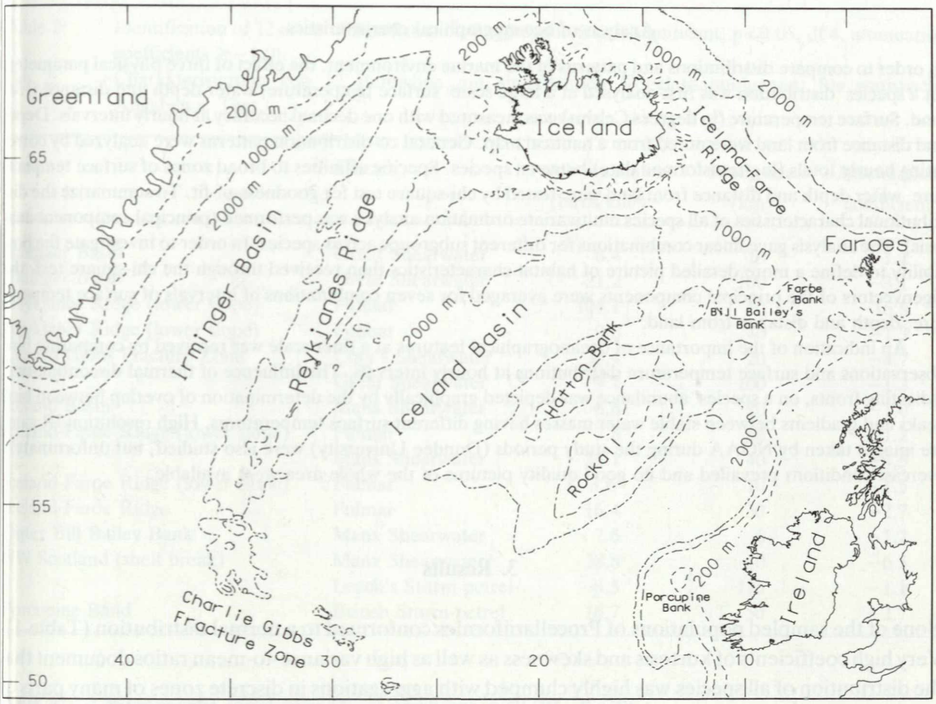


Fig. 3: The bathymetry of the study area.
Abb. 3: Tiefenzonen des Untersuchungsgebiets.

eastern parts of the area were covered from 14 to 21 July and 26 to 27 July, and in 1989 three ships covered most of the area during the period 14 July to 14 August. All birds except ship- and whale-followers were recorded in a 300 m wide transect to one side of the ship extending forward and abeam. Birds on the water were recorded continuously in 10-minute periods. To limit the bias introduced by movements of flying birds, snap-shot counts of these were performed at intervals following Tasker *et al.* (1984). We found that the suggestion by Tasker *et al.* (1984) to limit the use of binoculars affected sighting efficiency negatively. In order to avoid underestimation (especially of storm-petrels on the water), we therefore chosed to make more or less continous use of binoculars within the transect. Position and speed were noted at least once per hour, and interpolated to ten-minute periods.

A total of 2965 ten-minute periods of observation along approx. 9000 kms of line transect were carried out in fair weather and good conditions. Observations performed during fog or during wind speeds above Beaufort 6 were excluded.

Each species' distribution was analysed by computing the following statistics based on birds recorded within transect: mean abundance per 10-minute interval (sitting and flying birds combined), variance, skewness, kurtosis and Kolgomorov D statistic of goodness-of-fit to a normal distribution. Maps were made showing the mean abundance of each species in rectangles measuring 30′ N/S x 60′ E/W miles. These estimates were based on mean bird densities per square kilometre. The general strength of aggregation of each species was indicated by the variance-to-mean ratio. Indentification of large scale patches of significant concentrations of birds was made per species using a regression against distance model (Schneider 1982). Aggregations were distinguished from passing flocks and background variation in counts by identifying each one hour period (approx. 10 nautical miles) with a significantly higher mean density than that of the five nearest hours (approx. 50 miles transect distance on both sides of the peak). This procedure tested for a significant decrease in density with increasing distance from each high count. The slope of the regression line provided a coefficient of the decrease in density, when moving away from each abundance peak. The size of each patch was indicated by the length of the transect(s), which crossed the concentration.

Analysis of oceanographical characteristics

In order to compare distributions and patterns of the marine environment, the effect of three physical parameters on a species' distribution was first analysed at a large scale: surface temperature, water depth and distance from land. Surface temperature (in degrees Celsius) was measured with one decimal accuracy at hourly intervals. Depth and distance from land were noted from a nautical map. General co-distribution patterns were analyzed by correlating hourly totals (log-transformed data) between species. Specific affinities to broad zones of surface temperature, water depth and distance from land were tested by chi-square test for goodness-of-fit. To summarize the distributional characteristics of all species multivariate ordination analysis was performed (principal component analysis). The analysis gave linear combinations for different subgroups across species. In order to investigate the possibility to define a more detailed picture of habitat characteristics than received through the chi-square test, the eigenvectors of the principal components were averaged for seven combinations of intervals of surface temperature, depth and distance from land.

An indication of the importance of oceanographical features at a finer scale was received by comparing bird observations and surface temperature distributions at hourly intervals. The influence of thermal discontinuities, indicating fronts, on a species' abundance was depicted graphically by the determination of overlap between bird peaks and gradients between stable water masses having different surface temperatures. High resolution IR satelite images taken by NOAA during the study periods (Dundee University) were also studied, but unfortunately overcast conditions prevailed and no good quality pictures of the whole area were available.

3. Results

None of the sampled populations of Procellariiformes conformed to a normal distribution (Table 1). Very high coefficients of kurtosis and skewness as well as high variance-to-mean ratios document that the distribution of all species was highly clumped with aggregations in discrete zones of many parts of the study area. No general pattern of clustering in relation to shelf areas and surface temperatures could be identified.

Fulmar

The Fulmar was the most common Petrel species recorded during the study. The species had the highest variance-to-mean ratio (Table 1). It was seen throughout the area with the lowest mean densities over the deep basins (> 2000 m) in the central and eastern parts (Fig. 4). Five significant aggregations were found along the lower slopes (1000 m) of the Reykjanes and the Iceland-Faroe Ridges

Table 1: Dispersion and sample statistics. D:Norm is goodness-of-fit to a normal distribution.
Tab. 1: Statistische Angaben zum Untersuchungsmaterial; Näheres s. Text.

	n	Mean/ 10-minute	Ratio s^2/mean	Skewness	Kurtosis	D:Norm ($p<0.01$)
Fulmar	4685	1.58	46.3	14.8	255.7	0.427
Cory's Shearwater	178	0.06	41.2	45.9	2282.0	0.505
Great Shearwater	1423	0.48	24.2	14.7	280.1	0.472
Sooty Shearwater	336	0.11	4.0	16.0	372.4	0.497
Manx Shearwater	1186	0.4	33.8	21.4	606.0	0.456
British Storm-petrel	563	0.19	12.6	16.5	325.3	0.482
Leach's Storm-petrel	415	0.14	17.9	25.9	888.2	0.505

Table 2: Identification of 12 areas of significant bird aggregations (r is significant, $p<0.05$, df 4, attenuation coefficients ≥ -1.0).

Tab. 2: Charakterisierung von 12 Bereichen mit signifikanten Vogelansammlungen; für statistische Angaben s. Text.

Area	Species	Patch maximum (birds/km²)	Patch size (km)	Attenuation coefficient
Irminger Basin	Great Shearwater	6.4	10	−1.1
Irminger Basin	Great Shearwater	21.2	100	−3.1
Reykjanes Ridge (lower slope)	Fulmar	104.1	60	−16.8
Reykjanes Ridge (lower slope)	Fulmar	9.0	40	−1.3
Charlie Gibbs Fracture Zone	Cory's Shearwater	30.4	20	−4.7
	Great Shearwater	7.7	100	−1.3
Iceland Basin	Manx Shearwater	6.6	20	−1.0
Iceland-Faroe Ridge (lower slope)	Fulmar	7.8	80	−1.2
	Manx Shearwater	31.1	40	−4.5
Iceland-Faroe Ridge (lower slope)	Fulmar	3.6	10	−1.5
Iceland-Faroe Ridge	Fulmar	16.4	30	−2.7
Outer Bill Bailey Bank	Manx Shearwater	7.6	6	−1.2
NW Scotland (shelf break)	Manx Shearwater	38.8	40	−6.3
	Leach's Storm-petrel	8.5	115	−1.1
Porcupine Band	British Storm-petrel	16.7	50	−2.7

Table 3: Inter-specific correlations (* r is significant, $p<0.001$, df 610).

Tab. 3: Interspezifische Korrelationen (* r signifikant, $p<0.001$, df 610).

	Fulmar	Cory's Shearwater	Great Shearwater	Sooty Shearwater	Manx Shearwater	Storm Petrel
Fulmar						
Cory's Shearwater	0.01					
Great Shearwater	−0.01	0.18*				
Sooty Shearwater	−0.02	0.61*	0.15*			
Manx Shearwater	−0.01	0.01	−0.03	0.05		
British Storm-petrel	−0.02	−0.01	−0.03	−0.01	−0.01	
Leach's Storm-petrel	−0.01	−0.01	−0.02	0.01	0.01	0.05

(Table 2). The extent of these aggregations ranged from 30 to 80 km. A massive concentration of Fulmars was crossed 400 km southwest of Iceland along the western slope of the Reykjanes Ridge; the densities of birds rose during two hours by a factor 100. Outside these areas, discrete peaks in the abundance were found far south on the Charlie Gibbs Fracture Zone (CGFZ), along the shelf break off Ireland and over the 2000 m isobath off Scotland.

The species' distribution was not correlated with any of the other species (Table 3), although it shared the frontal zone in the CGFZ with the large shearwaters, and shared an area of high abundance over the southern slopes of the Iceland-Faroe Ridge with the Manx Shearwater. The only clear picture of habitat association that can be received by the chisquare test is the majority of birds (51%), which were recorded in cold waters (Table 4). A more detailed picture was received from the prin-

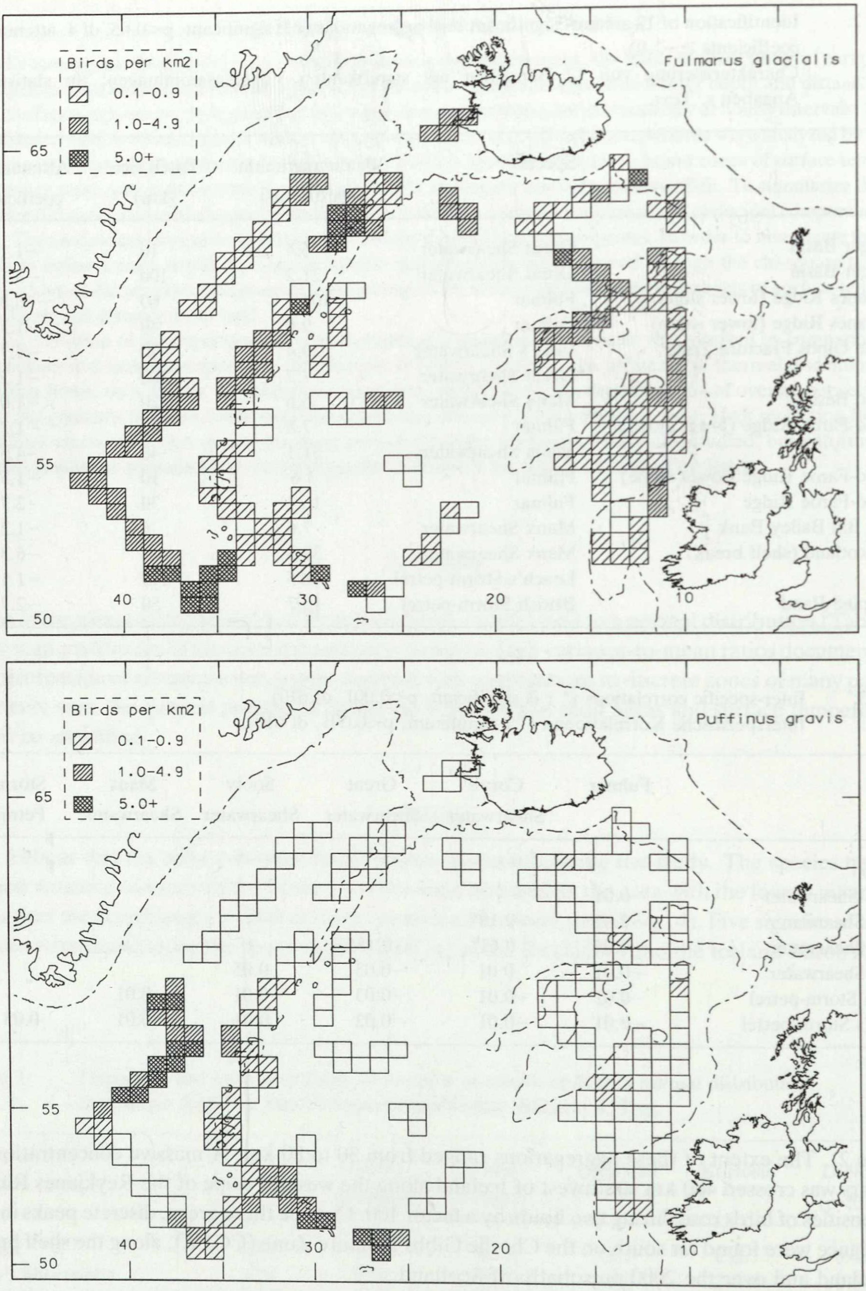
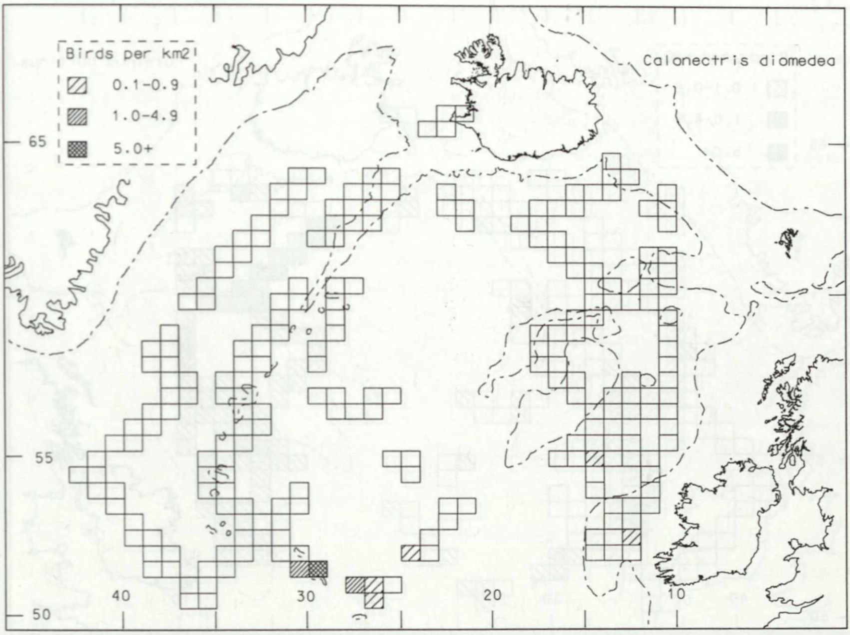
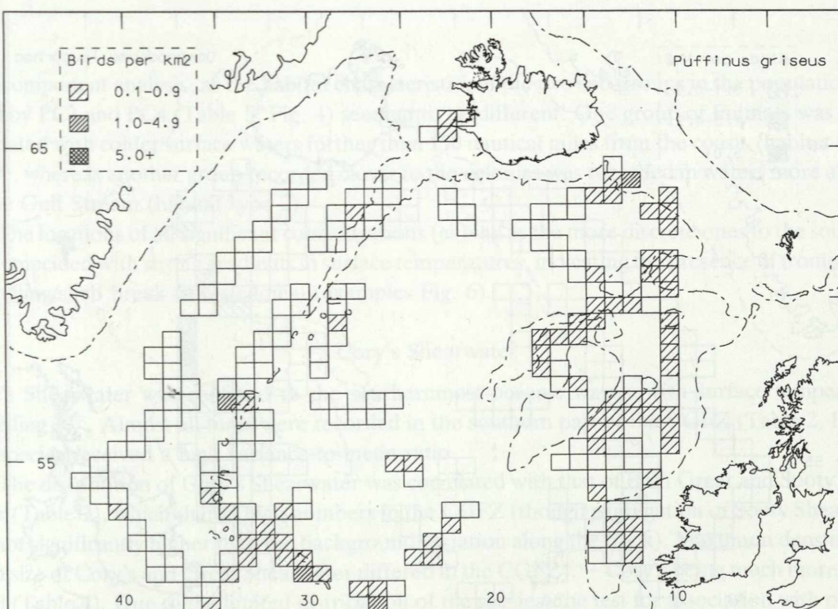
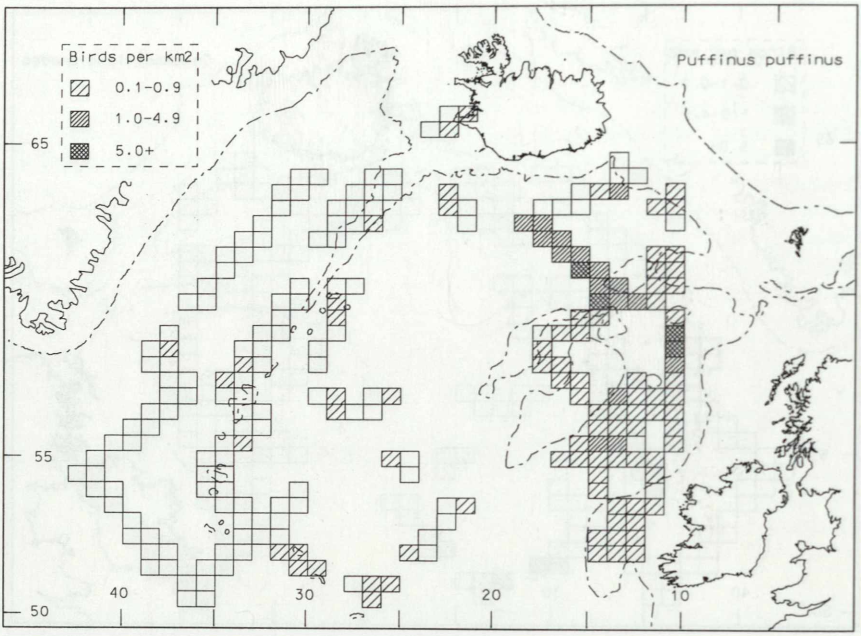


Fig. 4: Patterns of distribution of the seven Procellariiformes studied. Mean densities of birds per km². Th 1000 m depth contours (see Fig. 3) are indicated.

Abb. 4: Die Verbreitungsmuster der 7 untersuchten Vogelarten. Darstellung der durchschnittlichen Anzah von Vögeln pro km²; Tiefenlinien wie in Abb. 3.


Birds per km2
0.1-0.9
1.0-4.9
5.0+
Calonectris diomedea
65
55
50
40
30
20
10


Birds per km2
0.1-0.9
1.0-4.9
5.0+
Puffinus griseus
65
55
50
40
30
20
10



Birds per km2
0.1-0.9
1.0-4.9
5.0+
Puffinus puffinus
65
55
50
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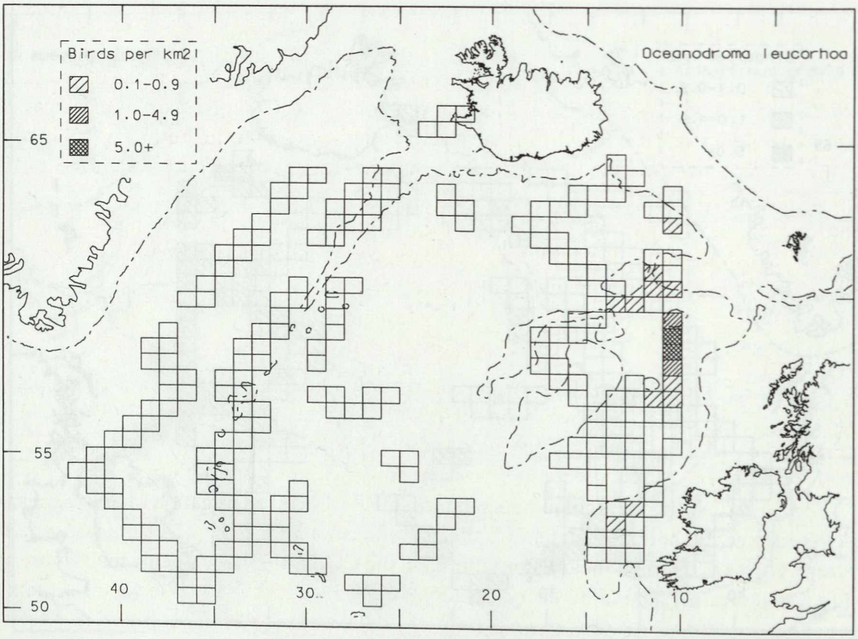

Birds per km2
0.1-0.9
1.0-4.9
5.0+
Oceanodroma leucorhoa
65
55
50
40
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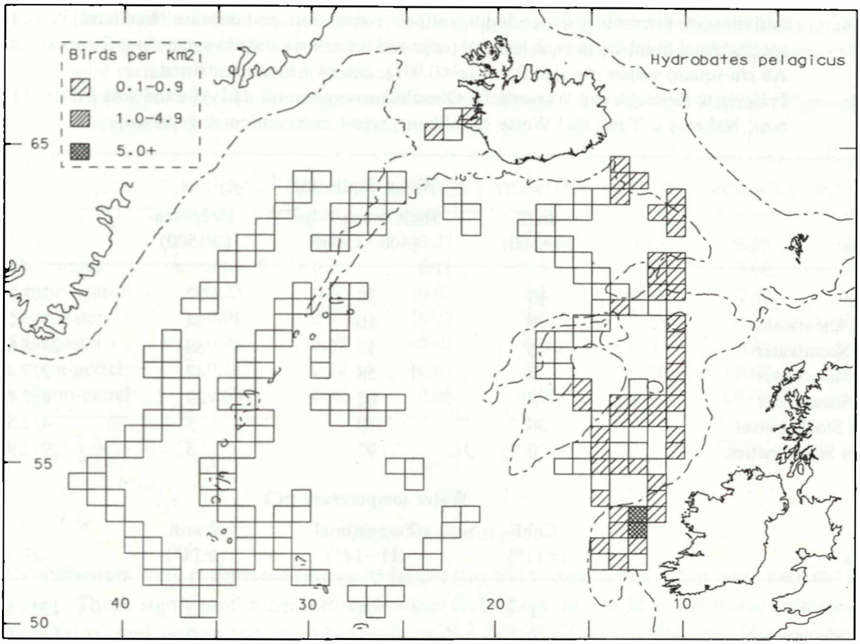
20
10



cipal component analysis, as the habitat characteristics of the two sub-groups in the population indicated by PC3 and PC4 (Table 5, Fig. 4) seemed to be different. One group of Fulmars was clearly associated with colder surface waters further than 150 nautical miles from the coasts (habitat types 6 and 7), whereas another group recorded closer to the colonies was recorded in waters more affected by the Gulf Stream (habitat type 2).

The locations of all significant concentrations (as well as the more discrete ones to the south and east) coincided with strong gradients in surface temperatures, indicating the presence of frontal zones (upwelling/shelf break fronts/eddies) (examples Fig. 6).

Cory's Shearwater

Cory's Shearwater was confined to the southernmost oceanic waters with surface temperatures exceeding 13°. Almost all birds were recorded in the southern part of the CGFZ (Table 2, Fig. 4). The species received a high variance-to-mean ratio.

The distribution of Cory's Shearwater was correlated with that of both Great and Sooty Shearwater (Table 3), which shared high numbers in the CGFZ (though aggregation of Sooty Shearwater was not significantly higher than the background variation along the track). Maximum densities and patch size of Cory's and Great Shearwater differed in the CGFZ), – Cory's being much more aggregated (Table 4). Due to the limited distribution of the species, the test for association with physical parameters clearly reflected the environment of the fracture zone; far from land in deep, sub-tropical water masses. The distribution of the other two large shearwaters was much wider than that of the Cory's Shearwater, and accordingly their overall distributions were not identical.

Several seamounts of limited geographical extension (peaks/ridges less than 3 kms in length) and a gradient in surface temperature (from 15° to 16°) (Fig. 6) were encountered in the area of concentration.

Table 4: Affinities for intervals of water depth, surface temperature and distance from land. Percentage of species' total numbers in each interval (adjusted for effort) and chi-square test for goodness of fit. All chi-square values are significant ($p<0.001$), except where mentioned.

Tab. 4: Präferierte Bereiche von Wassertiefe, Oberflächentemperatur und Abstand vom Festland (in Prozent, Näheres s. Text; chi^2-Werte signifikant, wenn nicht anders angegeben).

Species	Water depth (m) Shelf (0–400)	Shelf break/ridge (400–1500)	Deep sea (≥1500)	x^2
Fulmar	35	38	27	203.2
Cory's Shearwater	0	16	84	275.2
Great Shearwater	0	12	88	2388.8
Sooty Shearwater	0	58	42	227.4
Manx Shearwater	9	62	29	657.7
British Storm-petrel	36	59	5	452.5
Leach's Storm-petrel	0	97	3	972.9

Species	Water temperature (°C) Cold (<11°)	Transitional (11–14°)	Warm (≥14°)	x^2
Fulmar	51	24	25	1223.4
Cory's Shearwater	0	1	99	1398.1
Great Shearwater	53	10	37	1909.1
Sooty Shearwater	5	46	49	423.2
Manx Shearwater	2	85	13	1905.1
British Storm-petrel	3	18	79	725.1
Leach's Storm-petrel	1	97	2	1239.7

Species	Distance from Land Close (200)	Medium (200–400)	Distant (≥400)	x^2
Fulmar	28	33	39	144.1
Cory's Shearwater	0	4	96	408.6
Great Shearwater	1	2	97	3188.2
Sooty Shearwater	32	36	32	2.8 (ns)
Manx Shearwater	61	26	13	1166.5
British Storm-petrel	38	62	0	818.6
Leach's Storm-petrel	95	5	0	2897.2

Table 5: Results of the ordinal analysis (principal component analysis) of bird abundance (daily totals). The loading of each species is shown for all seven components. The proportion of each component of the total variance is indicated in brackets.

Tab. 5: Ergebnisse einer Hauptkomponenten-Analyse für die Anzahl von Vögeln (Tagessummen; Angaben für 7 Komponenten, Näheres s.Text).

Species	PC1 (26%)	PC2 (23%)	PC3 (15%)	PC4 (14%)	PC5 (13%)	PC6 (6%)	PC7 (4%)
Fulmar	−0.17	−0.08	0.73	0.67	−0.13	−0.05	−0.01
Manx Shearwater	0.63	−0.27	0.11	−0.11	0.03	0.09	0.71
Cory's Shearwater	0.23	0.62	−0.07	0.15	−0.23	0.69	−0.011
Great Shearwater	0.01	0.37	0.27	−0.08	0.88	0	0.04
Sooty Shearwater	0.38	0.55	−0.07	0.06	−0.20	−0.71	0
British Storm-petrel	0.11	−0.14	−0.61	0.71	0.31	−0.02	0.05
Leach's Storm-petrel	0.63	−0.36	0.08	−0.08	0.11	−0.09	−0.71

Great Shearwater

Great Shearwaters were common along parts of the two westernmost lines, but were rare in the rest of the area. Three significant concentrations were identified: two in the cold water masses of the Irminger Basin, and one in the southern part of the CGFZ (Table 2, Fig. 4). The species' high variance to-mean ratio was caused by these very high counts (Table 1).

The occurrence of Great Shearwater was correlated with that of both Cory's and Sooty Shearwater (Table 3), which shared high numbers in the CGFZ, though their specific area of concentration did not overlap completely. Due to high numbers found in the Irminger Basin, Great Shearwater was also associated with cold, deep waters.

Great Shearwater data were split into two components by the principal component analysis (Table 5). The three large shearwaters received high loadings on PC2, while only Great Shearwater had a large eigenvector value on PC5. Plotting the eigenvectors of PC2 and PC5 as mean values per habitat (Fig. 5) showed that the data from the ridges in warmer waters (habitat type 4) seemed segregated from the rest of the data.

The concentration within the Irminger Basin was located in the vicinity of the front between cold and temperate water (9°−10°, Fig. 6). The second concentration in the CGFZ was related to the warm water mass (> 16°).

Sooty Shearwater

Sooty Shearwater was observed throughout most of the area in low densities except in the cold waters of the Irminger Basin (< 9°, Fig. 4). None of the aggregations crossed were significant, and contrary to the other three Shearwater species no large groups of birds were seen, which resulted in a much lower variance-to-mean ratio than the other six species (Table 1).

As mentioned for Cory's and Great Shearwater, all three shearwaters were common in the CGFZ, and their general distributions were correlated (Table 3). Compared to both Cory's and Great Shearwater, Sooty Shearwater was more commonly associated with shelf break and ridge areas closer to land, and compared to Great Shearwater it seemed to avoid the colder waters off east Greenland. The prinicipal component analysis gave high scores to Sooty Shearwater on the first two components. The plot of eigenvectors of PC1 and PC2 per habitat indicated that the main difference

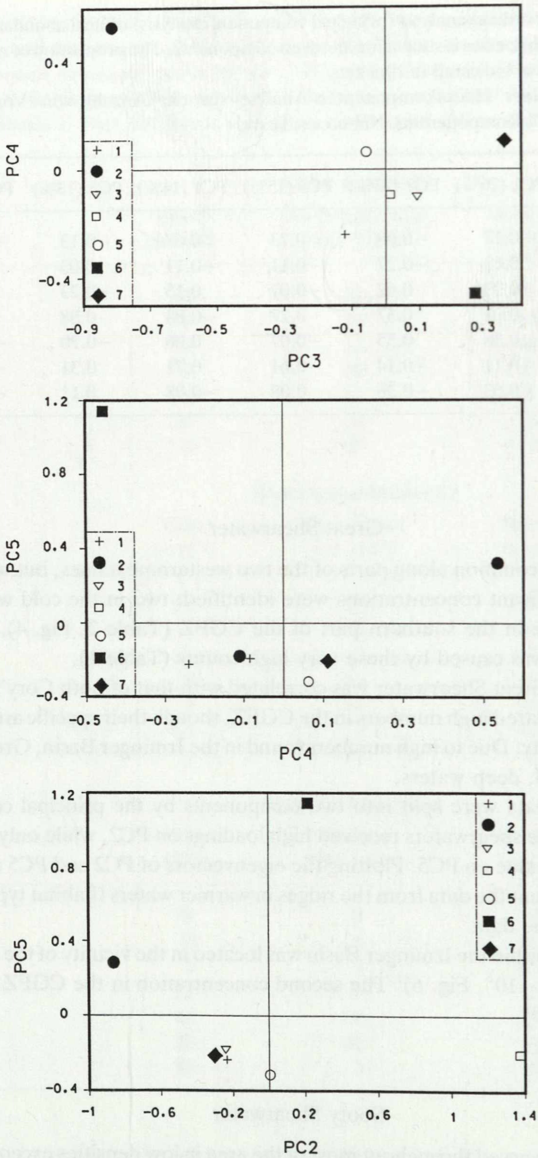


Fig. 5: Plots of habitat characteristics of selected principal components. The mean load of the eigenvectors is shown per habitat type. Type 1: ≥12°C, <150 nautical miles from land, ≥1500 m depth – type 2: ≥12°, <150 n.miles, <1500 m – type 3: ≥12°, ≥150 n.miles, ≥1500 m – type 4: ≥12°, ≥150 n.miles, <1500 m – type 5: <12°, <150 n.miles, <1500 m – type 6: <12°, ≥150n.miles, ≥1500 m – type 7: <12°, ≥150 n.miles, <1500 m.

Abb. 5: Darstellung von Habitatcharakteristika ausgewählter Hauptkomponenten. Dargestellt ist die durchschnittliche Ladung von Eigenvektoren für Habitattypen.

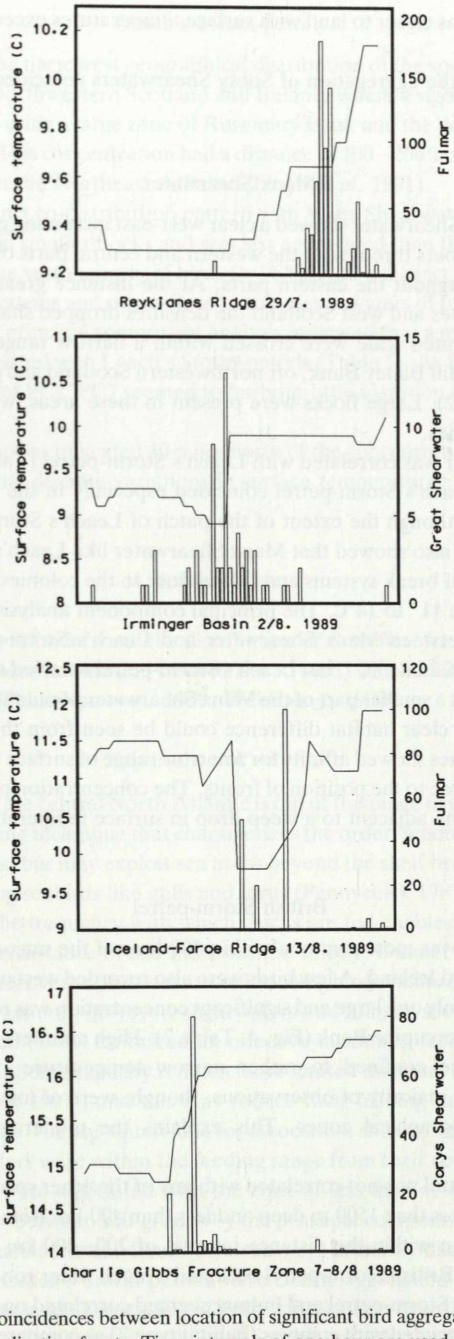


Fig. 6: Examples of coincidences between location of significant bird aggregations and gradients in surface temperature indicating fronts. Time intervals of one hour are used on the X-axis.

Abb. 6: Beispiele für das Zusammenfallen von bedeutenden Vogelansammlungen und Gradienten in der Oberflächentemperatur, die Fronten anzeigen. Die X-Achse gibt Zeitintervalle von einer Stunde an.

was birds in PC1 from areas closer to land with surface temperatures exceeding 12° (Faroes, Britain and Ireland).

In the fracture zone the aggregation of Sooty Shearwaters coincided with the front to waters above 16°.

Manx Shearwater

The distribution of Manx Shearwater showed a clear west-east increasing gradient. Flying birds were scattered in very low numbers throughout the western and central parts of the study area, while the birds were common throughout the eastern parts. At the distance greater than 600 km from the larger colonies in the Faroes and west Scotland the densities dropped sharply (Fig. 4). Four significant concentrations of limited scale were crossed within a narrow range of surface temperatures around 12° on the Outer Bill Bailey Bank, off northwestern Scotland and along the edges of the Iceland-Faroe Ridge (Table 2). Large flocks were present in these areas, which all lie approximately 200 km from major colonies.

The Manx Shearwater was correlated with Leach's Storm-petrel (Table 3). The distribution of Manx Shearwater and Leach's Storm-petrel coincided especially in the area of high densities off northwestern Scotland, although the extent of the patch of Leach's Storm-petrel was much larger (Table 2). Chi-square test also showed that Manx Shearwater like Leach's Storm-petrel was significantly associated with shelf break systems and ridges close to the colonies in the area of transitional surface temperatures from 11° to 14°C. The principal component analysis resulted in a refined picture of the correlation between Manx Shearwater and Leach's Storm-petrel. Manx Shearwater received high loading on PC1 and PC7, but Leach's Storm-petrel received a strongly negative loading on PC7. This indicates that a smaller part of the Manx Shearwater population was not correlated with Leach's Storm-petrel. No clear habitat difference could be seen from the plot of PC1*PC7.

Even though the species showed affinity for a narrow range of surface temperatures, the areas of concentration were not close to the position of fronts. The concentration off Scotland was located 20 miles from a turbulent zone adjacent to a steep drop in surface temperatures further to the north.

British Storm-petrel

The British Storm-petrel was most common within 400 kms of the major breeding colonies in the Faroes, western Britain and Ireland. A few birds were also recorded west of 12° W close to the southwestern part of Iceland. Only one large and significant concentration was recorded, located in a well-defined area around the Porcupine Bank (Fig. 4, Table 2). High numbers (≥ 10 birds per 10-minute period) in this area were confined to rather narrow temperature (14.2°–14.3°) and depth (150–300 m) ranges. The majority of observations, though, were of low numbers for much wider geographical and oceanographical zones. This explains the moderate variance-to-mean ratio (Table 1).

The British Storm-petrel was not correlated with any of the other species. It was primarily associated with warm waters less than 1500 m deep and less than 400 km from land (Table 4). A total of 62% of the birds was seen within the distance interval of 200–400 km from land. Compared to Leach's Storm-petrel, the British Storm-petrel occupied a much wider zone near the breeding areas. As mentioned, the British Storm-petrel and Fulmar seemed correlated on PC4 (Table 5). This component reflected birds associated with colonies (habitat type 2) as compared to PC5, which reflected birds from more remote areas (habitat type 6).

No features of finer scale indicating fronts or turbulence could be determined from the temperature distribution of the surface waters of the Porcupine Bank.

Leach's Storm-petrel

Leach's Storm-petrel had the narrowest geographical distribution of the species examined. This species was only recorded off northwestern Scotland and Ireland, where a significant concentration was recorded within an area covering a large zone of Rosemary Bank and the deep waters to the south of the bank (Fig. 4, Table 2). This concentration had a distance of 100–200 km to St Kilda, which is the only known large colony in the Northeast Atlantic (Lloyd *et al.* 1991).

The species had a distinct co-distribution pattern with Manx Shearwater off northwestern Scotland, although it was seen in smaller flocks and was less aggregated than this species (Table 3). The chi-square test associated the vast majority of birds (> 95%) with a distinct habitat identical to Manx Shearwater's: shelf break systems and ridges close to colonies in waters of transitional surface temperatures. As mentioned, the principal component analysis indicated that a minor portion of the Manx Shearwaters were not correlated with Leach's Storm-petrels (Table 5). As for this species the habitat affinity depicted from plot of PC1*PC7 seemed to harbour little variation from the picture given by the chi-square test.

The existence of a front was indicated 40 miles north of the concentration off Scotland in a generally turbulent area, showing discrete variations in surface temperatures.

4. Discussion

The following is an attempt to understand the distribution of *Procellariiformes* beyond the shelf and offshore waters. Hence it does not include birds closer to land, which have already been subject to extensive seabird surveys (Danielsen *et al.* 1990, Webb *et al.* 1990).

Importance of colonies

One may question whether the central North Atlantic is out of the range of adult petrels feeding their chicks. Due to the flap-gliding technique that characterizes the order, feeding birds are not restricted to coastal or off-shore areas, but may exploit sea areas beyond the shelf break, that are out of reach for other species of breeding seabirds like gulls and terns (Pennycuick 1987). Brooke (1990) stated, that during chick-feeding the frequency with which chicks are fed enables the Manx Shearwater to exploit areas at a maximum distance of 360 km from the colony. Dunnet & Ollason (1982) on the basis of analyses of ringing recoveries and controls of breeding birds mentioned a maximum record of 466 km for the Fulmar. In general, however, shearwaters and fulmars seem to feed much closer to the colony. Furness & Todd (1984) estimated an effective maximum feeding range for fulmars at 120 km. The storm petrels' gliding capacity is much more limited than that of the Shearwater species and the Fulmar (Pennycuick 1987), and this may reduce their feeding ranges as compared to the shearwaters and the Fulmars. The chi-square test for association showed that most of the two storm-petrels and Manx Shearwaters were within the feeding range from their colonies, and a fair proportion (63%) of the fulmars were associated with the zone of less than 400 km distance.

Measuring correlations between sub-groups by the principal component analysis provided indications that only Manx Shearwaters and Leach's Petrels were primarily distributed in relation to the location of their colonies. Leach's Storm-petrels were clearly aggregated in the near-colony areas within 200 km distance from land. The studies of Petrel distribution over the inner shelves adjacent to the British and Faroese colonies showed that large numbers of Manx Shearwaters but only few British Storm-petrels are found here (Webb *et al.* 1990 and Danielsen *et al.* 1990). Concentrations of British Storm-petrel in the North Atlantic have mainly been described on the outer shelves (Danielsen *et al.* 1990, this study, Leopold pers. comm.), indicating major concentrations off the

Faroes and off south and western Ireland. As the number of non-breeding adults of Manx Shearwater is very small (Brooke 1990), the Manx Shearwaters scattered at low densities beyond 400 km from colonies may be immatures. The finding of a fair proportion of Fulmars and British Storm-petrels more than 200 kms from land in areas with different characteristics than areas near colonies may indicate large populations of non-breeders. However, knowledge of the ratio between non-breeding adults/immatures of petrels at sea is very limited. A study by Dunnet *et al.* (1979) indicated that a large proportion of the population of Fulmars consists of non-breeders. In this light it is interesting that 62% of the British Storm-petrels were actually recorded more than 200 kms from land.

Large scale habitats

Within the ranges of measurements taken during the surveys, the distribution of the seven Petrel species may be viewed from the general characteristics of their physical environment like large-scale changes in surface temperature and sea depth. As reflected primarily by the principal component analysis, the distribution of all species could be viewed in at least two dimensions characterized by a combination of depths and surface temperatures. Identification of common characteristics of local breeders and visitors proved difficult, and the examined species showed segregation rather than overlapping distributions. Segregation among pelagic seabirds has been demonstrated along the western frontal boundary of the Gulf Stream (Haney 1986a). In studies carried out in the Indian Ocean and the Southern Ocean, Summerhayes et al. (1974) and Pocklington (1979) showed that both diversity and abundance of marine birds were correlated with different water types defined by surface temperature and salinity.

We found that the Fulmar was more affected by water surface temperatur than water depth, as most birds were recorded in the colder waters in the study area. Significant concentrations of one group of Great Shearwaters showed affinity for the core of the Gulf water in the CGFZ (> 16°). Concentrations of Great Shearwaters in the eastern part of the North Atlantic have been recorded later in August at the shelf break off France (Bourne 1986), but numbers in the eastern part in general seem to fluctuate (Hutchinson 1989). Cory's Shearwater was more closely related to the CGFZ than any of the other species, but seemed more related to the frontal zone than to the warm water mass. Large fluctuations in numbers reaching northwestern Europe may be linked to variations in inflow of warmer water masses from the south (Jones & Tasker 1982). Cory's Shearwaters seen at the same latitude off Canada in July (mainly *C. d. borealis*) are believed to be subadults on late passage from their wintering quarters off South Africa (Brown 1986).

Water temperature also affected the distributions of Manx Shearwaters, Leach's Storm-petrels and British Storm-petrels, as they were rare in cold waters. The only true geographical and habitat overlap found in this study may be the co-occurrence that Manx Shearwater showed with Leach's Storm-petrel close to the colonies to the northwest of Scotland. Like Leach's Storm-petrel, the majority of Manx Shearwaters were in near-colony areas near the shelf edge with surface waters influenced by the Gulf Stream. These characteristics fit well with areas off northwestern Scotland, especially with St Kilda, west of Scotland, which is located very close to the shelf break. British Storm-petrels occupied a zone with much wider oceanographical characteristics than both Manx Shearwaters and Leach's Storm-petrels.

Unlike the other species Sooty Shearwaters were divided into two groups separated mainly by water depth characteristics: one in shelf areas and one in deep areas, and the species avoided cold water masses east of Greenland. The low variance-to-mean ratio, the lack of flocks on the water and the fact that no significant aggregations were found in the study area underline the weak affinity between this species and the deep areas of the North Atlantic Ocean. Large concentrations in the North Atlantic have so far only been recorded in the extensive shallow waters of the Scotia Shelf and Grand Banks in May-July (Brown 1986) and between north and western Britain and the Faroes in the east in

July-September (Tasker *et al.* 1987, Danielsen *et al.* 1990, Webb *et al.* 1990). Brown *et al.* (1981) discussed the differences in the distribution of the two South Atlantic shearwaters with broad overlap in their diets and suggested, that throughout their non-breeding range in the Atlantic they seem to minimize competition by avoiding complete distribution overlap. Competition rather than habitat differences may also explain the segregation of the species during this study. On the other hand, the dependence on shelf and shelf break areas seems to be a consistent feature of non-breeding Sooty Shearwaters, as judged from the huge concentrations recorded in these environments off California (Briggs & Chu 1986).

Small scale habitats

Although an impression of the Petrel species' distribution and segregation across the North Atlantic was received, it is conceivable that information of these species' small-scale variation was lost during the surveys. Seabird variability and hence habitat preferences changes with the geographical scale on which the analysis is based (Schneider & Duffy 1985).

Due to the large distance between the study transects, the majority of our results reflect mainly coarse scale habitats. On the other hand, our comparisons of bird and surface temperature distributions present evidence of aggregations of Fulmar, Cory's, Great and Sooty Shearwater in the vicinity of meso scale phenomena like frontal zones between different water masses. These findings add to the expanding general evidence that frontal barriers between water masses form the principal habitats for many seabird species in both shelf, shelf-break and oceanic areas (e. g. Kinder *et al.* 1983 (Berings Sea), Ainley & Jacobs 1981 (Ross Sea), Haney & McGillivary 1985b (South Atlantic Bight)).

Five significant concentrations of Fulmars were located at fronts to colder water masses along the edges of the Reykjanes and Iceland-Faroe Ridges. Our surveys further indicated that the peak occurrences of Great Shearwater southeast of Greenland coincided with the position of fronts to the colder water masses. No fishing activities by commercial trawlers were recorded in these concentration areas, which supports the evidence that the distribution of the Fulmar is primarily controlled by oceanographic features (Brown 1970, Durinck et al. 1993).

Our observations of Cory's Shearwaters correspond well with earlier studies showing that the species at these latitudes mainly is distributed further to the south along the edges of the Gulf Stream than Great Shearwaters, as has been reported near the Scotian Shelf and Grand Banks (Brown 1986). Thermal fronts along the Gulf Stream, like in the Charlie Gibbs Fracture Zone, have also been found by Haney & McGillivary (1985a) to support Cory's Shearwaters, which due to their reduced diving capacity are dependent on surface fronts.

No observed small-scale features seemed to influence the distributions of Manx Shearwaters and the storm-petrels. Despite the fact that concentrations of both storm-petrels occurred over the shelf and the shelf edge, no evidence of fronts was gathered in their immediate vicinity. The distribution of Leach's Storm-petrel was found by Haney (1986b) to be particularly affected by upwelling in the Gulf Stream of southeastern United States. The shallow Porcupine Bank of Ireland had the only concentration of British Storm-petrel, where weak upwelling has been described (Dickson & McCave 1986).

5. Zusammenfassung

Im Nordatlantik (Abb. 1) wurde die Sommerverteilung von *Procellariiformes* erfaßt. Die Daten, die 1987 und 1989 in großem Umfang gesammelt wurden, wurden auf Korrelationen zwischen den Arten und mit ozeanographischen Daten untersucht. Insgesamt wurden 9000 km Transekt-Strecken mit Schiffen zurückgelegt, wobei die

Teilstrecken 50–500 km auseinanderlagen. Sieben Arten wurden häufig angetroffen, und ihre Verbreitung wies Schwerpunkte auf. Die meisten beobachteten Konzentrationen lagen am Rande von Kontinentalsockeln und in der Nähe von ozeanischen Höhenrücken neben dem Golfstrom. Mit Ausnahme des Eissturmvogels *Fulmarus glacialis* hatten kalte Oberflächentemperaturen einen negativen Einfluß auf die Verbreitung der meisten Arten. Die Wellenläufer *Oceanodroma leucorhoa* waren innerhalb von 100 km um die Hauptkolonie auf St. Kilda konzentriert. Sturmschwalben *Hydrobates pelagicus* wurden in einem küstennahen Streifen von etwa 400 km angetroffen, Eissturmvögel und Schwarzschnabel-Sturmtaucher *Puffinus puffinus* in Abständen von über 1000 km von den nächsten Kolonien, wobei die Schwarzschnabel-Sturmtaucher nur bis etwa 600 km von der Küste häufig waren.

Eissturmvögel und Sturmschwalben, die mehr als 200 km von Kolonien entfernt beobachtet wurden, gruppierten sich offenbar in Gebieten mit anderen ozeanographischen Charakteristika als solche Vögel, die in der Nähe von Kolonien beobachtet wurden. Die ozeanographischen Charakteristika im Bereich von Konzentrationen von Schwarzschnabel-Sturmtauchern und Wellenläufern waren recht ähnlich.

Die Verbreitung des Großen Sturmtauchers *Puffinus gravis*, des Dunklen Sturmtauchers *Puffinus griseus* und des Gelbschnabel-Sturmtauchers *Calonectris diomedea* überschnitten sich nur wenig mit der der anderen Arten, die hauptsächlich im südlichen Bereich des mittel-atlantischen Höhenrückens angetroffen wurden. Die drei letztgenannten Sturmtaucher bevorzugten zudem leicht unterschiedliche ozeanische Habitate.

6. References

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