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Effects of hydrographic and meteorological factors on seasonal seabird abundance in the southern North Sea

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ABSTRACT: We examined the influence of both season and hydrographic and meteorological factors on seabird abundance in the southern North Sea. Seabirds were counted from ships in a study area of 27.8 × 32.8 km on 407 d from 1990 to 2007. Two hydrographic and 5 meteorological parameters were taken from archived data. The relationships between bird abundance and abiotic parameters were investigated by generalised additive models for 3 distinct seasons. The species in the study area exhibited different seasonal patterns. While some species were present year-round, others occurred only at certain periods. Despite these substantial changes in abundances, the nature of the interactions between bird abundances and abiotic parameters did not vary much between seasons. All 5 meteorological and 2 hydrographic parameters significantly influenced the abundance of seabird species, though to a different degree. The single factors that most often had a significant influence in the single models were wind field, sea surface temperature anomaly, sea surface salinity anomaly and air pressure change. The quantitative composition of the seabird community differed significantly between onshore wind and offshore wind conditions. It is assumed that hydrographic parameters are relevant for the birds by determining their foraging habitats and that atmospheric parameters influence flight conditions during foraging and migration.

KEY WORDS: Seabird · Hydrography · Meteorology · Phenology · Wind · Monitoring

INTRODUCTION

Various studies have investigated the influence of abiotic and biotic factors on the distribution and abundance of seabirds at sea (for reviews see Hunt 1990, Schneider 1991). Processes involved vary from 100s of metres to 1000s of kilometres in spatial ranges and from hours to years in temporal ranges, reflecting the influence of different oceanographic features and processes affecting prey availability to seabirds (Hunt & Schneider 1987). Less attention has been paid to the influence of meteorological factors, except for wind direction and wind speed (Furness & Bryant 1996, Weimerskirch et al. 2000). Recent advances in global weather data availability have enabled analyses of how seabirds cope with large-scale weather patterns, e.g. the use of low and/or high pressure systems for movements and foraging flights (Nicholls et al. 1997, Spruzen & Woehler 2002). However, at small temporal and spatial scales, little is known about the respective effects of hydrographic and meteorological factors on seabird abundance, namely in coastal areas with high environmental variability, such as the southeastern North Sea (Markones et al. 2008). There, in particular, *Larus* spp. gulls often show highly divergent patterns on a day to day basis. This could be expected, to some degree, since the study area in question, the Inner German Bight, is an area of very high hydrographic variability, comprising the transition zone between the less saline and turbid Continental Coast Water Mass and the more saline and transparent Central North Sea Water Mass (Becker et al. 1983). In this system, fresh-

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water influx is enhanced during offshore easterly and southerly winds, while seawater influence is increased when westerly winds occur. Garthe (1997) and Markones (2007) showed that the distribution of several seabird species correlated with the occurrence of these 2 main water masses. The nearshore-dominating Continental Coast Water Mass was the preferred habitat of common gulls *Larus canus*, while northern fulmars *Fulmarus glacialis*, black-legged kittiwakes *Rissa tridactyla* and common guillemots *Uria aalge* were significantly associated with the Central North Sea Water Mass, which becomes dominant in the deeper north-western part of the study area. Changes in bird assemblages may be a consequence of sometimes rapid variations in hydrographic and/or meteorological parameters. Also, species may differ in their response to these changes, as well as in their choice of habitat, especially pelagic versus coastal seabirds. Furthermore, habitat requirements of seabirds undergo a seasonal pattern. During the breeding period, the activity range of birds is restricted by the availability of suitable nest sites and parental duties (incubation shifts and chick provisioning). During spring and autumn, distribution patterns are often influenced by moulting, migration, or dispersal (Stone et al. 1995). In winter, movements are generally less pronounced, though, e.g., cold spells may induce some movement, especially in waterfowl species (Elkins 1988, Ridgill & Fox 1990). In consequence, different influences of abiotic factors on the distribution and abundance patterns of seabirds among the different seasons may occur (Markones 2007).

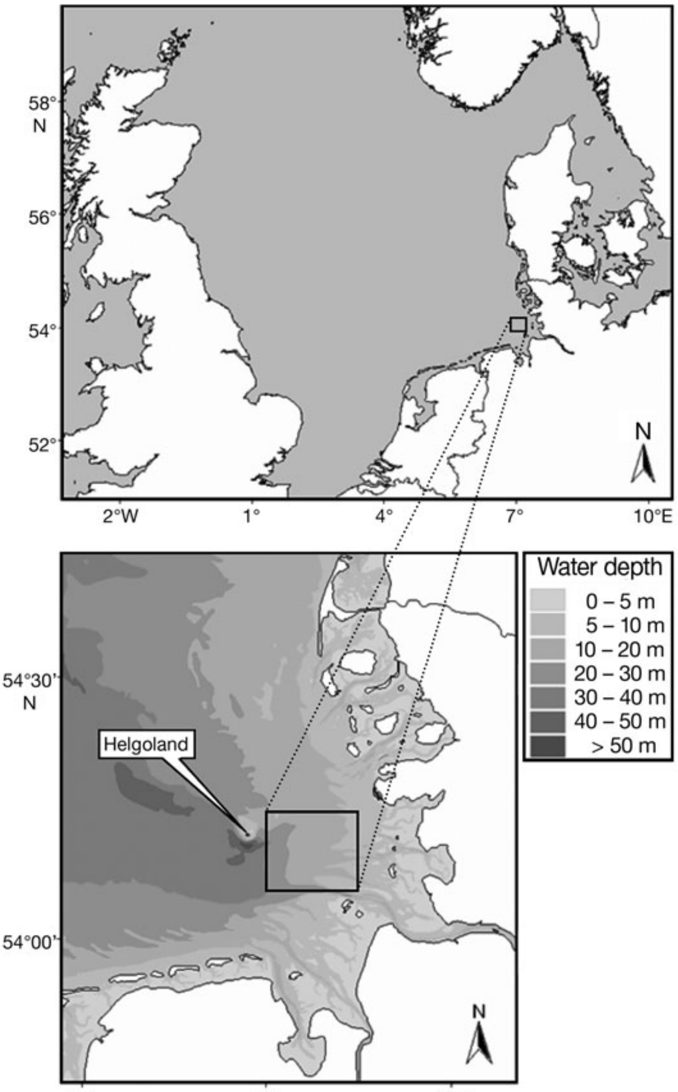

Fig. 1. Location of the study area 'HELBOX' (Helgoland box). The upper panel shows the location in the North Sea; the lower panel shows more details from the southeastern North Sea. The label 'Helgoland' represents both the island and the station 'Helgoland Roads'

In the present paper, we thus investigate to what degree seasonal, hydrographic and meteorological factors influence seabird abundance in the Inner German Bight (southern North Sea). We concentrate our efforts on an intensively surveyed study site at the transition between coastal and marine influences. A high level of survey effort has been carried out under variable environmental conditions. We relate key hydrographic and atmospheric parameters to bird abundance to assess which factors predominantly influence the abundance of the different seabird species during different seasons. We also investigate whether these factors may influence seabird community composition. Finally, we evaluate the consequences of our findings for seabird monitoring programs, processes of selection and delineation for marine protected areas and climate change predictions.

MATERIALS AND METHODS

Study area. The study area is a 27.8 × 32.8 km rectangular area located to the east of the island of Helgoland in the Inner German Bight (hereafter 'HELBOX'; Fig. 1). Both bird and environmental data were assembled for each day of ship-based observations, which covered at least 5 km^2 within the box area (5 km^2 as a minimum equals 1 h of counts at a ship speed of 9 knots and with 17 km of linear survey effort).

Bird data. Birds at sea were counted from ships, following the current international standard (Tasker et al. 1984, Camphuysen & Garthe 2004). All species were recorded within a transect strip of 300 m width set perpendicular to one or both sides of the steaming vessel. The width of 300 m was estimated according to the range-finding method of Heinemann (1981) using callipers. For swimming individuals, the transect strip was subdivided into 4 bands (0 to 50, 50 to 100, 100 to 200 and 200 to 300 m) to allow for distance corrections. As flying birds move faster than the observation vessel, we used the snapshot method described by Tasker et al. (1984) to avoid overestimation of particularly mobile species. According to this technique, flying birds are, by convention, only recorded as within the transect when they fly over the area of the transect strip at the time of a snapshot count. Flying birds crossing the transect strip at other times and birds sighted outside the transect area were usually also recorded, but their numbers were not used for density calculations. During all surveys, geographic positions were automatically recorded every minute with a hand-held GPS (global positioning system)-recorder. Counts were only conducted and used for analysis when visibility was good enough to survey the entire transect area and beyond (minimum visibility: 1 km) and when other weather conditions such as wind, rain and spray did not influence the counts.

To account for birds that were overlooked, especially in the outer transect area on the water, we applied the distance sampling methodology and calculated species-specific correction factors to estimate detection probability. To take into account clustering of birds (group sizes per observation), the time unit for analysis was set at a 1 min counting interval. We applied the half-normal function with cosine adjustment using the software Distance 5.0 (Thomas et al. 2006). Only for this analysis, were data based on all records from within the German Bight (not only from the HELBOX) since 1993. As the detectability of birds on water (i.e. birds that are swimming, resting, preening, etc.) changes with wave heights and white crests on the water (Duffy 1983), correction factors were calculated separately for each sea state. Sea states are coded to describe wave height and white water conditions (Beaufort scale; Dietrich et al. 1975). As sea state is recorded continuously during all bird counts, such a correction procedure takes into account the frequently changing conditions at sea. For species with low sample sizes and for sea states experienced rarely or with similar effects on detectability, correction factors were summarised for >1 sea state value. Common guillemot *Uria aalge* and razorbill *Alca torda* were combined because razorbill sample sizes were relatively low. Table 1 shows all correction factors applied for the analyses in the present paper. Correction factors were calculated by dividing the 300 m transect band by the estimated 'effective strip width' (in m; Buckland et al. 2001), as analysed by the software Distance 5.0. Abundances of flying birds were not corrected for distance as we assumed that, in contrast to swimming birds, all flying individuals within the area surveyed had been recorded completely.

Data on seabird abundance in the study area were analysed from the German Seabirds at Sea Database, Version 5.12, as of October 2008. In total, data for 407 d from July 1990 to May 2007 were available, summing to 4786.5 km^2 of survey effort (Table 2). Although days were not sampled on an exact schedule every year, data effectively covered the different years and months over the whole study period, so possible biases due to unequal distribution of observation days should have been minimised. The unit for analysing bird data was the 'day'. For each day, and separately for all species, abundance values were obtained by: (1) summing the total number counted in the transect, (2) dividing this number by the survey effort (km^2), and (3) multiplying this value by the correction factor (see above). We thus obtained species-specific density values.

As the (variable) influence of abiotic parameters was much more of interest than the seasonal cycle, we chose 3 distinct 'seasons' and pooled all data within

Table 1. Correction factors calculated by distance sampling methods for birds on water for different seabird species at different sea states (Beaufort scale). See 'Materials and methods' for procedure. Correction factors in bold were used for analyses. Seasonal patterns of the species present in the study area are also given (see Fig. 2)

Species	Taxon	Seasonal pattern	Sea state						
			0–1	2	3	4–7	0–2	3–7	0–7
Red-throated diver	*Gavia stellata*	c	–	–	–	–	**1.4**	**1.8**	1.7
Northern gannet	*Sula bassana*	a	–	–	–	–	–	–	**1.5**
Little gull	*Hydrocoloeus minutus*	d	–	–	–	–	**1.7**	**1.7**	1.7
Black-headed gull	*Larus ridibundus*	a	**1.6**	**1.8**	**1.9**	**2.3**	–	–	1.8
Common gull	*Larus canus*	b	**1.5**	**1.8**	**1.8**	**2.2**	–	–	1.7
Lesser black-backed gull	*Larus fuscus*	a	**1.4**	**1.5**	**1.6**	**1.8**	–	–	1.6
Herring gull	*Larus argentatus*	b	**1.5**	**1.6**	**1.7**	**2.2**	–	–	1.7
Great black-backed gull	*Larus marinus*	b	–	–	–	–	**1.7**	**1.9**	1.8
Black-legged kittiwake	*Rissa tridactyla*	b	**1.7**	**1.8**	**1.8**	**2.2**	–	–	1.9
Sandwich tern	*Sterna sandvicensis*	a	–	–	–	–	**1.8**	**1.8**	1.8
Common/Arctic tern	*Sterna hirundo/paradisaea*	a	–	–	–	–	**1.8**	**1.8**	1.8
Common guillemot	*Uria aalge*	b	**1.6**	**2.0**	**2.0**	**2.2**	–	–	2.1
Razorbill	*Alca torda*	c	**1.6**	**2.0**	**2.0**	**2.2**	–	–	2.0

Table 2. Number of observation days (upper value) and survey effort (lower value, in km^2) per month and year in the study area from 1990 to 2007

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1990	–	–	–	–	–	–	3	3	1	–	–	1	8
	–	–	–	–	–	–	24.4	34.5	19.4	–	–	17.1	95.4
1991	4	3	1	2	3	3	3	1	1	2	4	1	28
	43.9	35.0	08.3	19.1	34.0	47.6	30.8	21.7	05.9	17.6	37.1	08.9	309.9
1992	4	2	2	2	6	4	3	2	4	6	1	2	38
	44.8	15.4	21.0	16.4	67.4	38.8	32.7	25.3	37.5	52.0	06.8	26.6	384.7
1993	2	1	4	2	5	2	2	8	1	2	5	1	35
	23.5	08.3	43.4	29.1	62.6	16.4	32.6	93.3	08.4	28.2	55.1	9.0	409.9
1994	2	2	2	1	2	3	5	5	5	–	1	–	28
	16.3	15.4	21.3	09.5	19.4	29.1	80.3	49.0	56.3	–	9.0	–	305.6
1995	–	1	–	–	–	2	1	–	–	–	2	–	6
	–	09.2	–	–	–	24.3	08.3	–	–	–	14.4	–	56.2
1996	–	–	–	2	2	2	–	5	3	–	–	–	14
	–	–	–	16.6	20.3	21.4	–	52.9	38.2	–	–	–	149.4
1997	2	4	–	4	7	8	11	10	2	–	3	1	52
	16.3	29.7	–	29.2	75.9	71.8	135.7	112.6	19.8	–	25.1	08.5	524.6
1998	3	4	4	–	3	2	–	5	–	–	–	2	23
	25.5	32.3	38.7	–	66.5	19.5	–	51.2	–	–	–	17.9	251.6
1999	–	–	2	–	–	–	–	2	–	–	1	1	6
	–	–	16.0	–	–	–	–	92.7	–	–	08.9	08.6	126.2
2000	2	–	3	2	2	4	1	2	–	1	2	3	22
	16.8	–	24.2	26.6	26.2	44.7	06.5	17.0		07.8	16.3	25.0	211.1
2001	1	–	2	4	2	3	3	–	–	–	–	3	18
	08.5	–	20.7	42.2	61.8	25.4	32.7	–	–	–	–	27.9	219.2
2002	–	–	–	3	5	5	3	2	3	2	–	–	23
	–	–	–	27.5	51.6	42.9	26.0	16.6	26.6	20.6	–	–	211.8
2003	–	1	3	4	1	3	1	11	–	–	–	1	25
	–	11.0	34.5	79.4	07.7	26.0	05.9	194.4	–	–	–	8.0	366.9
2004	–	–	–	1	–	2	1	3	2	–	2	–	11
	–	–	–	12.2	–	23.7	19.5	44.7	25.3	–	36.2	–	161.6
2005	–	–	1	3	7	7	3	5	3	2	1	2	34
	–	–	07.6	29.2	93.1	109.5	50.0	90.5	50.7	38.4	08.5	18.3	495.8
2006	1	1	2	2	3	5	3	4	2	2	1	1	27
	08.8	14.8	17.1	28.7	38.3	75.0	52.8	54.0	39.6	15.2	09.1	09.8	363.2
2007	1	1	2	3	2	–	–	–	–	–	–	–	9
	07.1	15.7	31.3	49.5	39.8	–	–	–	–	–	–	–	143.4
Total	22	20	28	35	50	55	43	68	27	17	23	19	407
	211.5	186.8	284.1	415.2	664.6	616.1	538.2	950.4	327.7	179.8	226.5	185.6	4786.5

these. Seasons were defined to match the species presence in the study area (for species-specific seasons see Garthe et al. 2007). The periods of the year not covered by our analyses were eliminated, due either to insufficient sample sizes (i.e. the number of days at sea with sufficient coverage, e.g. spring) or because these were transient months associated with different 'seasons' for the different species (e.g. the second half of July partly represents the breeding period, and partly, autumn migration).

For each season, we included in the analysis those species that were present on at least 15 % of the observation days. The only exceptions were common eider *Somateria mollissima* and common scoter *Melanitta nigra*, which were excluded from the analysis in winter, as the study area is located clearly outside their foraging and resting areas and recordings were only from migrating birds. For the seasonal analyses, the species analysed in detail comprised 39 % (winter), 94 % (autumn migration) and 94 % (reproductive period) of overall seabird abundance. Ignoring the 2 sea duck species mentioned above, the values increased to 96 % (winter), 98 % (autumn migration) and 99 % (reproductive period). Divers (i.e. loons *Gavia* spp.) were defined as red-throated divers *Gavia stellata*, because 93 % of all divers identified to species and registered in the transect were of that species (69% of all divers were identified to species; n = 363 individuals). Common terns *Sterna hirundo* and Arctic terns *Sterna paradisaea* were pooled as commic terns. A total of 57% of all commic terns was identified to species (n = 1202 individuals). Although common terns were more numerous and made up 83% of all commic terns registered in the transect and identified to species, a relatively high percentage of non-identified individuals occurred on some observation days (in contrast to the case of the divers), so that simple species allocation was not regarded as adequate. In all other cases, proportions of unidentified birds were very small and therefore negligible (0.7% of common guillemot and razorbill and 0.03% of large gulls). Scientific names of the bird species follow Bauer et al. (2005).

Environmental data. In spite of having a large set of hydrographic and meteorological parameters, only those that were considered meaningful from a seabird biology and marine ecology point of view (Table 3) were selected. Thus, e.g., precipitation and visibility were neglected because, to the best of our knowledge, they do not generally affect seabird abundance directly. Also, strongly correlated factors were avoided, e.g. multiple measurements of the same or a similar parameter on a specific day. The variables finally selected for analysis were only weakly correlated, with a maximum Pearson correlation coefficient of 0.4 (Table 4). Furthermore, it was considered that the temporal resolution (e.g. 1 measurement per day) of some environmental parameters (e.g. air pressure) might not be appropriate, as they are fast changing. In such cases, ratios or means were calculated (see below).

Two hydrographic parameters, sea surface temperature (SST) and sea surface salinity (SSS; Table 3), were analysed from the Helgoland Roads time series (Franke et al. 2004, Wiltshire & Manly 2004) provided by the Alfred-Wegener Institute for Polar and Marine Research. These parameters were measured from a boat at a fixed place near the island of Helgoland once a day on working days. We interpolated values for days not sampled (weekends and public holidays). Helgo-

Table 3. Environmental parameters and their time scales as used in this study. The measurement frequency for each parameter is one value per day. SST: sea surface temperature; SSS: sea surface salinity; CET: Central European Time. ΔT: Temperature difference

Parameter	Unit	Explanation
SST anomaly	°C	Deviance of the SST value on a specific date (e.g. 1 April 2000) from its long-term mean for that date (e.g. mean for 1 April from 1990 to 2007)
SSS anomaly	psu	Deviance of the SSS value on a specific date (e.g. 1 April 2000) from its long-term mean for that date (e.g. mean for 1 April from 1990 to 2007)
Absolute air pressure	hPa	Mean of measurements from 07:00, 14:00 and 21:00 h CET on the observation day
Preceding air pressure change	hPa	Difference between 07:00 h CET on the day before the observation day and 07:00 h CET on the observation day
Concurrent air pressure change	hPa	Difference between 07:00 and 21:00 h CET on the observation day
Wind field	–	Combination of wind direction and wind speed on the observation day For wind directions (measured at 07:00 h CET) from the sea (SW, W, NW), the Beaufort-scaled wind speeds (measured at 07:00 h CET) were taken as positive values, while for wind directions from land (N, NE, E, SE, S), the Beaufort-scaled wind speeds were multiplied by −1
ΔT: water−atmosphere	°C	Difference between the SST value and the mean atmospheric temperature value on the observation day

Table 4. Cross correlations between the environmental parameters used for analysis. Correlation coefficients shown are based on Pearson correlations for the whole data set (407 observation days; see Table 1). SST: sea surface temperature; SSS: sea surface salinity. ΔT: Temperature difference

	SST anomaly	SSS anomaly	Absolute air pressure	Preceding air pressure change	Concurrent air pressure change	Wind field	ΔT: water−atmosphere
SST anomaly	–						
SSS anomaly	−0.137	–					
Absolute air pressure	0.028	0.025	–				
Preceding air pressure change	−0.073	0.118	0.404	–			
Concurrent air pressure change	−0.055	0.083	−0.117	0.147	–		
Wind field	0.005	0.055	0.024	0.130	0.120	–	
ΔT: water−atmosphere	−0.098	−0.008	0.061	0.042	0.104	0.020	–

land Roads is located only 6.5 km west of the study area. As we were not interested in the annual cycle of these parameters but rather in their deviance from the means, we calculated daily means for both, and used 'SST anomaly' and 'SSS anomaly' as the deviations from the long-term mean on the respective day. SST anomalies should indicate warmer or colder years; SSS anomalies should indicate influence of Continental Coast Water Mass (if SSS values are lower than on average) or Central North Sea Water Mass (if SSS values are higher than on average; see also Loewe et al. 2006). These different causes for changes in SST and SSS are also supported by the fact that SST and SSS were not correlated ($r = -0.003$, $df = 4187$, $p = 0.846$, Pearson correlation; data from 1 January 1990 to 31 May 2007).

Meteorological data were obtained from the German Weather Service (DWD). They were selected to reflect important atmospheric parameters possibly influencing seabird behaviour, e.g. when foraging and migrating (all times are given according to Central European Time; Table 3): (1) absolute air pressure (means of measurements from 07:00, 14:00 and 21:00 h on the observation day), (2) preceding air pressure change (from 07:00 h on the day before the observation day to 07:00 h on the observation day), (3) concurrent air pressure change (from 07:00 to 21:00 h on the observation day), (4) wind field (see below) and (5) the temperature difference between SST and the atmospheric temperature on the observation day. The last parameter was based on observations by Haney & Lee (1994), who suggested that air–sea heat flux and ocean wind fields may have a strong influence on offshore dispersal of gulls by facilitating energy-efficient flying under certain conditions. For the wind field, the selected variable includes a quantitative combination of direction and speed, scaled to highlight an onshore/offshore axis. For wind directions (measured at 07:00 h) from the sea (SW, W, NW), the Beaufort-scaled wind speeds (measured at 07:00 h) were taken as positive values, while for wind directions from land (N, NE, E, SE, S), the Beaufort-scaled wind speeds were multiplied by –1.

Statistical analysis. The comparison of bird abundance and abiotic parameters was done on a daily basis; bird abundance was obtained from our own data set on seabirds at sea (see 'Bird data' above), and abiotic parameters were gleaned from archived materials (see 'Environmental data' above and Table 3). The relationships between bird abundance and abiotic parameters were investigated using generalised additive models (GAMs; Hastie & Tibshirani 1990, Wood 2006). Influences of the hydrographic and meteorological parameters on seabird abundance in the study area were tested separately for each species and season. GAMs with quasi-Poisson error distribution were performed using the MGCV package (Wood 2008) of the open source software package R 2.8.1 (R Development Core Team 2008). As the data set was based on counts, the Poisson function should usually form the basis of the analysis (Zuur et al. 2007). However, to prevent overdispersion, an underlying quasi-Poisson function was selected in the model frame. Models were selected using backward selection and exclusion of non-significant predictor variables (applying the ANOVA function with *F*-statistics). To avoid over-fitting of models (Meynard & Quinn 2007), only seasons with an adequate sample size were used (≥80 observation days), rare species were disregarded (see 'Bird data' above) and the degrees of freedom for curve smoothing were restricted to 4. Models were validated applying 10-fold cross-validations, which were repeated 10 times. We calculated the root mean-squared error of prediction (RMSEP) and the correlation between observed values and the values predicted during the cross-validation procedure (r^2) to obtain measures of model performance.

As the wind field is considered a central element responsible for the distribution of water masses and also influencing bird flight behaviour, we investigated whether onshore wind versus offshore wind conditions may lead to differences in the quantitative composition of the seabird community. Analysis was performed for winter only, as this is the period during which the least migratory movements are expected and when no birds commute between colonies and feeding grounds. We tested whether the (daily) species abundance values differed between 52 d with offshore conditions (wind from land towards the sea) and 32 d with onshore conditions. We conducted a Monte Carlo permutation test with 1000 permutations, based on a detrended correspondence analysis (DCA). A dummy variable wind (0 for onshore wind, 1 for offshore wind) was introduced and tested for significance to the quantitative species data. This test was undertaken using the package 'vegan' (Oksanen et al. 2008) in R. Significance levels were set to 0.05 for all analyses.

RESULTS

Seasonality

The species in the study area exhibited different seasonal patterns. While some species were present year-round, others occurred only at certain periods. Principally, all species can be divided into 4 groups as exemplified in Fig. 2: (a) species that occur from spring to autumn and breed on islands or along the coast near the study area, but leave the study area in winter, e.g. *Larus fuscus*; (b) species that occur year-round and breed nearby, e.g. *L. canus*; (c) species that occur from

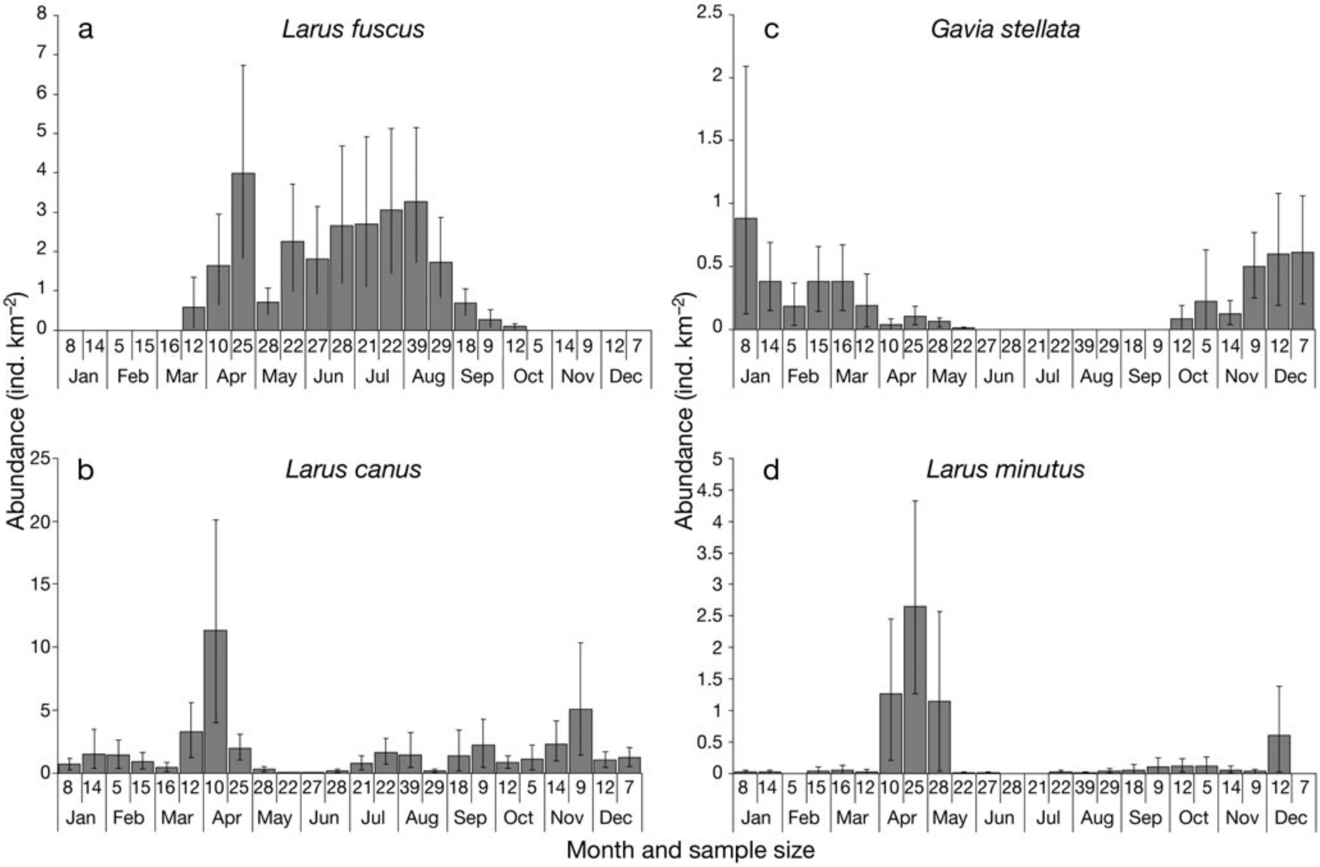

Fig. 2. Abundance patterns of 4 seabird species over the annual cycle. Each month is split into 2 halves, with the number of days from 1990 to 2007 as sample size indicated below the *x*-axis. Means and 95% confidence intervals are based on bootstrapping the original values 10 000 times: (a) lesser black-backed gull *Larus fuscus*, (b) common gull *L. canus*, (c) red-throated diver *Gavia stellata*, (d) little gull *L. minutus*

autumn to spring, including the winter period, but leave the area for breeding, e.g. *Gavia stellata*; and (d) species that predominantly occur during the autumn and spring migration periods and have a clear bimodal distribution, e.g. *L. minutus*.

Influence of hydrographic and meteorological parameters on seabird abundance

All 5 meteorological and 2 hydrographic parameters significantly influenced the abundance of seabird species in the study area in the southeastern North Sea, though to a different degree (Table 5). Except for the common guillemot during the reproductive period, the GAMs found at least 1 abiotic parameter explaining considerable variance in species abundance. Overall, the 2 hydrographic parameters were significant in 54% of all species/season combinations, while the 5 atmospheric parameters were significant in 44% of these combinations. The single factors that most often had a significant influence in the single models were wind field, SST anomaly, SSS anomaly and preceding air pressure change (Table 5).

Two typical patterns are explained in more detail. Species responded differently to the wind field, with species such as the common gull *Larus canus* being significantly less abundant during onshore wind conditions, while the opposite was true for the black-legged kittiwake *Rissa tridactyla* (Fig. 3). Especially during autumn migration, but also during the 2 other periods, species were often significantly more abundant when air pressure was high and/or increased, as shown for the black-headed gull *L. ridibundus* (Fig. 4). These responses were apparent in several species.

For all models the results of the cross-validation were characterized with a low r^2 (<0.1) and a large RMSEP.

Seabird community and wind field

The quantitative composition of the seabird community in the HELBOX area differed significantly between onshore wind and offshore wind conditions in winter

Table 5. Influence of 5 atmospheric and 2 hydrographic variables on abundances of the most common seabird species in the study area based on generalised additive models. Analyses are shown for winter (November to February; n = 84 observation days; total effort = 809.9 km), autumn migration (August to September; n = 95 observation days; total effort = 1277.8 km) and the reproductive period (mid-May to mid-July; n = 99 observation days; total effort = 1189.8 km). –: non-significant results; $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$; SST: sea surface temperature; SSS: sea surface salinity. ΔT: temperature difference

Taxon	Species presence (% of days)	Total ind. seen (n)	Deviance explained (%)	Absolute air pressure	Air pressure change Preceding	Air pressure change Concurrent	Wind field	ΔT water–atmosphere	SST anomaly	SSS anomaly
Winter										
Gavia stellata	67	239	17.7	–	*	*	–	–	–	–
Hydrocoloeus minutus	18	56	78.8	**	***	***	–	**	**	***
Larus canus	80	1140	31.2	–	–	*	***	–	–	–
Larus argentatus	71	914	71.5	–	–	***	*	***	***	–
Larus marinus	69	500	25.1	–	–	*	*	*	–	–
Rissa tridactyla	50	329	73.4	–	*	***	***	–	***	–
Uria aalge	63	457	47.5	***	–	–	–	–	***	–
Alca torda	17	24	14.4	–	–	–	–	–	–	*
Autumn migration										
Larus ridibundus	46	1491	69.1	***	***	–	**	**	–	**
Larus canus	56	827	29.7	–	***	–	–	–	***	–
Larus fuscus	85	1797	42.6	–	***	–	–	***	–	**
Larus argentatus	77	1685	20.1	–	–	–	**	–	*	–
Larus marinus	54	276	41.6	–	–	–	*	**	*	**
Rissa tridactyla	62	1191	65.2	–	***	***	*	–	***	
Sterna sandvicensis	53	247	46.7	–	***	–	**	*	–	***
Sterna hirundo/paradisaea	73	692	23.8	**	–	–	*	–	*	–
Reproductive period										
Sula bassana	16	33	28.4	–	***	**	–	–	–	–
Larus ridibundus	33	129	60.2	–	***	*	**	***	*	***
Larus canus	24	173	51.7	–	***	–	*	**	–	***
Larus fuscus	93	1744	49.7	–	**	**	**	–	*	***
Larus argentatus	72	951	42.3	***	–	–	–	–	***	**
Larus marinus	24	47	55.4	**	–	–	*	***	**	*
Rissa tridactyla	60	659	12.5	–	–	–	–	–	–	*
Sterna sandvicensis	54	196	25.0	**	*	**	–	**	*	–
Sterna hirundo/paradisaea	43	214	37.1	–	–	–	**	–	***	*
Uria aalge	57	306	0	–	–	–	–	–	–	–

($r^2 = 0.27$, n = 84 d, $p = 0.033$, detrended correspondence analysis with Monte Carlo permutation). During onshore wind situations, common guillemots *Uria aalge* and black-legged kittiwakes constituted much higher percentages than during offshore wind situations, while common gulls and herring gulls *Larus argentatus* occurred in higher percentages during offshore wind situations (Fig. 5).

DISCUSSION

Influence of season and abiotic parameters

The different seabird species exhibit different seasonal patterns in the southern North Sea. Interestingly, despite substantial changes in abundances, the nature of the relations between bird abundances and abiotic parameters did not vary much between seasons. However, the highest deviances explained by the GAMs were only achieved in winter and during autumn migration. This substantiates that breeding birds are restricted in their spatial distribution, as they have to commute regularly to their breeding colonies for territorial and nest defence, incubation and chick provisioning. Thus, they are bound to stay within their foraging range, thereby possibly masking 'ideal' habitat relationships (Garthe 1997, Markones 2007).

The seabird assemblage in the study area consists mostly of highly mobile and frequently flying species. It can consequently be expected that, on the one hand, hydrographic parameters are relevant for the birds, determining the foraging habitats and options, and, on the other hand, atmospheric parameters, influencing flight conditions during foraging and migration. Flying in adverse conditions is energetically expensive, and birds may avoid extensive movements under such conditions (Haney & Lee 1994). The significant influence of air pressure was revealed in several species. High air pressure per se generally coincides with 'good weather', i.e. clear skies and good visibility, which facilitates orientation, whereas low pressure

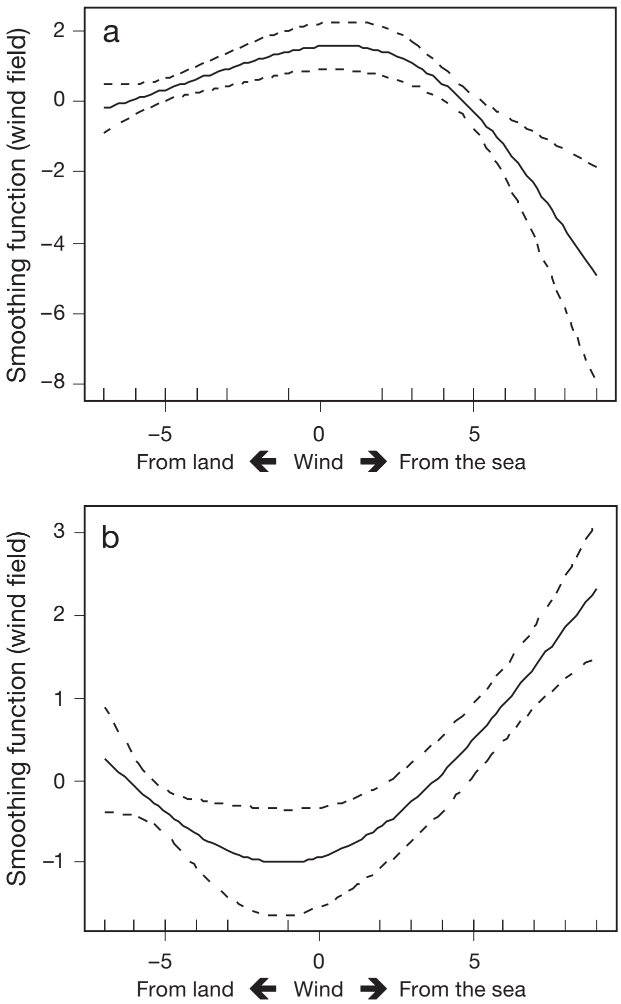

Fig. 3. Generalised additive model (GAM) smoothing curve fitted to partial effects of explanatory variables on abundance of (a) common gulls *Larus canus* and (b) black-legged kittiwakes *Rissa tridactyla* in winter. Density is represented as a function of the variable 'wind field'. Dashed lines show 95 % confidence intervals around the main effects. Common gull: $F = 6.368$, $p < 0.001$; black-legged kittiwake: $F = 18.572$, $p < 0.0001$

is associated with precipitation and poor visibility. Periods of high pressure are thus often characterized by high migration intensities, though some species are observed migrating beneath, above, or even in clouds (Richardson 1990). Others migrate only when all orientation cues are available (Nilsson et al. 2006). This may hold true not only for birds on migration, but also for offshore foraging flights of coastal birds, such as gulls and terns, during the breeding season. Our variable 'wind field' is a particularly important factor for 2 reasons. First, wind speed and wind direction are known to influence or determine when and where birds are able to fly (Woodcock 1940, Manikowski 1971, Furness & Bryant 1996). Although we did not sample many days with wind speeds >7 on the Beaufort scale (i.e. >17 m s^{-1}), even wind speeds of 10 to 15 m s^{-1} may have strong effects on field metabolic rates (Gabrielsen et al. 1987) and flight performance (Spear & Ainley 1997). Strong winds also reduce foraging options (Dunn 1973, Finney et al. 1999). In the southeastern North Sea strong winds reduce commercial fishing activity and thus the availability of discards for scavenging seabirds and, for gulls, are correlated with high proportions of resting (Markones et al. 2008). Second, the wind regime steers the distribution of the water masses in the German Bight and is thus a proxy for maritime versus coastal/freshwater conditions. Consequently, this factor significantly changed the composition of the community in the study area, with pelagic species, such as common guillemot and black-legged kittiwake, dominating during sea wind conditions, while coastal species, such as common and herring gull, dominated during land wind conditions. It is somewhat surprising that the 2 hydrographic parameters were not significant in more models. A possible reason is that the Helgoland Roads station is only partly a good indicator for the study area; unfortunately, no other stations or data sets were available throughout our time series. Sea surface salinity may also be an important indicator of fronts (Skov & Prins 2001, Markones 2007), but frontal occurrence and related bird distribution are much smaller scale processes in space and time and thus were not detectable by our analysis.

Responses to the environmental parameters varied between species, but also between seasons within the same species. There was a tendency for the diving species (divers, auks) to respond to fewer atmospheric parameters than the other species that forage in flight. This would make sense as flying is much more vulnerable to adverse weather conditions than diving. On the other hand, most species showed stronger responses to atmospheric conditions during the main migration period from August through September than, e.g., during the breeding period (see the discussion above).

Methodology

There are constraints when studying seabird distributions at sea from ships in relation to environmental conditions, as adverse conditions affect the ability to detect and census certain species. We tried to circumvent this problem by only using count data when visibility was good enough for overlooking the transect area and substantially beyond, and when other weather conditions such as wind, rain and spray were not affecting the counts. We calculated sea-state-dependent correction factors to adjust counts for birds overlooked in the outer transect area. However, Ron-

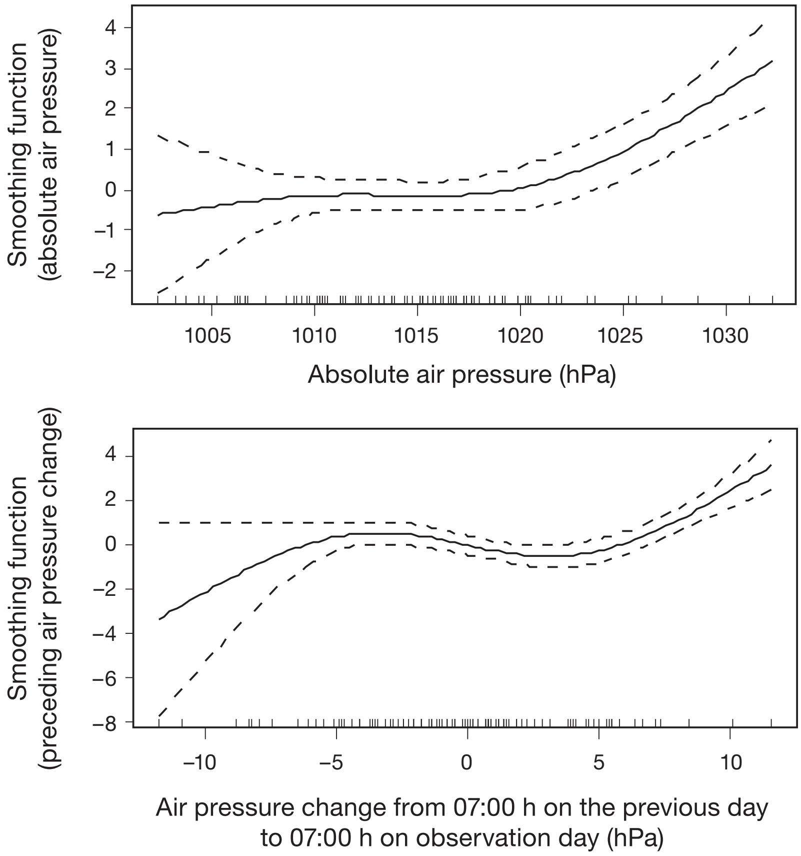

Fig. 4. Generalised additive model (GAM) smoothing curve fitted to partial effects of explanatory variables on abundance of black-headed gulls *Larus ridibundus* during autumn migration. Density is represented as a function of the variables (a) 'absolute air pressure' and (b) 'preceding air pressure change'. Dashed lines show 95% confidence intervals around the main effects. Absolute air pressure: $F = 14.702$, $p < 0.0001$; preceding air pressure change: $F = 18.309$, $p < 0.0001$

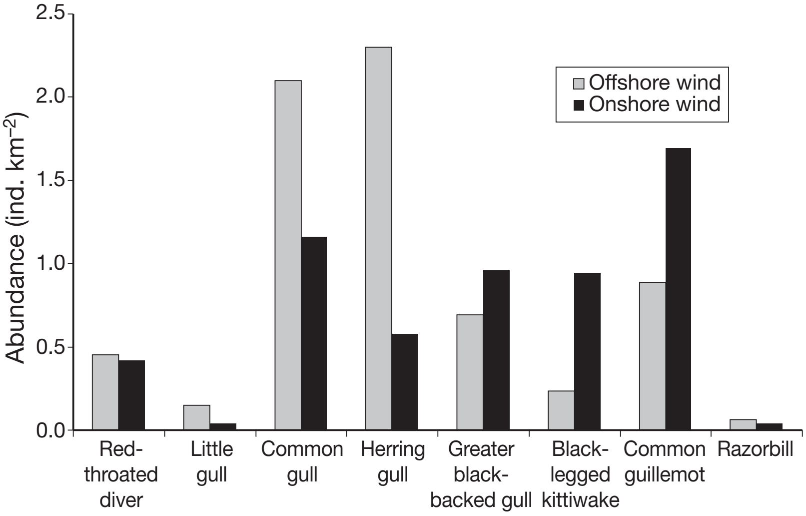

Fig. 5. Composition of the seabird community in winter during offshore and onshore wind conditions. For taxonomic names, see Table 1

coni & Burger (2009) point out that the basic assumption for this methodology, seeing all birds in front of the boat near the transect line, may be violated in some species that are difficult to detect. Fortunately, no such species (e.g. small auks) occurred in considerable quantities in our study area. Hyrenbach et al. (2007) highlight the need to test survey techniques for different survey platforms, as the latter provide different advantages and disadvantages for detecting birds. The authors also showed that cloud cover and sea state may affect census properties. We accounted for the latter effect by calculating different correction factors for different sea states.

This analysis focused on the influence of major hydrographic and atmospheric parameters on the abundance of seabird species during 3 different seasons. Such comprehensive analyses are associated with advantages and disadvantages. To establish a baseline of the influence of abiotic conditions on seabird abundance, it is advantageous to investigate the influence of these factors on all species during different periods of the annual cycle. However, sample sizes could never be large enough to test the whole suite of possible factors, interacting effects and their combinations. Thus, a pre-selection of pertinent parameters is unavoidable, in our analyses as well as in others.

Some important parameters were not included in this analysis, although they are known to affect seabird abundance and distribution patterns. Fish trawler abundance data were not available at the required temporal and spatial resolution. Previous analyses have shown that trawler distribution may influence the distribution of some seabird species feeding on discards (Camphuysen et al. 1995, Garthe 1997), but more complex analyses revealed that this factor is not related in a straightforward manner to seabird abundance and that it interacts strongly with various other factors (Markones et al. 2008). The influence of tides (Becker et al. 1993, Schwemmer & Garthe 2008) and the time of day (Burger 1983, Markones et al. 2008) were excluded, as they are also very complex. Furthermore, in an 18 yr data set, trends in numbers over time do occur. Although such trends were detected for the German Bight (Garthe & Schwemmer 2005), they did not appear to be strong enough to affect our analyses. Generally, results of GAMs have to be treated with care, as indicated by high prediction errors and low correlation between observed values and values predicted during cross-validation procedures. Thus, they may be sufficient to explain the factors causing the observed variance in seabird abundance, but not to enable predictions. Further species-specific analyses would be required focussing on certain parameters in more detail.

Implications for monitoring programmes, marine protected area delineation and climate change predictions

The findings from our analyses have some strong implications for other issues. First, seabird at sea monitoring programmes need to take different weather scenarios into account to obtain the full picture, not only patterns from high-pressure, low-wind scenarios. This is particularly relevant for aerial surveys that can only be conducted when the sea state is very low, as birds otherwise cannot be distinguished from wave crests (Camphuysen et al. 2004). Such conditions often occur during passages of (ridges of) high pressure systems, often in combination with easterly winds, that in turn enhance the abundance of coastal species, such as black-headed gulls and common gulls, and may also trigger migration (Hüppop et al. 2006). Furthermore, it needs to be considered how representative such surveys are, especially for certain species that respond strongly to atmospheric parameters.

Similar implications hold true for the identification and delineation of marine protected areas, especially those designated for seabirds that are not related to fixed bottom structures but to hydrographic features such as water masses and fronts. The preferred habitats of such species vary in location and extent with changing hydrographic and meteorological parameters (Markones 2007); thus, habitat models need to be incorporated into recommendations for locations of protected areas (Louzao et al. 2006). Protected areas for seabirds in the Exclusive Economic Zone of Germany have recently been designated, as demanded by the EU Birds Directive (Garthe 2006), but such approaches assume that the distribution of birds does not change over time. Changes in seabird abundance and distribution may, however, occur as a consequence of substantial changes in the North Sea ecosystem (Beaugrand 2004, Edwards & Richardson 2004).

Finally, statistical models such as those developed in the present paper will enable predictions, for example on the consequences of climate change. Scenarios will consider future changes in environmental parameters, such as wind fields, pressure systems and SST (Christensen et al. 2007). From the data shown here we can expect substantial effects of future climatic changes on the composition of the seabird community in the southern North Sea, due to the link between relevant environmental parameters and seabird distribution. This prediction is further supported by the fact that climatic and hydrographic parameters are known to significantly affect seabird demography (Sandvik et al. 2008).

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