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PATTERNS OF CO-OCCURRENCE OF CETACEANS AND SEABIRDS IN THE NORTH EAST ATLANTIC

Henrik Skov*, Jan Durinck*, Finn Danielsen* & Dorete Bloch+

*Ornis Consult Ltd, Vesterbrogade 140
DK-1620 Copenhagen V, Denmark

+Natural History Museum, FR-100 Tórshavn
Faroe Islands

ABSTRACT

This paper seeks to use the results of combined cetacean and seabird surveys for investigating levels of correlation between species of whales and birds. The distribution of cetaceans and seabirds recorded during the Faroese cruises of the North Atlantic Sightings Survey (NASS) in July-August 1987 and 1989 is analysed. The study area covered the Norwegian Sea south of 68° N from East Iceland to 2° E, the sea between East Iceland and the Faroes from 20° W to 2° E and the seas west of Scotland and Ireland to 20° W.

Simultaneously sampled data on cetaceans and seabirds were analysed at different geographical scales, and compared by relating individual species to oceanographical variables derived from Principal Component Analysis of depth and surface temperature characteristics. Surprisingly, most species were correlated with two factors accounting for less than five percent of the oceanographical variation, and the majority of species appeared clustered in shelf areas of colder surface temperatures (< 9° C). Water mass independence was apparent in breeding bird species but not in cetacean species with which they were correlated, and we argue that this difference may be due to a strong influence from the position of colonies on bird distribution. The larger species of cetaceans observed in deep oceanic waters showed little or no relation to bird species.

INTRODUCTION

Recently, a number of coordinated surveys of cetaceans covering large ocean areas have been carried out concurrently with surveys of seabirds, but mostly at a somewhat larger scale. And contrary to most seabird mapping programmes whale surveys have often been undertaken from dedicated vessels. Although research programmes have been designed for investigating whale-bird interactions concerning a limited number of species (e.g. Au & Pitman 1988, Obst & Hunt 1990), the potential use of international sightings surveys for receiving improved data on the distribution of seabirds has been little explored.

We wished to use the North Atlantic Sightings Surveys (NASS) in 1987 and 1989 for gathering data on seabird abundance in the North Atlantic. Seabird observations were carried out from the Faroese vessel *Hvitiklettur* for six weeks during July-August 1987 and for three weeks during July-August 1989 from the Faroese vessel *Ólavur Halgi* and the Icelandic vessels *Árni Friðriksson* and *Barðinn*. The purposes were a) to produce quantifiable information on seabird distribution for a vast sector of the North East Atlantic, and b) to correlate distributions of cetaceans and birds. The distribution of seabirds and cetaceans recorded during NASS has been published independently in a number of papers (e.g. Danielsen *et al.* 1990, Sigurjónsson *et al.* 1989, 1990). This paper seeks to merge the data on whales, dolphins and seabirds observed from *Hvitiklettur* and *Ólavur Halgi*, and view the distributional patterns from a different (mainly oceanographical) angle. Such correlations are probably the only means by which one can obtain a general overview of the ecological relationships between cetaceans and seabirds over a wide geographical range. The degree of distributional overlap or seggregation of species can be identified by using oceanographical characteristics as vectors.

The design of the NASS-87 and NASS-89 surveys permitted comparisons of seabird and cetacean data with oceanographical data. Associations between cetaceans and seabirds at a small-scale (close proximity) could not be thoroughly investigated during the NASS surveys, as these direct seabird-cetacean interactions must be studied at a small distance. During NASS, only the target species (principally the *Balaenoptera* species and Pilot Whale *Globicephala melas*) were closed in on, while a substantial part of the observations of other species were made while on passing mode (Sigurjónsson *et al.* 1989, 1990).

Determination of zones of overlap or clusters of cetaceans and seabirds in the North East Atlantic can prove important both to the future conservation and utilization of stocks, and may provide links to important food sources and key food webs exploited by many species.

MATERIAL AND METHODS

Observation procedures and survey strategies

This study was conducted in the North East Atlantic in July-August 1987 and 1989 (Fig 1.). A total of 5600 n. miles were cruised in 1987 and 4800 n. miles in 1989. During both surveys the coverage included areas south of 68° N from East Iceland to 2° E, the sea between East Iceland and the Faroes from 20° W to 2° E and the seas west of Scotland and Ireland to 20° W. Proportionally more effort was channelled into areas close to and north of the Faroes in 1987 compared to 1989. The oceanography of the large area from west of Ireland to north of the Faroes is dominated by the Gulf Stream - North Atlantic Current, which runs in a northeasterly direction over the ridges on both sides of the Faroes (Hansen 1985).

Surface temperatures in August decrease from the south to north from 15° to 9° C (Krauss 1955). The smaller area covered north of 62° N is dominated by the East Iceland Current with surface temperatures in August in the range between 6° and 9° C. Accordingly, the study area spans a surface temperature gradient from 6° to 15° C. The Iceland Faroe Ridge, the Rockall Bank and the Porcupine Bank form major shelf areas far from land, while the coastal areas southeast of Iceland, around the Faroes and west of the British Isles form the shelf areas close to the land.

Although Fin Whale *Balaenoptera physalus*, Minke Whale *Balaenoptera acutorostrata* and Pilot Whale were the target species, all cetacean sightings were recorded. The same line-transect strategy was used in 1987 and 1989, and the recording procedures of both cetaceans and birds were almost identical during the two surveys. Both ships had a standard crew of four whale observers and one bird observer on the roof. The cruising speed of the ships was 8.5-9.5 knots. In general, observations were only maintained in conditions up to Beaufort 4-5 and when visibility exceeded 1 n. mile, but occasionally observations were made during poorer conditions.

At each whale sighting time of observation, ship's position and bearing to the sighting and the distance to the whale were recorded (Sigurjónsson *et al.* 1989). In order to limit counting of birds along the cruise lines, bird records were only made within one transect having a fixed width of 300 meters, extending ahead of the ship in a 90° degree sector. Recordings were split into intervals of 10-minutes. In order to limit the bias introduced by flying birds, snap-shot counts of these were performed at intervals following Tasker *et al.* (1984). Ship's position, bearing and speed were recorded hourly, at way points and start of closing tracks. Surface temperature was recorded at the start of each hour. Water depth was noted from a nautical map.

Data analysis

Only species meeting the following conditions have been included in the analysis: whale species, with a total of at least 10 observed individuals and seabird species, with at least 100 observations. The resulting 10 cetacean and 11 bird species are listed in Table 1. The selected species include species that are relatively uncommon in the eastern part of the North Atlantic compared to areas west of the study area. To limit the bias introduced by poor conditions, only 10-minute periods, where windspeeds were below Beaufort 4 and visibility exceeded 1 n. mile, were retained for analysis. A further selection of data was made in order to avoid the possible over-representation of birds associated with the target species (cetaceans) by excluding the observations made during the closing tracks to the animals. Therefore, all whale and bird observations analysed can be regarded as recorded during transects of passing mode. The effect of fishing activities on bird distribution was limited by excluding all birds observed feeding at trawlers.

Because of the limited size of the database produced by selection procedures, no analysis of differences between the two years was made, and for the same reason details of (feeding) behaviour were not considered. A normality test (Kolmogorov) was performed on 10-minute totals, as well as calculations of kurtosis and skewness values. The distributional characteristics of each species were first examined by computing the mean, maximum and variance values at the 10-minute interval. To study the dependence of the species' variability on the size of interval or sample units, an index of clustering (variance-to-mean ratio) was calculated for four different scales: 1.5 n. miles, 10 n. miles, 50 n. miles and 150 n.miles. Inter-correlation (Pearson correlation) between species was then performed at the scale, where the aggregation of most species peaked. Before correlation analysis was made, all densities were transformed by log. (x+1).

To identify common environmental gradients to view the distribution of all species along, we performed Principal Component Analysis (PCA) on oceanographical measures for each latitudinal band of 60 n. miles. The major orthogonal patterns of variation gave combinations of three intervals of surface temperature (6-9° C, 9-12° C and 12-15° C), and four intervals of water depth (0-400 m, 400-800 m, 800-1500 m and ≥1500 m). All variables were expressed as proportions. The factor scores for each principal component were averaged for each latitudinal band and correlated with the mean densities of the selected species using linear regression. The resulting correlation coefficients formed units in three-dimensional plots, which made it possible to depict graphically the position of species in relation to the principal components.

RESULTS

A mean abundance of 14.7 birds and 1.2 cetaceans was recorded per 10-minute period. The Fulmar *Fulmarus glacialis* and Puffin *Fratercula arctica* accounted for 71% of the bird abundance, while Pilot Whale, White-sided Dolphin *Lagenorhynchus acutus* and Common Dolphin *Delphinus delphis* accounted for 93% of the whale abundance (Table 2).

The Kolmogorov test showed that the sample of all species was highly non-normal ($p < 0.01$), and all species had high coefficients of skewness (> 7.6) and kurtosis (> 86). The high variance-to-mean ratios found in most species except Great Skua *Stercorarius skua*, Fin Whale, Sperm Whale *Physeter macrocephalus*, Northern Bottlenose Whale *Hyperoodon ampullatus* and Harbour Porpoise *Phocoena phocoena* indicate that among the dominating species of seabirds and cetaceans a patchy dispersion pattern was present (Table 2). All species except White-beaked Dolphin *Lagenorhynchus albirostris* showed a significant increase in patchiness with decreasing degree of resolution (Table 2, Fig. 2). Thus, correlations between species were based on the 150 n. miles unit size, the result is shown in Table 3. Significant inter-correlations were found between breeding bird species recorded in large numbers on the inner shelf, not far from breeding colonies: Fulmar, Gannet *Sula bassana*, Kittiwake *Rissa tridactyla*, Arctic Tern *Sterna paradisaea*, Guillemot *Uria aalge* and Puffin. The Harbour Porpoise, White-sided Dolphin and Pilot Whale seemed correlated with members of the "Inner Shelf group", as did the Minke Whale, whereas the White-beaked Dolphin was correlated with Gannet only, as it was only recorded on the shelf northwest of Scotland close to the gannetry of Sct. Kilda. The Bottlenose Dolphin *Tursiops truncatus*, the Common Dolphin and the larger species of cetaceans showed no or little relation to the "Inner Shelf group". Another inter-related group could be identified among birds found in abundance both on the Faroe Shelf, on the banks south of the Faroes and near the edge of the shelf south and west of the Faroes and west of Scotland, hence overlapping with the first group; Fulmar, Gannet, Leach's Petrel *Oceanodroma leucorhoa*, Storm Petrel *Hydrobates pelagicus*, Manx Shearwater *Puffinus puffinus*, Sooty Shearwater *Puffinus griseus*, Great Skua, Kittiwake, Arctic Tern and Guillemot. Cetaceans related to this "outer shelf group" included Pilot Whale and Bottlenose Dolphin *Tursiops truncatus*, and to a lesser degree White-sided Dolphin and Harbour Porpoise. The coefficient of Pilot Whale and Bottlenose Dolphin correlation was high, as small groups of Bottlenose Dolphins were seen with the large herds of Pilot Whales recorded in 1987 (Bloch & Lockyer 1988).

Fin Whale was correlated with two cetacean species recorded mainly close to the shelf edge and in deep waters: Bottlenose Whale and Common Dolphin. No bird species was clearly related to this "deep water group", but Great Skua showed some relation to Fin Whale and Common Dolphin.

The Sperm Whale was not correlated with any of the bird species, nor with other cetaceans.

The PCA of oceanographical measures for 20 lattitudinal bands extracted six factors with eigenvalues exceeding 0.06 (Table 4). Together these factors explained the total variation (100%) in oceanography, as measured by depth and surface temperature characteristics. PC1 and PC2 were the major factors explaining two thirds of the variation, while the two minor components PC5 and PC6 explained less than 5%. PC1, PC3 and PC5 described mainly different temperatures associated with shallow and shelf waters. PC1 described the surface temperature interval between 9° and 12° C for both shallow (< 400 m) and shelf waters (4-800 m), while PC3 was the only component to describe warm waters of variable depth and PC5 described the temperature interval below 9° in shelf and shelf edge zones. PC2, PC4 and PC6 had relatively less loading on the surface temperatures, and described mainly differences in depth. PC2 described deep waters (≥ 1500 m) associated with cold surface water. PC4 described shallow waters (< 400 m) with little temperature association, while PC6 as the only component described only depth characteristics.

The 20 linear regressions of the six PCA-derived oceanography measures on densities of the 10 cetacean and 11 bird species revealed only three significant relationships (Table 5). Fulmar and Gannet were correlated with PC6 (independence of surface temperature characteristics) and Common Dolphin was highly correlated with PC1 (shelf waters ≥ 9° and < 12° C). In general, species could be related with more than one factor, and the total explained variation ranged from 11.4% (White-beaked Dolphin) to 83% (Common Dolphin). By plotting all r coefficients, the appearence of each species' relative position in relation to the total oceanographic measures was improved (Fig. 3). The three "depth" components 2, 4 and 6 did not segregate species into discrete clusters, but rather gave the impression of a scattered distribution. Looking at the species included in the "Inner Shelf Group" (= group 1) and the "Outer Shelf Group" (= group 2) it appears, that in general PC6 (temperature independence for all depth categories) influenced most species, especially birds (with the exception of Puffinus species and Common Tern). Of the cetaceans concidered as members of group 1 and 2 only Minke Whale and Bottlenose Dolphin were influenced by PC6. PC2 (deep oceanic water, cold temperatures) and PC4 (shallow waters of cold and warm temperatures) were only of importance to Storm Petrel and White-sided Dolphin. The slightly inter-related group of Fin Whale, N Bottlenose Whale, Common Dolphin and Great Skua (= group 3) had low coefficients with PC6, and had only slightly similar position on the plot by sharing small coefficients with PC2 and PC4. The White-beaked Dolphin - Gannet correlation could not be well depicted by PC2, 4 and 6, the Gannet being closer to members of group 1 and 2, to which it was also correlated. Also the Sperm Whale showed weak relations to PC2 and 4, and seemed related to PC6.

The "surface temperature factors" segregated species more effectively (PC1, PC3, PC5). Detailing again the position of members of the groups 1 and 2 only Gannet and Storm Petrel were influenced by PC1 (≥ 9°and < 12° surface temperatures for shallow and shelf waters), while the majority of both cetaceans and birds were clustered at moderate to high coefficients with PC5 (the shelf and edge waters with surface temperatures below 9°) and having no relation with PC1. PC3 (warm surface water) affected also the distribution of Fulmar and White-sided Dolphin. Members of group 3 were positioned far from each other, when plottet against PC1, 3 and 5. Common Dolphin was at the far left of the graph, representing correlation with temperate and warm surface waters. Northern Bottlenose Whale was most related to PC3, Great Skua most related to PC1 and Fin Whale had a low coefficient with all three components. When viewed by these three components Gannet was closer to White-beaked Dolphin than to the members of group 1 and 2. The Sperm Whale showed relations with cold shelf and edge waters (PC 5).

Table 6 expresses the adjusted proportion of each species recorded in oceanic and shelf regimes, and the proportion recorded in waters below and exceeding 12° C. More cetacean than bird species had a high proportion of records in deep waters, as only Leach's Petrel and Manx Shearwater were primarily observed in the oceanic parts. With the exception of Leach's Petrel, Fin Whale and Common Dolphin, which were primarily seen in waters of surface waters above 12°, all species examined had relatively high proportions of their populations in both warmer and colder waters.

DISCUSSION

The pronounced differences in dispersion patterns and abundance of the analysed species of birds and cetaceans indicate the presence of clusters in at least 15 of the 21 species examined (Table 2). With the exception of Storm Petrel, the highest degree of clustering was observed in the numerically dominant species; Fulmar, Gannet, Leach's Petrel, Manx Shearwater, Sooty Shearwater, Kittiwake, Guillemot, Puffin, Pilot Whale, White-sided Dolphin and Common Dolphin. Surveys of marine birds have documented that birds at sea form large feeding aggregations in areas of enhanced productivity/availability of prey (Schneider 1982, Duffy 1983, Briggs *et al.* 1984, Abrams & Griffiths 1981). By using meso-scale units as a basis for correlations between species and with marine parametres, important variation in the distribution at the smaller scale may be lost. Fronts and local upwelling may affect both the productivity and availability of prey in surface waters (Schneider & Duffy 1985), and hence the information received through this study lacks details on coarse-scale and smaller scale habitats.

Surface-temperature and water depth were used as the primary factors determining species groups. Although these parameters may not directly affect the occurrence of cetacean and bird species, they may indicate a relationship to relative productivity of different water masses and shelf areas. Table 6 provides strong indications that in general, cetaceans were distributed in a wider depth spectrum than birds. For most of the whale species recorded, we found as many or more in the deep oceanic parts as at the edges and over the slopes of the shelves, while only a minority of bird species had populations in the deep areas. Due to the position of their breeding colonies, most seabirds breeding in the North East Atlantic experience large distances to areas beyond the shelf edge, and consequently the largest aggregations at this time of the year are normally found in shelf waters (Danielsen *et al.* 1989, Webb *et al.* 1990). The reason why comparatively more birds of Leach's Petrel and Manx Shearwater were seen in oceanic waters may be that the majority of the records of these two species were made close to the colonies at Sct. Kilda, where the shelf breaks close to the island. The same indication of major differences in the bird and whale distribution could not be given by the spectra of surface temperatures (Table 6).

Because of the strong affinity for shelf areas in most of the seabirds, it is not surprising that many species, which are common breeding birds both on Iceland, Faroes and west Scotland, were inter-related. Pearson correlation revealed relations between species within two major overlapping groups, which were assigned to the inner and outer shelf areas, respectively. When correlating members of these groups to oceanographic measures by PCA, relatively well depicted patterns of co-occurrence were identified. Most of the species in the two groups were related to the least components (PC5 and PC6), accounting for less than 5% of the total oceanographical variation. Contrary to the birds, the cetaceans of the two groups were not related to PC6, which measured total independence of surface temperatures for all depth sections. Most birds and cetaceans within the group, though, were related to the fifth component, measuring cold surface temperatures of the shelf waters.

Two models may explain the discrepancy in cetacean and bird distribution within group 1 and 2; birds might be aggregated at coarse-scale phenomena occuring within the temperature intervals (fronts, local upwelling etc). It is unlikely, though, that dolphin species should not at all exploit such phenomena. Rather, as an effect of the location of their breeding colonies, many birds were unable to feed in more productive water masses far from land. This model is likely to explain the paucity of group 1 and 2 seabirds in areas rich in cetaceans species with which they were related, as well as the paucity of birds in deep areas. Colonies probably affects seabird distribution during the breeding season stronger than both physical and biological phenomena (Skov *et al.* in prepp). The cold spectrum af surface temperatures on the shelf may provide most of the birds concerned with important food sources during the breeding season, but as the independence of water masses seem to be a strict bird characteristic, it is likely that this component (PC6) include areas with limited food sources. Food competition between breeding birds seems evident within short ranges of large colonies as is indicated by the distances between large colonies (Furness & Birkhead 1985), and by the dispersion of birds from the near colony areas after the breeding season (Danielsen *et al.* 1989).

Although Fin Whale, N. Bottlenose Whale and Sperm Whale shared large proportions of sightings in deep waters (> 75%), only Fin Whale and N. Bottlenose Whale were correlated, and as viewed by the PCA the co-occurrence of the two species was weak. Concidering the possible feeding depth of Sperm Whale (Leatherwood & Reeves 1983), it may be questioned whether surface temperature characteristics affect its distribution at the meso scale. Weak relations were also identified between Fin Whale, Common Dolphin and Great Skua. Common Dolphin was abundant in warm Atlantic waters, where Fin Whale (Sigurjónson *et al.* 1989) and Great Skua was recorded.

Common Dolphin and White-beaked Dolphin seemed to have the narrowest habitat characteristics of all species, as they only occured in warm and cold shelf areas, respectively.

Our findings support the idea, that cetaceans and seabird distribution in the North East Atlantic overlap with respect to geographical area, shelf and surface water characteristics measured at the meso scale. Bird colonies, though, seemed to complicate the determination of common features to correlated species. Whether the location of bird colonies actually obscured the identification of bird-cetacean clusters may be tested by combined surveys during the non-breeding seasons, as the coming NASS 91/92 survey in wintertime. Future research is needed on the cluster identified in the colder portions of the shelf waters, both with respect to temporal and spatial persistence. As more data from these types of surveys are analysed, a more precise definition of species assemblages and habitat structures will be possible.

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Table 1.

List of selected species of cetaceans and seabirds, followed by species codes used in figures and tables.

Scientific name	Species name	Species code
Fulmarus glacialis	Fulmar	FUGLA
Sula bassana	Gannet	SUBAS
Oceanodroma leucorhoa	Leach's Petrel	OCLEU
Hydrobates pelagicus	Storm Petrel	HYPEL
Puffinus puffinus	Manx Shearwater	PUPUF
Puffinus griseus	Sooty Shearwater	PUGRI
Stercorarius skua	Great skua	STSKU
Rissa tridactyla	Kittiwake	RITRI
Sterna paradisaea	Arctic Tern	STEPA
Uria aalge	Guillemot	URAAL
Fratercula arctica	Puffin	FRARC
Balaenoptera physalus	Finwhale	BAPHY
Balaenoptera acutorostrata	Minke Whale	BAACU
Physeter macrocephalus	Sperm Whale	PHMAC
Globicephala melas	Long-finned Pilot Whale	GLMEL
Hyperoodon ampullatus	Northern Bottle-nosed Whale	HYAMP
Tursiops truncatus	Bottle-nosed Dolphin	TUTRU
Lagenorhynchus albirostris	White-beaked Dolphin	LAALB
Lagenorhynchus acutus	Atlantic White-sided Dolphin	LAACU
Delphinus delphis	Common Dolphin	DEDEL
Phocoena phocoena	Harbour Porpoise	PHPHO

Table 2.

Abundance and dispersion statistics. I is intensity of aggregation (variance-to-mean ratio) measured at four measurement intervals: 1.5, 10, 50 and 150 n. miles. r is correlation coefficient for increasing I with increasing measurement interval. S shows significanse of r: * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$.

	Mean	Max	I-1.5 nm	I-10 nm	I-50 nm	I-150 nm	r	S
FUGLA	4.01	1000	184.64	232	281.59	412.29	0.9925	***
SUBAS	0.58	120	23.66	67.27	164.14	420.69	0.9993	***
OCLEU	0.23	120	31.43	70.84	220.69	493.51	0.9969	***
HYPEL	0.41	40	8.56	28.98	74.5	88.58	0.87	***
PUPUF	0.63	131	51.41	107.12	252.98	201.76	0.567	*
PUGRI	0.52	361	147.92	268.64	440.45	455.57	0.78	***
STSKU	0.07	6	1.57	1.88	3.54	4.89	0.963	***
RITRI	1.15	189	52.55	114.58	160.6	205.31	0.903	***
STEPA	0.11	20	6.36	10.35	19.82	34.07	0.988	***
URAAL	0.55	179	48.82	174.5	210.3	237.37	0.73	**
FRARC	6.5	8000	4211.44	8474.88	9005.07	9496.18	0.611	*
BAPHY	0.02	12	3.5	5.22	5.92	12.05	0.988	***
BAACU	0.008	2	1.25	1.4	1.36	1.87	0.962	***
PHMAC	0.005	3	1.8	1.67	2.44	2.86	0.943	***
GLMEL	0.83	500	236.78	250.77	339.98	361.43	0.873	***
HYAMP	0.004	3	2.5	2.67	4.29	5.5	0.96	***
TUTRU	0.013	12	9.23	18.5	44.84	43.8	0.757	***
LAALB	0.021	29	16.19	16.62	19.26	17.67	0.322	NS
LAACU	0.11	80	48.64	56.77	68.4	104.68	0.998	***
DEDEL	0.18	110	45.28	46.25	66.27	97.83	0.995	***
PHPHO	0.011	5	2.73	3.71	3.95	5.03	0.946	***

Table 3.
Inter-specific correlations (Pearson) at 150 n. miles scale. * marks significanse at $p < 0.05$, df 31.

	FUGLA	SUBAS	OCLEU	HYPEL	PUPUF	PUGRI	STSKU	RITRI	STEPA	URAAL	FRARC	BAPHY	BAACU	PHMAC	GLMEL	HYAMP	LAALB	TUTRU	LAACU	DEDEL	PHPHO
FUGLA																					
SUBAS	0.54*																				
OCLEU	0.16	0.25																			
HYPEL	0.43*	0.54*	0.48*																		
PUPUF	0.27	0.37*	0.5*	0.44*																	
PUGRI	0.33	0.24	0.44*	0.51*	0.74*																
STSKU	0.27	0.38*	-0.2	0	0.16	-0.1															
RITRI	0.59*	0.53*	0.36*	0.38*	0.48*	0.38*	0.35														
STEPA	0.38*	0.28	0.15	0.1	0.41*	0.34	0.42*	0.6*													
URAAL	0.46*	0.23	0.25	0.32	0.22	0.45*	0	0.57*	0.39*												
FRARC	0.64*	0.3	0.2	0.24	0.14	0.37*	0	0.67*	0.39*	0.8*											
BAPHY	0.01	0.03	-0.1	-0.2	0.26	0	0.32	0.11	0.29	-0.2	-0.2										
BAACU	0.18	0.11	0.23	0.2	0.11	0.13	0.03	0.36	0.01	0.34	0.35	-0.1									
PHMAC	0.02	0	0.18	0.01	0.25	0.14	-0.2	0.07	0.04	-0.1	0.06	-0.2	0.03								
GLMEL	0.15	0.04	0.5*	0.33	0.33	0.38*	0.07	0.31	0.34	0.16	0.11	0.09	-0.2	0.04							
HYAMP	-0.1	-0.2	-0.2	-0.3	-0.2	-0.3	0	-0.1	0.02	0	0	0.48*	0.16	-0.2	-0.1						
LAALB	0.22	0.54*	0.05	0.1	0.03	0	0	0.07	-0.1	0.22	0.16	-0.1	0.23	-0.1	-0.1	-0.1					
TUTRU	0	0	0.62*	0.32	0.37*	0.4*	-0.1	0.21	0.02	0.04	0	0.12	0.03	-0.2	0.68*	-0.1	-0.1				
LAACU	0.17	0.13	0.1	0.21	0.34	0.48*	0.12	0.35	0.4*	0.38*	0.33	0.21	0.21	0.26	0.26	0.15	-0.1	-0.1			
DEDEL	-0.1	0.26	-0.1	0.1	0.21	0	0.3	-0.1	-0.1	-0.5	-0.5	0.4*	-0.3	0.04	0.02	-0.1	-0.1	0.01	-0.08		
PHPHO	0.31	0.1	0.34	0.16	0.26	0.31	-0.2	0.33	0.09	0.35	0.47*	-0.3	0.06	0.25	0.05	-0.2	-0.1	0	0.21	-0.2	

Table 4.

Principal Component Analysis of oceanographical variables. Only factor loadings > 0.1 are shown.

Variable	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
Surface temperature:						
6-9° C		0.586		0.276	0.602	
9-12° C	0.551					
12-16° C			0.372	0.187		
Water depth:						
0-400 m	0.48			0.806		0.152
400-800 m	0.37		0.652		0.427	0.455
800-1500 m				0.120	0.238	0.628
1500+ m		0.492	0.110			0.607
Eigenvalue	2.44	2.29	1.36	0.62	0.24	0.06
% variance	34.8	32.7	19.4	8.8	3.5	0.9
Cumulative %	34.8	67.5	86.9	95.7	99.1	100

Table 5.

Linear regressions of PCA-derived habitat measures on cetacean and bird densities. Only r values > 0.1 are shown. * marks significanse at $p < 0.05$, ** at $p < 0.01$, *** at $p < 0.001$, df 20.

	PC1	PC2	PC3	PC4	PC5	PC6	r^2-sum x 100
FUGLA			0.267		0.154	0.494*	41.4
SUBAS	0.396					0.457*	50.3
OCLEU						0.306	38.7
HYPEL	0.365	0.149		0.278		0.354	40.2
PUPUF					0.291		39.9
PUGRI					0.23		23.3
STSKU	0.138			0.102			11.7
RITRI					0.119	0.12	15.4
STEPA					0.134		42.6
URAAL						0.253	19.8
FRARC					0.171	0.135	29.2
BAPHY							16.1
BAACU						0.215	27.1
PHMAC					0.338		21.7
GLMEL					0.264		28.1
HYAMP			0.17				22.2
TUTRU					0.164	0.19	34.0
LAALB						0.141	11.4
LAACU			0.145	0.12	0.188		32.1
DEDEL	0.736***		0.224				83.0
PHPHO					0.27		20.5

Table 6.

Adjusted proportions (%) of species in depth and surface temperature sectors. Species names refer to codes given in Table 1.

	≤ 1500 M	≥ 1500 M	≤ 12°	≥ 12°
FUGLA	77	23	73	27
SUBAS	87	13	25	75
OCLEU	12	88	9	91
HYPEL	82	18	42	58
PUPUF	29	71	26	74
PUGRI	91	9	87	13
STSKU	54	46	40	60
RITRI	65	35	48	52
STEPA	55	45	42	58
URAAL	95	5	95	5
FRARC	96	4	95	5
BAPHY	9	91	13	87
BAACU	41	59	53	47
PHMAC	21	79	23	77
GLMEL	61	39	62	38
HYAMP	15	85	63	37
TUTRU	27	73	31	69
LAALB	100	0	100	0
LAACU	35	65	37	63
DEDEL	31	69	0	100
PHPHO	79	21	62	38

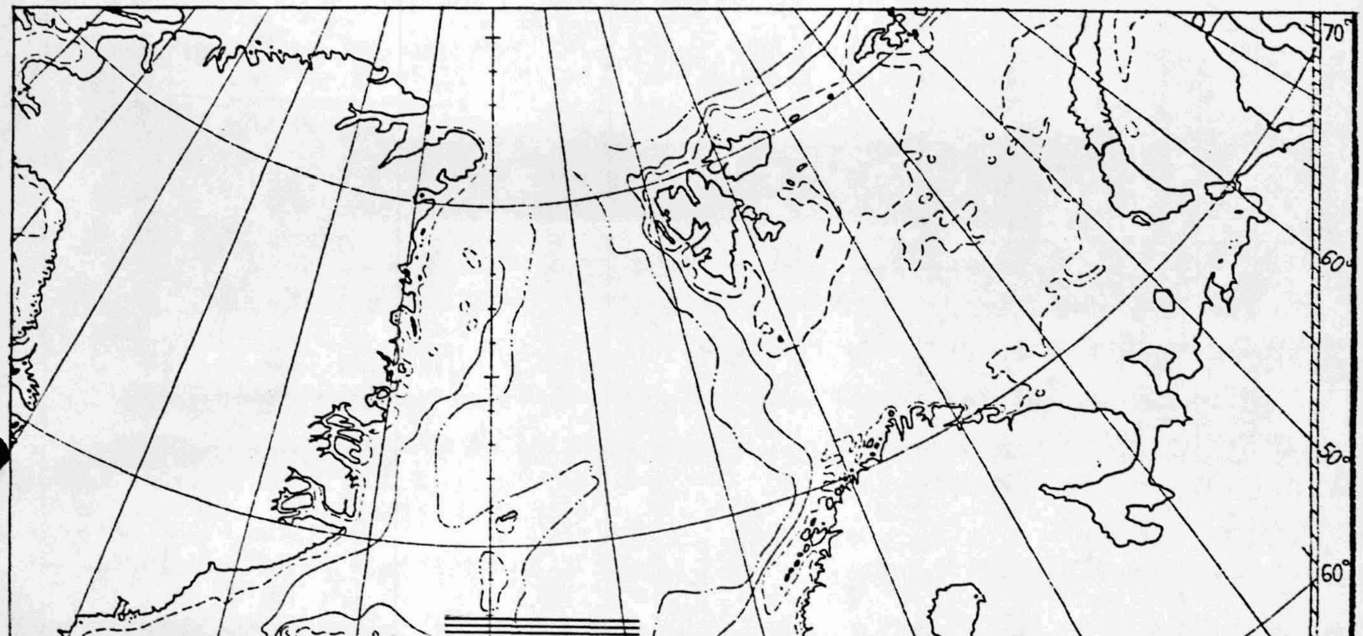

Figure 1.

Study area.

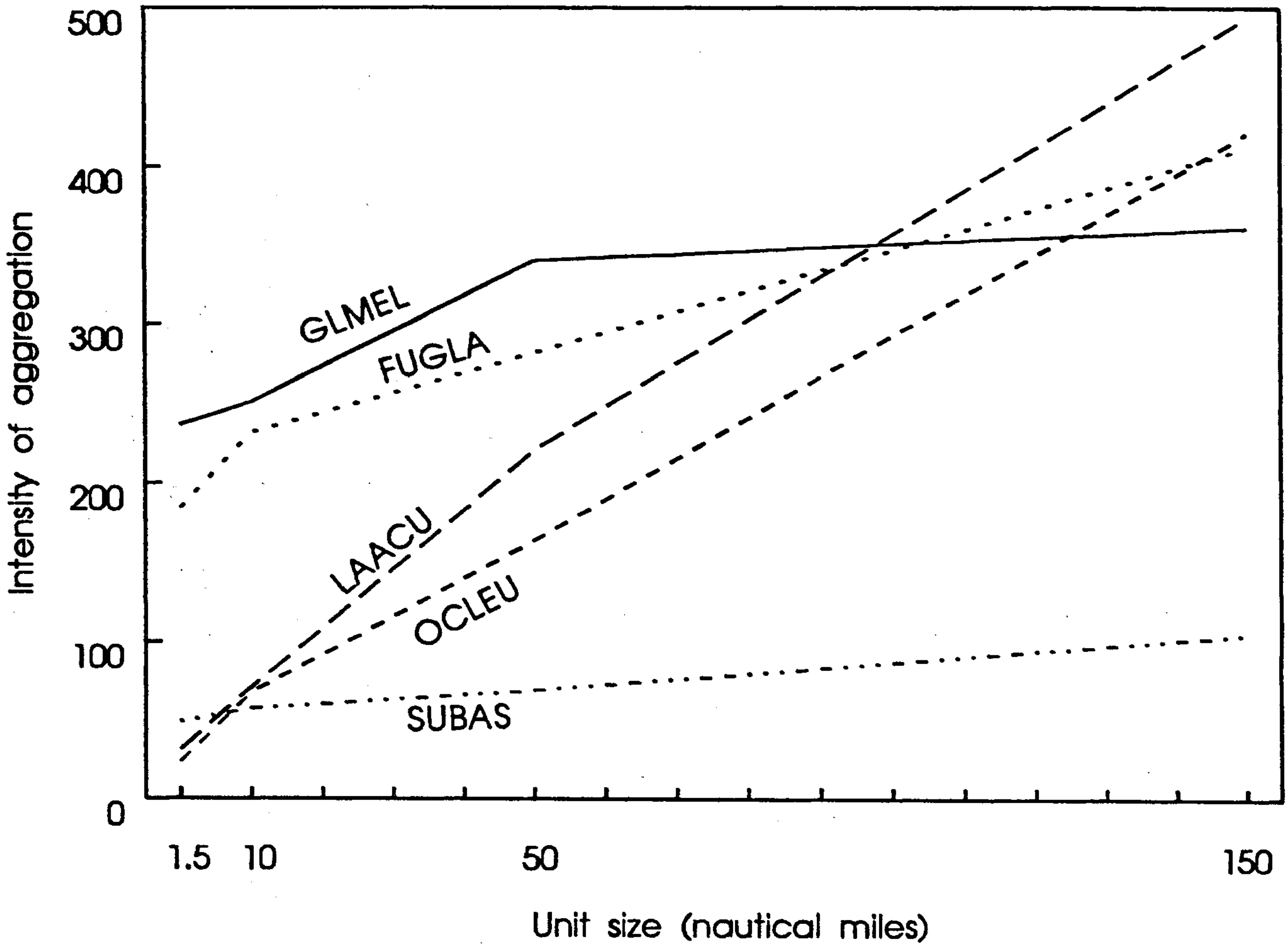

Figure 2.

Examples of increase in variance-to-mean ratio with interval unit.

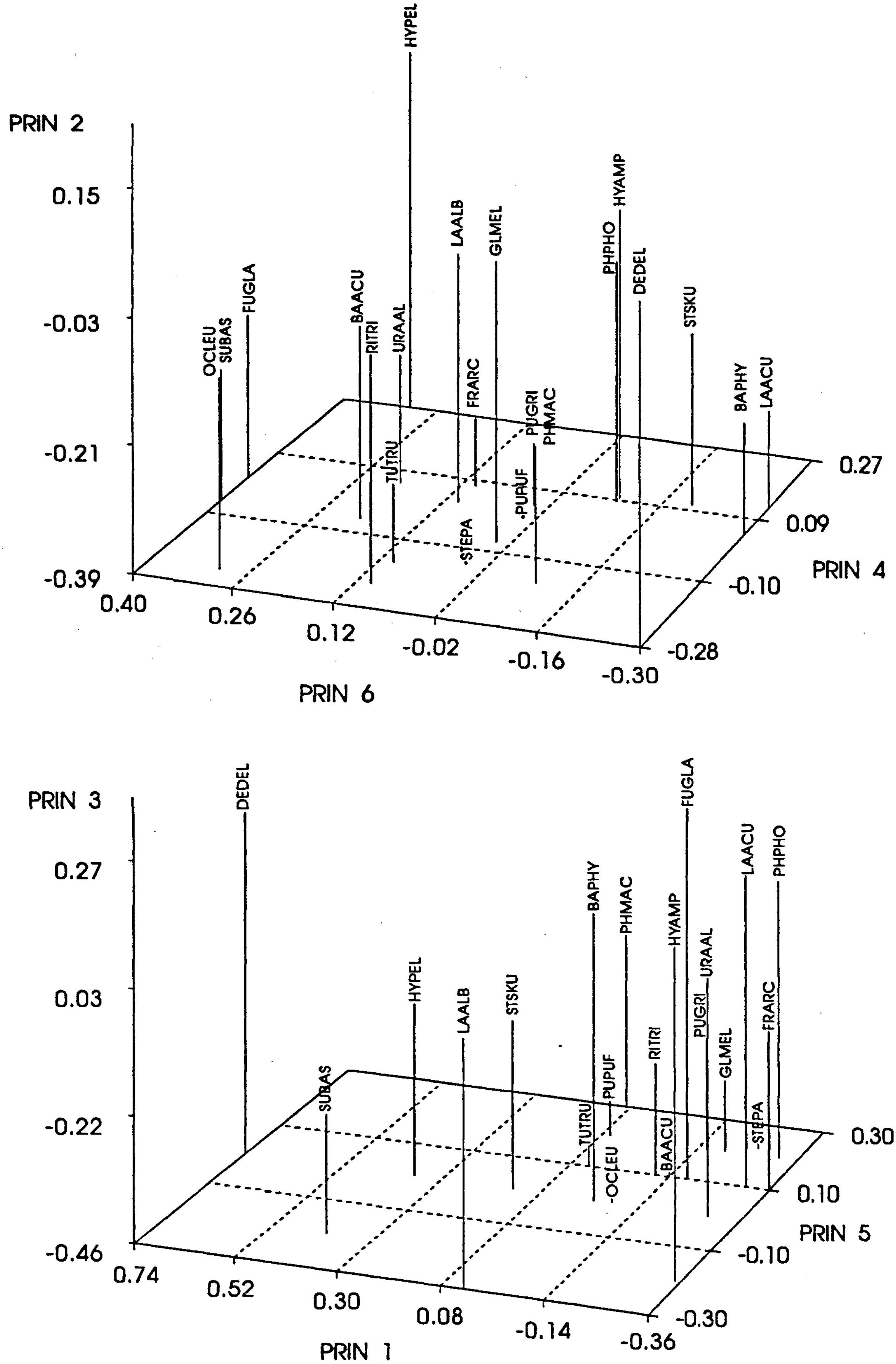

Figure 3.

Plots of specific correlations with PCA-derived habitat measures.